AN ABSTRACT OF THE DISSERTATION OF

Seth Michael White for the degree of Doctor of Philosophy in Fisheries Science
presented on September 10, 2008.
Title: How the Animals Found Their Places: Pattern Detection, Experimentation, and Epistemology in a High Desert Stream Fish Assemblage.

Abstract approved:

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Hiram W. Li

I examined the relative roles of biotic and abiotic factors in structuring redband trout *Oncorhynchus mykiss* distributions in the South Fork John Day. I first examined the relationship between the biological traits of the fish assemblage and riparian-geomorphic features in context of prevailing theories of stream ecology stemming from the river continuum concept (Chapter 2). I found that fish traits and habitat characteristics were related to one another in a different manner according to the spatial scale of observation (watershed, tributary, and reach scales) and that mode of species coexistence (niche overlap, niche partitioning, and non-associative) was correlated more strongly with the distribution of traits than with environmental features, suggesting that biotic interactions play an important role in structuring the fish assemblage. Next, I described the 'behaviorscape' of redband trout foraging and aggression in context of prevailing foraging theory (Chapter 3, Part I). I found that redband trout behaviors could be described in terms of expected energetic gains and losses and potentially predation risk, with 'risky' behaviors yielding higher expected energetic gains in habitats with abundant structural refugia. These findings raised the questions of how fish growth and foraging behavior would be affected by increased food resources, questions which I addressed via a supplemental feeding experiment in two streams (Chapter 3, Part II). I observed nearly an order of magnitude increase in instantaneous growth rates of redband trout *O. mykiss* and a potential competitor, juvenile Chinook salmon *O. tshawytscha*, upon feeding, demonstrating that food is a limiting factor for salmonid growth in this system. Also upon feeding, redband trout foraging and aggression increased in a stream with no heterospecifics, lower discharge, and colder water temperature, but not in a stream with

the opposite characteristics. These findings suggested that *O. mykiss* and *O. tshawytscha* may coexist in a state of interactive segregation, contrary to the common wisdom that the two species are selectively segregated and have therefore evolved fully-distinct habitat preferences. To acquire further evidence for this hypothesis and to elucidate the role of competitor densities on habitat selection at local scales (which would in turn affect fish distribution patterns at larger scales), I employed a multi-species habitat selection model (Chapter 4). Redband trout habitat selection of enriched patches was negatively affected by conspecific densities as expected, but positively affected by juvenile Chinook densities, a finding that I attribute to habitat effects or heterospecific attraction. Redband trout foraging and aggression decreased in the presence of both conspecifics and heterospecifics, and aggression appeared to decrease with supplemental feeding. These contrary results between the former and latter experiments testing for aggression as a response to feeding are explained via the manner in which food was delivered to the stream, pulsed at dawn and dusk versus delivered evenly over time, respectively. In the concluding chapter (Chapter 5), I make the case that restoration practices acknowledging a broad range of potential drivers for species distributions—including behaviorally-mediated biotic interactions among the fish assemblage—will better serve a broader range of restoration goals.

How the Animals Found Their Places: Pattern Detection, Experimentation, and Epistemology in a High Desert Stream Fish Assemblage

by
Seth Michael White

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APPROVED:

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Major Professor, representing Fisheries Science

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Head of the Department of Fisheries and Wildlife

_____

Dean of the Graduate School

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

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Seth Michael White, Author

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CONTRIBUTION OF AUTHORS

Drs. Hiram W. Li and Guillermo R. Giannico were the lead investigators on the larger South Fork John Day redband trout project, and were involved in project coordination, project design, and data collection in all the manuscript chapters of this dissertation (Chapters 2-4). Luis Francisco Madriñán contributed to the design and data collection of Chapter 2. Ian A. Tattam and Nicholas Weber contributed to the design and data collection of Chapter 3.

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This dissertation is dedicated to Leňa. She knows why.

Děkuji moc.

HOW THE ANIMALS FOUND THEIR PLACES: PATTERN DETECTION, EXPERIMENTATION, AND EPISTEMOLOGY IN A HIGH DESERT STREAM FISH ASSEMBLAGE

CHAPTER 1

GENERAL INTRODUCTION

> How the Animals Found Their Places, Northern Paiute (as reported by Ramsay 1980)
>
> In the old time Coyote was boss.
> Coyote said, “Bear, you better stay in the mountains.”
> Deer said, “I want to go live in the mountains too!”
> Sucker said, “I want some water.”
> Duck said he wanted water too.
> Swan said, “Look at me, I am growing pretty now;
> see, I am white all over.”
> Bear pounded the ground.
> “Ground,” he said, “who is talking about me?”
> Ground said, “Indian talks pretty mean,”
> so Bear went out and bit him.
> “I want to stay here in the rocks,”
> said Mountain Sheep.
> “I like to feel the ground,” Rock said,
> “I like to stay here in one place and not move.”
> Sagebrush said he felt the same way.
> This is Coyote’s story.

Explaining the distribution and abundance of organisms has been one of the central goals of ecology since its inception (Worster 1994), and probably since before ecology emerged as a formal discipline. The Northern Paiute story “How the Animals Found Their Places” is one such early attempt to make sense out of a seemingly random distribution of plants and animals, an effort to describe and justify patterns in nature that can appear overwhelmingly chaotic. Although the stories we tell to explain patterns in nature might serve many spiritual, aesthetic, or moral purposes, there is also a very

practical reason for being able to explain the distribution of organisms: prediction. We want to be able to predict how plants and animals are distributed in nature—in both time and space—so that we can make better choices as a human society about how to live without unnecessarily detracting from the natural world (McGill et al. 2007). While a general consensus may not exist regarding what is "unnecessarily detracting" from nature, there are still several questions that many agree would be easier to answer given better predictive abilities, including: To what degree can we use natural resources and expect them to be there for us and future generations? Is there a way in which humans and the rest of nature can coexist so that that nature will provide for not only our vital needs (Næss 1989) and vice versa, but also for the aforementioned spiritual, aesthetic, and moral values? And finally, as our society attempts to correct the mistakes of its past, to what degree will efforts at restoring nature prove effective?

The human relationship with salmon in the Pacific Northwest is a case in point. Although salmon, steelhead, and trout have evolved over millennia in this geologically-active region and have developed several adaptive traits and behaviors enabling their survival in harsh environmental conditions, many populations are nonetheless threatened by human-related activities such as dam building, timber harvest, cattle grazing, irrigation, fishing, hatcheries, urbanization, and introductions of non-native species (Behnke 2002). Humans have a long history with salmonids *Oncorhynchus* spp. in this region—beginning with harvest by American Indians and later Europeans and other settlers, and culminating in our present position, poised to decide the fate of salmon and other river life (Lichatowich 1999)

The 'redband trout,' of the South Fork John Day River, the focal population of this study, are considered a primitive evolutionary line of *O. mykiss* that probably cannot be traced to a single ancestor due to their complex lineage of alternating periods of population isolation and convergence (Behnke 2007). Although not currently considered a formal subspecies, redband trout appear to be morphologically and biochemically differentiated from rainbow trout in coastal streams, discrepancies which reveal themselves in the unique genetics of several populations east of the Cascade Mountains (Currens et al. 2007). These fish are also referred to as 'redband-steelhead trout' because

their populations yield both resident trout and anadromous steelhead (Behnke 2002), just one indicator of the diverse life history forms possible in these populations.

Although the John Day River system in eastern Oregon is one of the largest undammed rivers in the U.S., its watershed harbors several wilderness areas, and the South Fork maintains protection via a Wild and Scenic designation, populations of redband trout are still faced with many problems there that are implicated in the decline of their populations. Namely, the John Day River and many of its tributaries (including the South Fork) are listed as 303d water quality limited streams due to elevated temperatures. Many areas in this basin experience severe cattle grazing, irrigation diversions, and other forms of habitat degradation that have contributed to the listing of *O. mykiss* as Threatened under the Endangered Species Act (Federal Registry Office 71FR834). Although much effort and resources have been devoted to restoring these and other salmonid populations in the Columbia River basin, the labors have typically met with varied or minor successes (ISAB 2003).

There are of course several probable reasons why restoration efforts are not always effective—including political, social, and economic obstacles—but another potential reason is that we lack a sophisticated enough understanding of the organism's ecology to allow predictions. We would like to predict, for example, the impacts of different kinds of forest management practices, or the effects of particular restoration projects, on salmonid populations. That our predictive ability remains poor may seem surprising to the public given the tremendous resources dedicated to adipose-finned fish in the Pacific Northwest. But many ecologists recognize that nature is complex, and that more basic and applied science is needed. Here we have a paradox: on one hand, we have spent a tremendous amount of resources on salmon research and recovery ($150 million as reported over a decade ago by Naiman et al. 1995, and currently $4-8 billion as per Pete Bisson and Hiram Li, pers. comm.) but on the other hand, we often lack the ability to make accurate predictions even regarding the most basic behaviors.

I suggest that one explanation for this phenomenon is that fisheries scientists—and probably scientists in many disciplines—find themselves entrained in prescribed

patterns of thought and pre-ordained methods of investigation, which I will term the Cartesian perspective, rather than seeking out new and holistic ways of understanding ecological systems, which I will call the integrated perspective (Table 1.1). The difference between the Cartesian versus integrated perspectives includes, respectively, the reduction of whole systems into parts versus recognizing and studying the whole (Sagoff 2003); using the accepted tools and perspectives from a single discipline versus drawing from multiple disciplines (Fisher 1997); employing only classical hypothesis testing versus the additional use of pattern description (Lawton 2000), multivariate analyses (McCune and Grace 2002), and information-theoretic approaches (Stephens et al. 2007); and elevating the voice of science to one of supreme authority versus recognizing science as just one of many narrative forms (Allen et al. 2001) (Fig. 1.1).

My assumption is that by drawing on the relative strengths of both of these perspectives (rather than criticizing or praising a particular approach), knowledge created by fisheries scientists can better contribute to both ecological theory and practical conservation and restoration programs. My approach was to recognize the holistic nature of the system under study—redband trout in the South Fork John Day River—by examining the role of both biotic and abiotic factors in structuring their distributions; using the complimentary perspectives of landscape ecology and behavioral ecology; employing a combination of classical, multivariate, and information-theoretic statistical approaches; and fully disclosing my process of generating hypotheses.

The overall goal of this study was to examine the relative role of biotic and abiotic factors in structuring redband trout populations in the South Fork John Day. Figure 1.2 illustrates my conceptual approach that proceeds via pattern description, hypothesis generation, experimentation, and finally re-informing my overall understanding of the broader pattern. Essentially, pattern detection at the landscape/watershed scale (Chapter 2) informed hypotheses that could be tested using mensurative/observational and manipulative experiments at the reach scale (Chapter 3), which in turn suggested hypotheses that were tested using a multi-species habitat selection theory in a single stream reach (Chapter 4). My objectives in Chapter 2 were to examine the relationship between the biological traits of fish and their environment in

context of prevailing theories of stream ecology (stemming from Vannote et al. 1980). Specifically, my objectives were to:

1) Describe multivariate patterns of biological traits of fish and patterns of habitat characteristics in the South Fork watershed,

2) Determine which traits are related to which habitat characteristics at multiple scales, and

3) Generate and test hypotheses about modes of species coexistence between disparate trait guilds.

Next, I combined the perspectives of behavioral ecology and the riverscape approach (Fausch et al. 2002) to elucidate the 'behaviorscape' of redband trout foraging and aggression in context of prevailing foraging theory (stemming from Stephens and Krebs 1986) and using methods that maximize the 'reality' of findings (as per Levins 1966) while minimizing observer disturbance to the organism. In Chapter 3, my objectives were to:

4) Describe multivariate redband trout foraging and aggressive behaviors in context of prevalent environmental conditions in the watershed, and

5) Examine the effect of food addition on redband trout growth, foraging and aggressive behavior, and potentially movement.

Results from the latter manipulative experiment (objective 5) indicated that contrary to previous research describing salmonids as organisms that regularly assess and move into optimal habitat patches (e.g., Gowan and Fausch 2002), redband trout and a potential competitor—juvenile Chinook salmon *O. tshawytscha*—did not make significant migrations among habitat units in response to addition of large amounts of food. In a concurrent study in this basin (Madriñán 2008), redband trout also moved infrequently in late summer. However, because my results about salmonid movement were inconclusive (the study design was optimized to detect the effects on fish growth

and behavior, not movement) and because a large body of work predicts that mobile organisms will select habitat based on the combination of resource availability and competitor densities (stemming from Fretwell and Lucas 1970; Fretwell 1972; and Rosenzweig 1979), I pursued the following objectives in Chapter 4:

6) Test the prediction that intra- and interspecific competitor densities will affect salmonid habitat selection of enriched patches, and

7) Test the prediction that intra- and interspecific competitor densities will affect redband trout foraging and aggressive behavior.

In the final chapter (Chapter 5), I summarize conclusions of each of these chapters in context of restoration principles for Pacific Northwest stream ecosystems.

This project complements an existing research framework designed to elucidate several ecological factors driving redband trout dynamics: to examine how physical habitat characteristics and water temperature drive their distributions (Madriñán 2008); to evaluate seasonal patterns of their migration, growth, and survival (Tattam 2006), and to correlate elevated stream temperatures with physiological responses (Feldhaus 2006). By expanding on these perspectives to include the potential biotic interactions among other fish that may be involved in structuring redband trout populations, I hope to add to a body of knowledge that will help to increase our predictive ability in this system.

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Tables

Table 1.1. Cartesian and integrated methods of conducting scientific investigations, with examples of the approach taken in this dissertation.

	Cartesian perspective	Integrated perspective	Perspective used in this dissertation
Ontological view of system	Reduction of the whole into parts	Recognition of whole systems (holism)	Consider not only multiple species, but also relative roles of biotic and abiotic factors at multiple scales
Research perspective	Using tools and perspectives of a single discipline	Using tools and perspectives of multiple disciplines	Combination of landscape and behavioral ecology perspectives; combination of mensurative and manipulative experiments
Quantitative tools	Classical hypothesis testing	Information-theoretic and multivariate approaches	Combination of hypothesis testing, model selection, and multivariate approaches
Narrative voice	Modern: science holds the key to knowledge, has all the ‘answers’	Postmodern: science is a narrative art, ‘answers’ depend on the storyteller	Recognizes the role of metaphor, e.g., the ‘landscape’ metaphor; full disclosure of where hypotheses came from

Figures

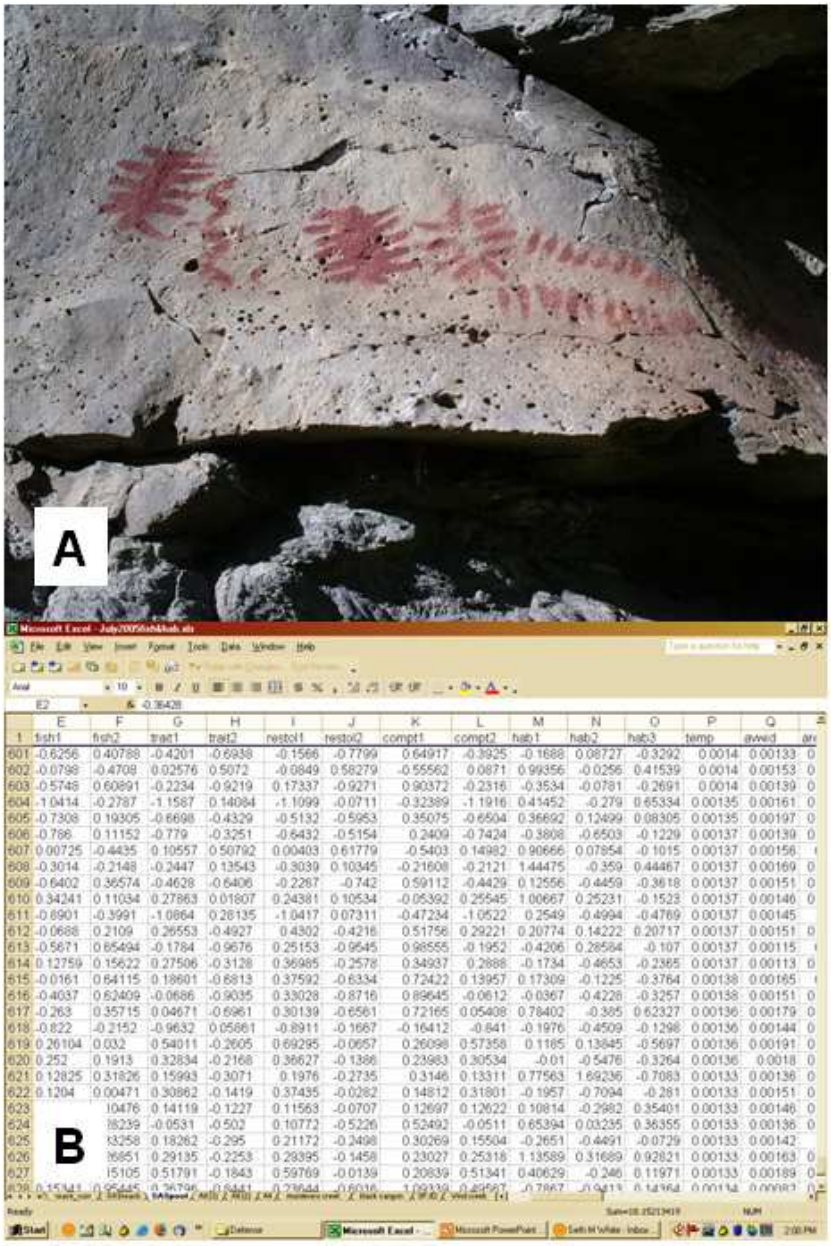

Figure 1.1. Two narratives in the South Fork John Day, eastern Oregon. The top picture (a) is rock art on a cliff overlooking Black Canyon Creek, a wilderness stream in the watershed, likely drawn by the Northern Paiute who most recently inhabited the area. The screenshot below (b) is raw data of fish assemblage distribution and habitat characteristics in the same river system. Both methods are an attempt to describe or make sense out of the natural world, and both have the potential to be equally compelling.

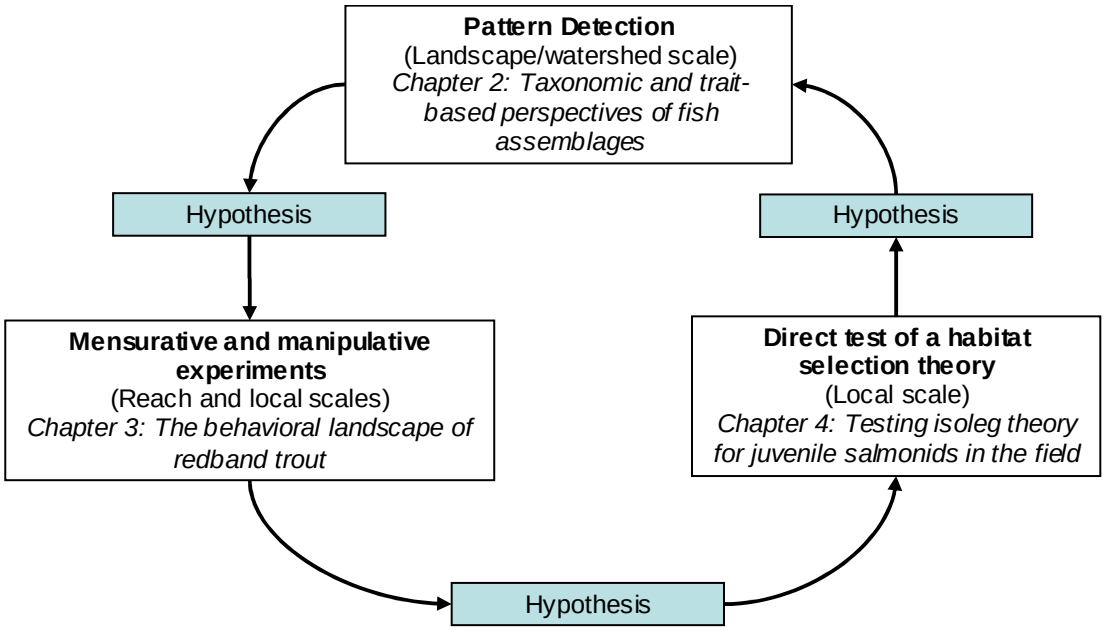

Figure 1.2. A model for understanding ecological systems, with references to chapters in this dissertation. The process begins with pattern description (top) which leads to hypotheses about larger-scale patterns. These hypotheses are subsequently tested using both observation (mensurative) and manipulative experiments at reach and local scales (left). New questions and hypotheses arise, which again are tested at smaller scales (right). Ideally, insights from smaller scale studies—because hypotheses were informed from larger-scale patterns—can provide new information about patterns at the largest scale.

Chapter 2

CAN A TRAIT-BASED APPROACH PROVIDE CLUES FOR COMMUNITY ASSEMBLY? A CASE STUDY IN AN EASTERN OREGON FISH ASSEMBLAGE

Abstract

Functional approaches to community ecology have the potential to provide more ecological generality and perhaps better predictive ability than the commonly-used 'species-specific' approach to modeling fish-habitat associations. I described the distribution of the fish assemblage in the South Fork John Day River, eastern Oregon, in context of the biological traits of fish species and multiple-scale environmental features (local habitat measures, reach-scale geomorphology, and remotely-sensed thermal imagery of surface water temperatures). Using readily-available information about biological traits such as water temperature preference, spawning mode, functional feeding group, and maximum size category, I derived alternative hypotheses about mechanisms driving assemblage structure at the watershed, tributary, and reach scales. Multivariate habitat indices were used as predictor variables and multivariate trait indices as independent variables in linear regression models that competed in a model selection context (Akaike's Information Criteria). Both fish trait and environmental ordinations provided interpretable ordination axes that formed significant regression models at all spatial scales. Fish traits, environmental conditions, and the way in which trait guilds were related to environmental features were distributed heterogeneously throughout the watershed, a finding opposed to prevailing theories of stream ecology that predict a gradual continuum of these processes. The nature of relationships between fish traits and environmental features seemed to be more affected by the types of traits present in particular locations than the distribution of environmental conditions in the basin, and therefore biotic factors (e.g., competition and predation) were potentially important drivers of species distributions in this system. These findings provide a basis for gaining insights from the kinds of snapshot-in-time, extensive distribution datasets that are becoming increasingly important in fisheries management and ecological research.

Introduction

> Conclusions drawn from descriptive studies are subject to the same problems as inferring the plot of a mystery novel by reading only the last paragraph.
>
> Li and Li 1996, p. 392, paraphrasing Johannes and Larkin (1961)

> So all life is a great chain, the nature of which is known whenever we are shown a single link of it.
>
> Sherlock Holmes, *A Study in Scarlet*

Explaining and predicting the distribution of organisms has been one of the main agendas throughout ecology's long history (Worster 1994). While ecologists pursue this otherwise worthy cause, global biodiversity is rapidly decreasing (Sala et al. 2000). Therefore, developing approaches for quickly assessing organism distribution, while simultaneously providing ecological insights about why those organisms are found where they are, is of paramount concern. In particular, biodiversity of freshwater fishes is currently undergoing rapid declines due to overexploitation, flow modification, habitat destruction, invasive species, and pollution (Harrison and Stiassny 1999; Dudgeon et al. 2006; Helfman 2007), a trend that is especially alarming because most of the world's fish biodiversity resides in freshwater ecosystems representing only one percent of the earth's surface (Lévêque et al. 2008).

Functional approaches to community ecology, focusing less on taxonomic and more on functional diversity, have gained recent attention and have the potential to increase our understanding of mechanisms driving community assembly rules (McGill et al. 2006; Shipley et al. 2006). This idea was captured by the words of Louis Sullivan, one of the founders of the Chicago School of Architecture, who coined the phrase, "Form follows function." Like the gargoyles of Prague Castle whose curved tongues funnel rain to the courtyard below, organism traits (e.g., fusiform morphology in salmonids) can be conceived of as solving particular environmental problems (e.g., strong current or long

migration distances). If the relationship of a particular trait is strongly correlated with the environment, this suggests that the organism's presence at a local site was constrained by that particular feature. However, biological traits can also be a residual feature of phylogenetic history or developmental constraints and so knowledge of which traits correspond with which environmental characteristics will help temper our “adaptionist thinking” (as per Gould and Lewontin 1979).

Functional approaches in freshwater ecology have been used to predict species additions to local habitats due to a spatial hierarchy of environmental and biotic filters (Poff 1997) and can provide a more mechanistic understanding of ecological relationships and perhaps better predictive ability than traditional species-specific habitat modeling. Statzner et al. (2004) demonstrated that currently-available knowledge of European stream invertebrate traits can help increase understanding of how communities are affected by multiple-scale environmental filters, and how the approach provides a richer framework for future research in ecology. A functional approach also promises to bridge the gap between our understanding of landscape pattern and our understanding of ecological processes important to organisms in the riverine environment (Wiens 2002). In contrast, taxonomic approaches to describing communities often fail to reveal functional diversity (Barnett et al. 2007), thereby concealing general patterns of communities that could lead to more predictive insights. This is especially important in freshwater aquatic ecosystems where several mechanisms such as biotic, abiotic, and spatial factors could potentially be implicated in driving observed patterns of “who is where” (Jackson et al. 2001). Even in relatively species-poor systems, examining species by species relationships can be complex because many of those relationships are nonlinear, and many species occur at abundances of vastly different scale (e.g., Fig. 2.1).

Recent advances in geographic information system (GIS) technology and spatial modeling of fisheries data (e.g., Nishida et al. 2007; Pichon et al. 2007) also have the potential to increase our understanding of general ecological patterns, but only if those studies move beyond pattern description. And although it is relatively easy to enter and display data in a GIS, many such approaches to modeling species-environment relationships are correlative in nature and lack a mechanistic explanation for how

organisms are distributed (Kearney 2006). The current study is an attempt to move beyond mere pattern description and into a richer understanding of species distributions, while at the same time retaining the ease and convenience of classic habitat modeling. Essentially, my approach was to examine patterns of fish assemblage distribution and assess multiple hypotheses regarding causal mechanisms driving those patterns. My primary assumption was that by examining the functional relationships between fish and their environment, I would be better able to make more ecologically-informed inferences about mechanisms than by examining taxonomic relationships with environment. If ecologists adopt the detective metaphor regarding how they should perform their job (Hilborn and Mangel 1997), then it follows that a good ecologist—like a good detective—should move beyond pattern description and towards more nuanced explanations of ecological phenomena.

My first objective was to describe the distribution of selected fish traits and environmental characteristics of the anadromous fish-bearing portion of a high desert stream, in context of important organizing principles of stream ecology. I proceeded by examining multivariate patterns in traits and habitat characteristics along the longitudinal profile of the South Fork John Day River in eastern Oregon. My second objective was to determine which suites of fish traits were most strongly correlated with environmental characteristics at the watershed, tributary and reach scales. I hypothesized that due to features of the environment that screen out particular traits at different spatial scales ("trait filters" as per Poff 1997), traits would be related to opposing sets of environmental characteristics at the watershed, tributary, and reach scales. I proceeded by using an information-theoretic approach (Burnham and Anderson 2002) to evaluate candidate models of trait-environment environments at each spatial scale. In evaluating the reach-scale models, I made the observation that trait-environment relationships could be categorized according to whether different trait guilds shared or partitioned different types of habitat according to prevailing ideas of species coexistence (Tokeshi 1999; Sommer and Worm 2002). I therefore became interested in whether traits or environment played a more important role in structuring these relationships. If traits played a larger role, that would suggest biotic interactions such as competition, predation, or other modes

of interaction are important in determining “who is where” in this stream. Conversely, if environment played a larger role in structuring these modes of coexistence, which would suggest that physical characteristics (e.g., water temperature and river geomorphology) play a strong role in determining “who is where.” Therefore, my third and final objective was to evaluate the relative strength of correlations between the distribution of traits versus environment and my designation of model types (niche partitioning, niche overlap, or non-associative). I proceed by conducting multivariate tests of group differences, with model types as response categories and traits versus environmental characteristics as explanatory variables.

In a broad sense, the overall strategy for objectives 1-2 is depicted in Figure 2.2. The first step was to compile information about fish traits in this system, then to combine those results with fish distribution data. I then performed ordinations of fish traits and habitat characteristics to derive indices for each (objective 1), and then modeled the relationship between those indices to discover which traits were related to which habitat characteristics (objective 2). These analyses were performed at the three spatial scales, and the final reach-scale models were used in an analysis (objective 3) to determine whether the distribution of traits or habitat had a greater influence on the mode of species coexistence.

Methods

Study area

This study was conducted in the South Fork of the John Day River and its two major tributaries, Murderer’s Creek and Black Canyon Creek, in northeastern Oregon (Fig. 2.3). The South Fork John Day is a stream impacted by cattle grazing, timber harvest, road building, and irrigation; but also containing within its watershed boundaries a wildlife refuge managed by the Oregon Department of Fish and Wildlife, Bureau of Land Management holdings, the Ochoco and Malheur National Forests, the Black Canyon Wilderness Area, and several private ranches (Loy 2001). The John Day River is one of

America's largest unimpounded rivers, and its South Fork maintains designation as a Wild and Scenic River.

Table 2.1 lists native fish species commonly encountered in the system; other native fish species include chiselmouth (*Acrocheilus alutaceus*), lamprey (*Lampetra* spp.), and two commonly-encountered species of cottids (*Cottus beldingi* and *C. rotheus*). The study of redband trout (*Oncorhynchus mykiss*) population listed under the Endangered Species Act (ESA) forms the sideboards of a larger project assessing the effects of temperature and other consequences of land use on fish distribution, growth, survival, and behavior (Li et al., unpublished data). A biogeographic analysis of fish species in the John Day and adjacent basins reveals a high degree of variation in assemblage composition in areas rich in geologic and hydrographic history (Bisson and Bond 1971).

I conducted this study at the basin, tributary, and reach scales in a similar manner as described in the categorization of spatial hierarchy in streams (Frissel et al. 1986). Studies at similar scales have proven effective for elucidating key patterns (Torgersen et al. 2006) and predicting critical habitat requirements (Harig and Fausch 2002) for stream fish. The spatial extent of the study was 72 river km of the South Fork John Day and its tributaries. This included the 45 river km of the mainstem South Fork below Izee Falls—the entire anadromous fish-bearing portion of the stream, with the exception of lower four river km where access to private land could not be obtained. I also surveyed the lower 19 river km of Murderers Creek and the lower eight river km of Black Canyon Creek up to the points where pools became too shallow or the gradient became too steep to survey, respectively. I conducted fish and habitat surveys at a snapshot in time: in midsummer at the approximate time of peak water temperatures and during low base flow conditions (Fig. 2.4) when fish were presumed to have settled in habitats to balance their physiological performance based on competitor densities, water temperature, food availability, and a suite of other potential factors (Jackson et al. 2001).

Surveys of fish distribution

Other researchers (Madriñán 2008) and I conducted spatially continuous, underwater visual surveys in order to document fish species distribution. Snorkeling has been demonstrated as an effective method for identifying longitudinal patterns in fish-habitat associations in streams (Thurow 1994; Mullner et al. 1998) and is also a relatively unobtrusive method, especially important when attempting to reduce impact on ESA-listed fish such as *O. mykiss* in the present study.

Multiple teams of trained snorkelers and note takers worked their way upstream through every pool in the study extent and every fifth riffle, totaling 1285 sampled habitat units and > 800 pools. Pools were the habitat unit of primary interest in this study because they have been shown to be energetically favorable as compared to riffles (Rosenfeld and Boss 2001). To a note taker on the stream bank, the snorkeler relayed estimates of fish counts by species and in the case of salmonids by length category. With three crews conducting surveys simultaneously, surveys were confined to a short time period (July 5 to July 21) in order to control for possible fish migration during the sampling window. Additionally, Madriñán (2008) found that during the mid-late summer season, radio-tagged *O. mykiss* in this system did not make significant migrations among local habitats. Because light conditions can affect underwater visibility, we consistently sampled between 0900 – 1700 hrs. Due to difficulty of observing sculpin (*Cottus* spp.) in the hyporheos during snorkel surveys and the resulting high probability of incorrectly classifying them as absent, these fish were not included in the analyses.

My method of relativizing the species and trait totals in data matrices prior to analyses (see ‘Data analyses’ section below) shifted the focus of inquiry towards the relative abundances of different members of the fish assemblage and their corresponding trait distributions. Therefore, my analyses were robust to discrepancies between fish counts derived from the rapid assessment technique and actual population abundances. Even so, a concurrent study in the South Fork John Day River relating mark-recapture population estimates to snorkel estimates reveals that snorkeling can be a precise, if not

accurate, tool for evaluating relative population sizes of the fish assemblage (Bayley et al., unpublished data).

Environmental data

Immediately after fish surveys of each channel unit, we collected environmental characteristics of pools using a modified version of Hankin and Reeves's (1988) protocol for sampling fish habitat along longitudinal profiles of rivers. We measured pool geometry (width at head, middle, and tail of pool; pool length; maximum depth of thalweg and tail) and calculated average pool width, total pool area, and residual pool depth (the maximum depth of a pool should it become isolated from others with declining water levels = maximum depth - tail depth). We visually estimated the percent of shoreline length having banks undercut ≥ 40 cm. As a proxy of large woody debris input from the riparian zone, we recorded the number of pieces of wood having stem diameter ≥ 10 cm (represent large wood in this river system) in contact with the pool. We visually estimated the size classes of dominant vs. subdominant substrates on a ranked scale (sand/silt/clay, small gravel, large gravel, cobble, boulder, or bedrock), and also ranked the degree of substrate embeddedness based on degree of difficulty freeing substrate from the stream bottom by hand (1-4 with increasing resistance). Using a hand-held GPS, we recorded the UTM (to 5-15 m accuracy) of each channel unit for later referencing in a geographic information system (GIS) database.

Maximum surface water temperatures of each pool were estimated using aerial, forward-looking infrared (FLIR) imagery on September 12, 2004—one year prior to collection of fish and habitat information—while water levels remained at base flows and temperatures near their annual peak. Although FLIR and fish-habitat data were derived from different years, the relative distribution of temperatures in this river system among years is relatively homogeneous (Madriñán 2008), as would be expected from the predictable annual hydrograph and seasonal average water temperatures (Fig. 2.4). Also, my method of relativizing habitat characteristics emphasized the proportional

relationships among environmental characteristics, not absolute values, and therefore I was confident in using 2004 FLIR data as a proxy for 2005 stream temperatures. FLIR has been successfully used to reveal relationships between water temperature and river biota relationships across entire river systems (e.g., Torgersen et al. 1999; Torgersen et al. 2006). Water temperature estimates from FLIR were calibrated using nearby stream gauging stations and with a series of submersible, automatic water temperature recorders distributed along the length of the South Fork and its tributaries. Further details on FLIR protocols for measuring stream surface water temperatures in general can be found in Torgersen et al. (2001); while details of the use of FLIR in a concurrent study in the South Fork John Day River are described by Madriñán (2008).

We categorized the river system into geomorphically and thermally distinct reaches using the hierarchical framework described by Frissel et al. (1986). Madriñán (2008) initially designated reach breaks with major changes in surface water temperatures and geomorphology using FLIR imagery and airborne light detecting and ranging (LiDAR) technology: change from valley to canyon, > 2% change in gradient, or major change in aspect or elevation; reaches were further partitioned if FLIR-based water temperatures differed by > 3ºC, resulting in a total of 22 reaches. For the reach-scale analyses of the present study, I grouped South Fork reaches into “meta-reaches” according to similarities in FLIR-derived maximum water temperatures, based on visual inspection of the longitudinal distribution of standardized water temperature by reach (Fig. 2.5). This grouping of mainstem South Fork reaches was desirable because reaches there were relatively short, and the subsequent reach lengths and variability in water temperatures were more comparable to those of the tributary reaches. The final number of river sections (reaches and meta-reaches) was three reaches each in Murderers and Black Canyon Creeks and seven meta-reaches in the mainstem South Fork, for a total of 13 river sections.

Compilation of trait information

I compiled readily-accessible information about fish species traits from field guides, published scientific literature, and data from the snorkel surveys. Here, I define trait to mean what recent authors have termed functional traits and ecological performances (Violle et al. 2007). I considered functional traits as characteristics that influence organism performance and fitness at the individual level (in this case: feeding group, spawning behavior, and maximum body length). I considered ecological performances as the response of individual performance to the environment (pollution tolerance and temperature preference). Regardless of terminology, both functional traits and ecological performances were employed in the analysis in an identical fashion, with each trait having one of multiple attributes (e.g., sensitive, intermediate, and tolerant are attributes of pollution tolerance) assigned to each species (Table 2.1).

A majority of the trait information was gleaned from Zaroban et al. (1999), who classified species attributes of Pacific Northwest fishes including sensitivity to siltation, turbidity, increased water temperature, and decreased dissolved oxygen ("pollution tolerance"); temperature classification of various life stages and physiological optima ("temperature preference"); and primary diets and distinguishing anatomy ("adult freshwater feeding group"). Using information compiled in Wydoski and Whitney (2003) and categories from Goldstein and Meador (2004), I also classified "reproductive strategy" for each species. Maximum body lengths for each species were derived from snorkel survey data. Although both anadromous and resident forms of redband trout are common in this system (Tattam 2006), both life history forms were considered a single taxonomic group. Traits of both anadromous and resident redband trout corresponded well within my designated trait categories (Table 2.1), including maximum body size—as resident and migratory *O. mykiss* were rarely observed > 250 mm during snorkel surveys, and these sizes correspond to length categories recorded for steelhead smolts in downstream migration traps from the South Fork John Day River (ODFW, unpublished data). Likewise, although Chinook salmon *O. tshawytscha* adults can reach much larger sizes than considered here, this species does not spawn in the South Fork tributary of the John Day River—rather, juveniles < 150 mm immigrate from the mainstem John Day

and use the South Fork for rearing only, typically from June through November (Jeff Neil, ODFW, pers. comm.).

Data analyses

The overall modeling strategy was to first generate matrices of fish traits and habitat characteristics, then derive multivariate axes multivariate axes for each, and finally relate the trait and habitat indices to one another using multiple linear regression (Fig. 2.2) for each of the three spatial scales. Following the notation of Legendre et al. (1997), data for fish, traits, and habitat were compiled into three separate matrices: matrix **A** (k x m) containing abundance information of k fish species at m pools, matrix **B** (k x n) describing n trait attributes of the same k fish species, and matrix **C** (p x m) containing information for p environmental variables. Rare trait attributes appearing in fewer than five percent of the pools were removed from the analysis. To arrive at the new matrix of species traits in each pool—matrix **D** (n x m)—I multiplied the species matrix **A** by the transposed trait matrix **B′**. I then calculated matrices of the direct relationship between fish species and environment, matrix **AC′** (k x p); and traits and environment, matrix **DC′** (n x p). I performed general relativizations of column totals (using Sørensen's distance measure) to account for disparate abundances of fish assemblage members in the case of fish and trait matrices **A** and **D**, and in order to account for the ranked scales of several habitat characteristics in the case of environmental matrix **C**. Environmental variables on continuous scales were natural log-transformed in order to meet assumptions of normality for subsequent Pearson correlations. After transformations, I removed habitat units that were strong multivariate outliers, having standard deviations $\geq$ 2.0 (Sørensen's distance) from each matrices **A**, **C**, and **D.**

To describe multivariate patterns in the distribution of fish traits and environmental characteristics of pools, I used nonmetric multidimensional scaling (NMS) (Kruskal 1964; Mather 1976). This ordination technique is an ideal method for ecological datasets because it avoids assumptions of linearity, can handle data on arbitrary scales,

relieves the zero-truncation problem, and allows freedom to choose any distance measure or relativization (McCune and Grace 2002). I first determined the appropriate number of axes by conducting preliminary NMS runs (Sørensen's distance) for each analysis. Preliminary runs stepped down from a 6-dimensional to a one-dimensional solution using random starting configurations, 10 runs with the real data, a designation of 200-500 iterations with a stability criteria of 0.0005, and 20 runs of randomized data for a Monte Carlo test. The number of dimensions for each analysis was chosen by examining scree plots of final stress vs. dimensionality. In each case I selected the lowest dimensionality where additional axes provided only incremental reductions in stress and the number of dimensions were significant at the $\alpha = 0.05$ level based on comparison with a Monte Carlo null model. I then performed a final, single NMS run using only the real data and the selected dimensionality and random starting configurations from preliminary runs.

To discover the nature of association between fish traits and environmental characteristics at multiple scales, I use a model selection approach (Burnham and Anderson 2002) to derive the most parsimonious, multiple linear regression models relating multivariate trait axes (dependant variables) to multivariate environmental axes (independent variables) using Akaike's Information Criterion (AIC) (Akaike 1973). I took advantage of the dataset's nested hierarchy of spatial scales, with data being collected at individual pools, which allowed me to average data by reaches for the watershed-scale analysis. At the watershed scale, the spatial extent of the model was the entire 72 km of surveyed river, and the grain was the 22 river reaches. At the tributary scale, the extent of each analysis was the extent of each tributary, and the grain was the individual pool, with sample sizes ranging from 124 – 300 pools. At the reach scale, the extent for each analysis also varied according to the extent of the particular river section and the grain was again the individual pool, with sample sizes ranging from 13 – 116 pools. Models were ranked according to their Akaike value adjusted for small sample sizes (AIC_c), with lower values indicating a more parsimonious model (Burnham and Anderson 2002), and by their Akaike weight (w_i) indicating the weight of evidence for the model given the data (Buckland et al. 1997).

I then classified the above regression models according to prevailing ideas of species coexistence (Fig. 2.6) (Tokeshi 1999; Sommer and Worm 2002), with "niche overlap" models exhibiting either a shared preference or avoidance of habitat by a trait guild; "niche partitioning" models exhibiting either a similar association of trait guilds with disparate habitat or disparate association with particular habitat; and "non associative" models exhibiting disparate association of trait guilds with disparate habitat, avoidance of disparate habitat, or only one trait guild contributing to a significant model at the $\alpha = 0.05$ level. To determine the relative influence of fish distributions vs. environmental characteristics on the type of model class at the reach scale, I examined which set of ordination axes best delineated groups of model classes. I employed multi-response permutation procedure (MRPP) (Mielke and Berry 2001), a nonparametric test for the hypothesis of no difference between pre-defined groups. I classified the aforementioned designation of the 13 river sections into the three model classes and ran two separate MRPP analyses: one testing for group differences based on trait ordination axes alone, the other testing for group differences based on environmental ordination axes alone. In both analyses I used a Euclidian distance measure, and distance matrices were rank-transformed.

All matrix manipulations and multivariate analyses were performed in PC-ORD v.5.19 beta (McCune and Mefford, n.d.), a software package specifically designed for analysis of ecological data. Multiple linear regression and model selection computations were performed is SAS v.9.1.3 (SAS, 2004).

Results

Objective 1: Multivariate patterns in fish traits and environmental characteristics

Nonmetric multidimensional scaling revealed intuitive patterns in both the distribution of fish traits and environmental characteristics. Ordination of sample units (pools) in fish trait ordination space (N = 686) resulted in a two-axis solution (Table 2.2a), with both axes explaining nearly three-quarters of variation in the dataset ($R^2 = 74.6\%$). Due to the

large number of strongly correlated traits, I interpreted trait axes based on Pearson correlations (r) > 0.50. Both trait axes could be described in terms of a fish's expected association with a gradient of physical conditions corresponding to the river continuum (Vannote et al. 1980) and terminology introduced by Bayley and Li (1992)—with the "rhithron" described as points on the continuum with faster currents, coarser substrates, and allochthonous sources of organic matter; and the "potamon" as slower currents, finer substrates, and autochthonous sources of organic matter. Trait axis 1, which I abbreviate as "COOLWATER," explained a large portion of the variation (R^2 = 40.9%) and was positively correlated with the following trait attributes: coolwater preference (Pearson's r = 0.73), broadcast spawner (0.73), intermediate pollution tolerance (0.71), invertivore (0.68), and small maximum body size (65-99 mm) (0.68). Trait axis 2, "COLDWATER," explained a large portion of the remaining variation (R^2 = 33.7%) and was positively correlated with the following trait attributes: sensitive pollution tolerance (Pearson's r = 0.76), simple nester (0.76), coldwater preference (0.74), and large maximum body size (200-250 mm) (0.72).

Ordination of sample units (pools) in environmental space (N = 662) resulted in a three-axis solution (Table 2.2b), with the cumulative axes explaining a large majority of variation (R^2 = 87.9%) in the dataset. Because there were fewer strongly correlated environmental variables, I interpreted environmental axes based on Pearson's r > 0.20. The three trait axes could be described in terms of Montgomery and Buffington's (1998) designation of reach-level channel types—with "response," "transport," and "source" characteristics corresponding to downriver, transitional, and headwater-type habitats, respectively. Environmental axis 1, "RESPONSE," explained over one-third of the variation (R^2 = 37.9%) and was positively correlated with pool size: pool width (Pearson's r = 0.62), pool area (0.68), maximum depth (0.65), residual depth (0.55); and large woody debris (0.61), embedded substrates (0.34), and water temperature (0.29). Environmental axis 2, "TRANSPORT," explained less than one-quarter of variation in the dataset (R^2 = 21.1%) and was positively correlated with undercut banks (Pearson's r = 0.65), residual pool depth (0.38), and maximum pool depth (0.22); and negatively correlated with the degree of embedded substrates (-0.33). Environmental axis 3,

"SOURCE," explained most of the remaining variation (R^2 = 28.8%) in the dataset, and was positively associated with large woody debris (Pearson's r = 0.67) and negatively associated with pool size: pool width (-0.55), pool area (-0.54), maximum pool depth (-0.40); and residual depth (-0.21) and water temperature (-0.46).

The scores of reach-scale multivariate trait and habitat indices were distributed heterogeneously throughout the South Fork John Day watershed (Fig. 2.7). The most apparent pattern in the distribution of traits was the low values of COOLWATER traits and disparately high values of COLDWATER traits in the highest reach of Murderers Creek (MC3) and throughout the entire length of Black Canyon Creek (BC1-3) (Fig. 2.7a). There was a corresponding reversal of this relationship in lowest reaches of the mainstem South Fork (SFm1-4), with high values of COOLWATER traits associated with low values of COLDWATER traits. COLDWATER traits also scored low in the lower portions of Murderers Creek (MC1-2), but without disparately high values of COOLWATER traits. One exception to this overall pattern was in the uppermost reaches of the mainstem South Fork (SFm7), a colder-than-average section of river (Fig. 2.5) that harbored high scores for COLDWATER traits. The most notable pattern in the distribution of habitat scores (Fig. 2.7b) was high values of SOURCE habitat in the upper section of Murderers Creek (reach 3) and throughout Black Canyon (BC1-3), and corresponding low values for SOURCE habitat throughout most the mainstem South Fork. The RESPONSE-type habitat was absent to rare in the aforementioned tributary reaches (MC3, BC1-3), and present in high to moderate quantities in the lower reaches of the mainstem South Fork (Sfm1-4). The TRANSPORT-type habitat was present mainly in the tributaries Black Canyon and lower two reaches Murderers Creek, while relatively absent in the mainstem South Fork and the highest section of Murderers Creek (MC3).

Objective 2: Multiple-scale relationships between fish traits and environment

The above multivariate analyses revealed two trait axes and three environmental axes, which determined the number of candidate models (R = 7) for all subsequent regression

analyses at the watershed, tributary, and reach scales. For each scale of analysis, the top models predicting both trait axis 1 and 2 are listed in Table 2.3. Although p-values are an artifact of classical hypothesis testing and are therefore irrelevant to some degree in a model selection context (Stephens et al. 2007), I only lent credence to relationships that were significant at the $\alpha = 0.05$ level because candidate models were not necessarily derived in an *a priori* fashion—that is, I expected that traits and environment would be somehow related and perhaps differentially across scales; but I did not hypothesize specific relationships, magnitudes, or direction of association. Thus, when interpreting the nature of association between traits and environment, models not significant at the $\alpha = 0.05$ criteria were considered to exhibit no notable relationship.

Overall, the ability of habitat types to predict trait guilds decreased with decreasing spatial extent. The average proportion of variance explained (adjusted-R^2) by watershed, tributary, and reach-scale models was 44, 26, and 17 percent, respectively. At the watershed scale, the strongest models predicting both the distribution of COOLWATER and COLDWATER traits among river sections were composed of the single environmental axis SOURCE, with COLDWATER traits *positively* associated with SOURCE-type pools ($p > 0.001$, $R^2 = 0.50$) and COOLWATER traits *negatively* associated with the same type of habitat ($p = 0.002$, $R^2 = 0.38$) (Table 2.3; Fig. 2.8a). The estimated probabilities that COOLWATER and COLDWATER models were the best model for the data at hand, given the set of models considered (Akaike weight, w_i) were $w_i = 0.41$ and 0.36, respectively.

At the tributary scale, models in Black Canyon were still relatively strong (as measured by adjusted-R^2; see Table 2.3a for subsequent model strengths, significance levels, and parameter estimates) in relation to the watershed scale models (Fig. 2.8b). A similar pattern in association among trait syndromes and SOURCE habitat emerged as at the watershed scale, but partitioning of habitat was stronger, with COOLWATER traits now positively associated with RESPONSE habitat, and COLDWATER traits negatively associated with REPONSE habitat, except in the Black Canyon tributary. An important effect of changing spatial scale was that in the Black Canyon tributary, the direction of association among COLDWATER traits and SOURCE habitat changed—decreasing the extent of analysis revealed a reversal in the relationship among traits and environment. In

both Murderers Creek and the mainstem South Fork, the association between COOLWATER traits and habitat types remained relatively strong (i.e., explained a reasonable proportion of the variance), but although all tributary-scale models were significant at the $\alpha = 0.05$ level, habitat types did not explain a large proportion of the variance in distribution of COLDWATER traits (largest $R^2 = 0.04$). For COOLWATER traits, Murderers Creek and South Fork mainstem models had a similar direction of association and relatively high proportion of variance explained by the habitat types as the tributary-scale model for Black Canyon. The only exception being that in Murderers Creek, COOLWATER traits were also positively associated with TRANSPORT habitat.

At the reach scale, there was a change in the nature of association between trait guilds and habitat in several areas (Table 2.3b). In only two out of the 13 river sections (Murderers Creek reach 1 and South Fork meta-reach 5) were models predicting the distribution of both trait groups not significant at the $\alpha = 0.05$ level. In Black Canyon reaches 1 and 2, both trait guilds were positively associated with RESPONSE habitat, and avoided SOURCE habitat, a pattern similar to the tributary-scale analysis in this stream. In Black Canyon reach 3, however, both trait guilds were positively associated with TRANSPORT habitat. In Murderers Creek reach 2, COOLWATER traits were positively associated with both TRANSPORT and RESPONSE habitats, while the distribution of COLDWATER traits was not significantly predicted by any of the habitat types. In Murderers Creek reach 3, COOLWATER traits were positively associated with all three habitat types, while COLDWATER traits were positively associated with only TRANSPORT habitats. In the South Fork mainstem, a majority of the models were described by the relationship of either trait guild with RESPONSE habitat (Table 2.3b)—positively with COLDWATER traits and negatively with COOLWATER traits. Compared to all other statistically significant models in the watershed, the ability of habitat types to explain variance in the trait distributions and the likelihood that the top model was the best model was relatively high in Black Canyon ($0.24 \leq R^2 \leq 0.53$; $0.55 \leq w_i \leq 0.75$) and somewhat variable in Murderers Creek ($0.05 \leq R^2 \leq 0.30$; $0.28 \leq w_i \leq 0.61$) and in the mainstem South Fork ($0.06 \leq R^2 \leq 0.38$; $0.30 \leq w_i \leq 0.61$).

Objective 3: Modes of species coexistence

All of Black Canyon and the highest reach of Murderers Creek (MC3) exhibited niche overlap (N = 4); whereas all other locations exhibited either niche partitioning (N = 2; SFm4 and SFm6), were non associative (N = 5; MC2, SFm1-3, and SFm7), or did not form significant models at the $\alpha = 0.05$ level (N = 2; MC1 and SFm5). MRPP tests of whether the distribution of trait scores or habitat scores influenced the type of model among the 13 reaches revealed that both types of ordination axes significantly delineated the model classes, but the designation based on traits had a stronger effect size (chance-corrected within group agreement, A = 0.48) and was significant at a higher level (p-value < 0.001) than the designation based on environment (A = 0.33; p-value = 0.01).

Discussion

Multivariate patterns in biological traits and habitat

Two major trait axes were discovered: COLDWATER traits described the attributes sensitive pollution tolerance, coldwater preference, simple nester, and large body size; while COOLWATER traits described the attributes intermediate pollution tolerance, coolwater preference, invertivore feeding mode, broadcast spawner, and small body size. These trait guilds also corresponded with Bayley and Li's (1992) designation of riverine habitats along a continuum from headwaters to mouth. Rhithron habitats are described as having faster and more variable currents, coarser substrates, and allochthonous sources of organic matter. Potamon habitat is described as having slower currents, finer substrates, and autochthonous sources of organic matter. Goldstein and Meador (2004) derived similar groups of traits from fishes in small streams and large rivers, trait groups they termed RIFFLE and RUN; but their analysis of trait-environment relationships was constrained by the use of cluster analysis—a useful approach for identifying major groups of traits, but one that does not take full advantage of the correlation structure among variables, as does NMS (McCune and Grace 2002). In Poff's (1997) original paper on landscape filters and species traits in streams, he hints that his description of the

effects of landscape filters on trait groups is simplistic because traits are often highly correlated; an issue he states will have to be dealt with in the future. The ordination approach used in the present study is a direct answer to Poff's (1997) concern. Another computational advantage of the trait approach is that information from rare species can be included in analysis if several rare species have similar functional attributes. For example, information about the traits of bridgelip suckers, largescale suckers, and mountain whitefish was incorporated into the trait matrix, even though each of the three species occurred in less than five percent of the sample sites and would have been necessarily excluded from a taxonomic analysis (McCune and Grace 2002).

Besides having similar analytical advantages as the above trait analysis, multivariate ordination of environmental characteristics formed ecologically-relevant axes in context of two important organizing principles in stream ecology: the river continuum concept (Vannote et al. 1980) and the process domains concept (Montgomery 1999). Vannote et al. (1980) described a gradient of conditions correlated with longitudinal position from headwaters to mouth of a river system, a conceptual framework that has been tested against competing theories of stream ecology for over two decades (Statzner and Higler 1985; Poff 1997; Montgomery 1999). In the present study, the RESPONSE axis described habitat with warm water, large and deep pools, abundant large wood, and embedded substrates; the TRANSPORT axis described habitat with deep pools, undercut banks, and substrates that were not embedded; and the SOURCE axis described habitat with cold water, small and shallow pools, and abundant large wood (Table 2.2b). These axes describe a gradient of conditions expected under the river continuum concept. And specifically, habitat types in this system corresponded with Montgomery and Buffington's (1998) designation of reach-level responses to land use and environmental change. In the present study, SOURCE habitats were small, cold, and appeared to be a source of large woody debris recruitment. TRANSPORT habitats were deep, had abundant undercut banks, and based on the lack of embedded substrates and low abundance of large woody debris could be conceived of as areas of sediment and debris transport. RESPONSE habitats were large, warm, had substrates embedded with fine sediment and had a relatively high abundance of large wood. The large wood in

RESPONSE habitats could have been recruited from upstream or from the nearby riparian area, but the sediments covering and embedded in substrates were likely transported from upstream habitats.

My designation of trait and environmental axes does not imply a continual gradient of habitat types along the stream's longitudinal profile—rather, major shifts in trait guilds and habitat types did not occur on a longitudinal gradient. Traits and environmental characteristics were instead distributed through the watershed in a heterogeneous manner; for example, SOURCE habitats were distributed in the upper reaches of Murderers Creek and Black Canyon as expected in the river continuum, but the same habitat type decreased upstream towards the upper reaches of the mainstem South Fork (Fig. 2.7b). This pattern was better explained by the process domains concept (Montgomery 1999), where discontinuities in environmental conditions and fish assemblage structure would be expected due to the spatial variability in disturbance patterns affecting ecosystem structure and dynamics. SOURCE habitats were distributed in a heterogeneous manner, most likely because of cold and warm water inputs at tributary junctions (Fig. 2.5) and potentially due to larger-scale geomorphic factors that I did not measure. Another body of theoretical work that describes similar inconsistencies in gradual changes along the river continuum is the serial discontinuity concept (Ward and Stanford 1983; Stanford and Ward 2001)—a concept originally intended to describe the disruption of ecological processes along the lateral, vertical, and longitudinal dimensions of the river continuum due to dams and other impoundments. This idea can be extended beyond impoundments to the influence of tributaries or other points of disruption along a river's gradient (Hiram Li, pers. comm.), such as those encountered in the present study. In fact, one of the tenants of the "riverscape" perspective (Fausch et al. 2002) is that the heterogeneity of processes occurring within a river system are just as important as—and sometimes more important than—the average value of responses visible by merely studying a system at a single, large extent.

The typical approach of interpreting species distributions involves first determining which species are related to which habitat, then making inferences about causal mechanisms for those distributions based on biological knowledge of each species

(e.g., Torgersen et al. 2006). In the present study, I incorporated biological knowledge of species directly into the analyses using the trait matrix (Table 2.1), an approach that allowed me to shorten the chain of inferential reasoning (Fig. 2.2). Multivariate ordinations of traits and environmental characteristics carried intuitive appeal based on their ease of interpretation, and had the added benefit of providing parameters for multiple regression analyses.

Multiple scale trait-environment relationships

Poff's (1997) initial discussion of the role of hierarchical filters determining local species occurrence included the issue of interacting linkages among habitat and traits at multiple scales, a problem that is yet to be resolved in the ecological literature. Johnson et al. (2007) recently stated, "Stream communities are structured by factors acting over multiple spatial and temporal scales. Identifying what factors are driving spatial patterns in stream communities is a central aim of ecology" (p. 939). I found that the nature of relationships among traits and environment changed with spatial scale, and that these relationships were heterogeneous throughout the watershed.

The goal of this paper is not to describe and justify in minutia the detailed relationships of traits and environment at each spatial scale and each location in the watershed, but rather to derive general principles and insights from a multiple-scale perspective. One such insight begins with the finding that explanatory power of models (R^2) tends to decrease with decreasing spatial extent of analysis. One method that fisheries scientists have used to justify using one spatial scale of analysis over another is to compare the relative ability of models at each scale to describe variation in the data, and to lend more credence to the top performing models according to this criterion (e.g., Harig and Fausch 2002). However, while searching for the appropriate scale of analysis, it will also be important to recognize that heterogeneity in ecological processes distributed throughout a watershed will lead to heterogeneity in the scaling of those

relationships—that there may be no consistent "best scale" of analysis (Fausch et al. 2002).

Case in point: although I found a general trend of decreasing explanatory power with decreasing spatial extent, it was often via analyses at smaller spatial extents where the most ecologically-interpretable findings were derived. For example, although there was a positive relationship among COLDWATER traits and SOURCE habitats at the watershed scale which explained a relatively large proportion of the variance, a reversal of this relationship was observed at the tributary scale in Black Canyon, with COLDWATER traits now negatively associated with SOURCE habitats (and positively associated with RESPONSE habitats), described by a weaker model. If managers were to embark on a watershed-scale restoration effort based on the results of the model at that scale, it would seem appropriate to modify or conserve habitats in a way that increased the proportion of SOURCE-type habitats. However, a more-refined understanding of fish-habitat associations would have been missed without looking more closely at Black Canyon, where COLDWATER traits—a guild including salmonids either listed under ESA (*O. mykiss*) or otherwise of management concern (Chinook *O. tshawytscha*)—were negatively associated with the same habitat. Black Canyon is a colder, higher gradient, and more forested tributary with a higher abundance of SOURCE habitats than others in the extent of this study, and fish with COLDWATER traits there are likely attracted to larger, deeper, and warmer habitats that provide conditions required to meet the physiological demands of a stream-dwelling ectotherm, such as reduced water velocities for conservation of energy that would otherwise be used for swimming (Trudel and Boisclair 1996), or increased temperatures that can provide conditions for optimal growth when food is plentiful (Elliot 1982).

Factors correlated with modes of species coexistence

Rather than present a lengthy discussion of the individual trait-environment relationships in each of the 13 river sections (Table 2.3b), I felt it was more informative to take a broad

view of the types of model results I encountered and describe how they were related to biotic and abiotic characteristics in the watershed. In classifying models, I drew on prevailing ideas of species coexistence (Tokeshi 1999; Sommer and Worm 2002). Tokeshi (1999) posits that whether species can coexist depends on two factors: the amount of niche overlap and how close to carrying capacity is a particular system. While I did not specifically address the issue of carrying capacity in this study, I did find a high degree of niche overlap in the Black Canyon tributary, and models relating traits with environment there were relatively strong ($0.24 \leq R^2 \leq 0.53$) compared to other parts of the watershed. Madriñán (2008) found that 68% of redband trout biomass in the drainage was concentrated in the Black Canyon tributary, which comprised only 7.4% of the total stream area. Steelhead-rainbow trout are competitively dominant over other fish species (Kelsey et al. 2002), and hence their population densities are likely to affect those of other fishes. According to Tokeshi's (1999) criteria, these clues suggest that competitive interactions have the potential to shape the structure of fish communities in the Black Canyon tributary, a question I feel is a worthwhile avenue for future research.

I discovered that the distributions of both traits and environmental ordination axes varied among model classes. I found that although both habitat and traits were significantly correlated with the mode of species coexistence, traits had a stronger effect than did environment, suggesting that the distribution of organisms was more important in determining the nature of trait-environment relationships than were the environmental conditions. This finding was counter to the predictions of the river continuum concept (Vannote et al. 1980), which anticipates that ecological process in rivers will form a gradient from headwaters to mouth. Lotrich (1973), for example, explained an increase in species diversity of fishes with increasing stream order due to a predictable increase in available habitat and subsequent decrease in environmental fluctuation. On the contrary, I found that trait distributions (Fig. 2.7a), environmental characteristics (Fig. 2.7b), and reach-scale niche relationships (Table 2.3b) were all distributed in a heterogeneous (though not random) manner throughout the watershed, and that no continual gradient existed.

These findings were also counter to predictions of the process domains concept (Montgomery 1999), which anticipates that similar ecological processes will emerge from spatially-adjacent domains of similar abiotic conditions. For instance, Grossman et al. (1998) found that variation in river flows had more impact on fish assemblage structure than did interspecific competition for space or predation. In the case of the present study, it was the distribution of organisms having particular traits that determined the nature of ecological relationships among fishes, not background environmental conditions. Like the process domains concept, Poff's (1997) conceptualization of trait filters also predicts that ecological relationships at local scales are subservient to larger-scale abiotic drivers such as geomorphology, flow regime, and temperature. While this may be true in many cases, the present results suggest that at the reach-scale, species distributions drove niche relationships while environmental conditions played a relatively smaller role.

Potential explanatory mechanisms for these contradictions include the idea that at smaller scales, biotic processes such as competition and predation may be more important that abiotic processes (Jackson et al. 2001). For instance, the timing and order of colonization of habitats can be more important than the particular environmental conditions in determining the nature of relationships among organisms (Barkai 1988; Strauss and Biedermann 2008). Additionally, Jackson et al. (2001) emphasized the idea that piscivory is more important than competition in streams and lakes, and that predation may lead to mutually exclusive distributions among fishes. I noted these types of mutually exclusive distributions in most areas of the watershed (Fig. 2.7a); one potential interpretation is that large-bodied fish of the COLDWATER guild were preying on the small bodied fish of the COOLWATER guild. In lower stretches of the mainstem South Fork, redside shiners (COOLWATER) have been found in stomachs of redband trout (COLDWATER) (Ian Tattam, pers. comm.). I consider these only possibilities at this point, and suggest the questions be pursued in future research.

Scope of inference and spatiotemporal scales

Our method of collecting spatially continuous information about fish and habitat characteristics allowed us to examine the changing nature of trait-environment relationships along the longitudinal profile of a relatively large (72 river km) stream network. Continuous sampling of large river networks has been used in other studies to discover fish-habitat relationships, primarily through the use of snorkel surveys (Torgersen et al. 2006), single-pass electrofishing (Kruse et al. 1998), and streamside visual estimates (White and Rahel 2008). These kinds of spatially continuous sampling techniques provide the additional benefit of a nested hierarchy of sample units, especially useful when factors at different scales are likely to differentially affect organism distribution, as is the case in stream ecosystems (Frissel et al. 1986; Poff 1997; Jackson et al. 2001). In the present study, I used individual pools as the sample units for reach-scale models, and used individual reaches as the sample units for the watershed-scale model in an effort to avoid over-representing sample size with non-independent samples (Hurlbert 1984) at the larger spatial scale.

Although the sample extent was relatively large in the present study, studies at even larger geographic scales that encompass multiple populations are often necessary to reveal factors affecting fish distribution (Rahel and Nibbelink 1999; Fausch et al. 2002). Especially when the community is the level of biological organization of interest, many researchers have emphasized patterns at regional or larger scales (Lawton 2000). MacArthur (1972) emphasized the need in ecology to search for repeated patterns, vs. the mere accumulation of facts. However, if community ecology is to move beyond pattern description and into process description (Noakes 1993; McGill et al. 2006), then optimizing spatial scales that are large enough to elucidate meaningful patterns yet small enough to make realistic inferences about mechanisms seems like the most fruitful path. Several recent studies and reviews have highlighted these ‘intermediate scales’ as important for inferring causes of fish-habitat associations (Harig and Fausch 2002; Fausch et al. 2002; Torgersen et al. 2006). Intermediate scales are also more practical units of study, and by using passive sampling techniques can be assessed fairly rapidly. In the present study, I was able to snorkel the 72 river kms with a small team of people in a

short time period, which was important for two reasons. First, it lent more confidence that fish distributions were not changing during the time of data collection. Second, these types of rapid techniques have the potential to provide managers with a tool for rapid assessment, important when management decisions require information that is often not available prior to a proposed activity (e.g., altering flow regimes, harvesting trees, or initiating cattle grazing).

Temporal scale is also an important consideration when making inferences about mechanisms driving species distributions, especially in streams where organisms may make seasonal migrations to complimentary habitats (Schlosser 1995) or the abundance of individuals varies dramatically by season or year (Johnson and Gage 1997). Pfister (1995) found that static regression models from a single census resulted in erroneous competition coefficients in a guild of tidepool sculpin, as compared to models from census data over multiple years and experimental manipulations. Although I recognize the importance of seasonal dynamics and annual variations in structuring fish populations, I felt that the 'snapshot in time' approach was useful for several reasons. First, as mentioned above, rapid assessment is an important tool for researchers and managers who need a quick and accurate way to document species distributions, especially in the absence of long-term data on population trends of less-commonly studied species (e.g., non-salmonids). Second, the choice of the mid-late summer sample period was based on the conviction that this time of year represents a bottleneck in physiological performance of many fishes. I chose a time period at the tail-end of the hydrograph when pool volumes were expected to be at their lowest and water temperatures at their highest (Fig. 2.4). All fish species in the present study have either coolwater or coldwater preferences (Table 2.1) and were therefore presumed to have settled into locations where they could best confront the combination of warm water conditions, competitor densities, and food availability, as has been demonstrated for late-summer distributions of salmonids in the Pacific Northwest (Stein et al. 1972; Torgersen et al. 1999).

The two conflicting quotes at the beginning of this paper best highlight the dilemma. On the one hand, inferring the causal mechanisms of patterns without long-term

studies or detailed experimentation can be tricky, as one can come to erroneous conclusions. On the other hand, as the novelist Thomas Wolfe noted, “Every moment is a window on all time,” and it follows that we should be able to glean *at least something* from observing current patterns. Shipley et al. (2006) demonstrated that in abandoned vineyards in southern France, a trait-based approach revealed important insights about plant community assembly without the use of Lotka-Volterra population dynamics, a method that becomes impractical in communities with more than a few species and in complex environments. Also, one can come to erroneous conclusions even after conducting long-term studies and detailed experiments (Roush 1995); correlative studies are a convenient first step in elucidating patterns and potential mechanisms for species distributions, especially when coupled with techniques that provide more generality such as the trait-based approach (McGill et al. 2006). Given the advantages of rapid assessment of species distributions and the ecological generality of the trait-based approach, the procedures described in this paper could be adapted by managers seeking an initial understanding of their system, or by researchers seeking to generate realistic hypotheses for future experiments.

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Tables

Table 2.1. Functional traits and ecological performances of fish species commonly encountered in snorkel surveys of the South Fork John Day River. * Trait information derived from Zaroban et al. (1999). Pollution tolerances are sensitive (S), intermediate (I), or tolerant (T). † Trait information derived from Wydoski and Whitney (2003) using categories of Goldstein and Meador (2004). Reproductive strategies are simple nester (SN), complex nester (CN), or broadcast spawner (BC). ‡ Maximum size categories from basin-wide snorkel survey, present study. Fish not included in this table but occasionally encountered in the South Fork are *Cottus rhotheus* and *C. beldingi*.

Fish species	Pollution tolerance *	Adult freshwater habitat *	Temperature preference *
Steelhead-rainbow trout *(Oncorhynchus mykiss)*	S	hider	coldwater
Chinook salmon *(Oncorhynchus tshawytscha)*	S	water column	coldwater
Redside shiner *(Richardsonius balteatus)*	I	water column	coolwater
Longnose dace *(Rhinichthys cataractae)*	I	benthic	coolwater
Speckled dace *(Rhinichthys osculus)*	I	benthic	coolwater
Mountain whitefish *(Prosopium williamsoni)*	I	benthic	coldwater
Bridgelip sucker *(Catostomus columbianus)*	T	benthic	coolwater
Largescale sucker *(Catostomus macrocheilus)*	T	benthic	coolwater
Mountain sucker *(Catostomus platyrhynchus)*	I	benthic	coolwater
Northern pikeminnow *(Ptychocheilus oregonensis)*	T	water column	coolwater

Table 2.1. Continued.

Fish species	Adult freshwater feeding group *	Reproductive strategy †	Spawning season †	Max size category (mm) ‡
Steelhead-rainbow trout *(Oncorhynchus mykiss)*	invertivore / piscivore	SN	spring	200-250
Chinook salmon *(Oncorhynchus tshawytscha)*	invertivore	SN	fall	100-150
Redside shiner *(Richardsonius balteatus)*	invertivore	BC	summer	65-100
Longnose dace *(Rhinichthys cataractae)*	invertivore	CN	summer	65-100
Speckled dace *(Rhinichthys osculus)*	invertivore	BC	summer	65-100
Mountain whitefish *(Prosopium williamsoni)*	invertivore	BC	fall	200-250
Bridgelip sucker *(Catostomus columbianus)*	herbivore	SN	spring	150-200
Largescale sucker *(Catostomus macrocheilus)*	omnivore	BC	spring	150-200
Mountain sucker *(Catostomus platyrhynchus)*	herbivore	BC	summer	150-200
Northern pikeminnow *(Ptychocheilus oregonensis)*	invertivore / piscivore	BC	summer	150-200

Table 2.2. Pearson correlations between axes from nonmetric multidimensional scaling and (a) trait attributes (N=686, Cumulative R^2=74.6%) and (b) habitat characteristics (N=662, Cumulative R^2=87.9%). In the trait analysis, attributes having Pearson correlations > 0.50 (marked with asterisk) were used in naming axes (capital letters); Pearson correlations > 0.20 were used in naming habitat axes. Cumulative and partial R^2 values are shown for each analysis and for each axis.

(a)

Trait	*Attribute*	Axis 1 (R^2=40.9%) COOLWATER	Axis 2 (R^2=33.7%) COLDWATER
Pollution tolerance	Sensitive	0.124	* 0.764
	Intermediate	* 0.708	-0.366
	Tolerant	0.431	-0.055
Temperature preference	Coolwater	* 0.733	-0.349
	Coldwater	0.151	* 0.742
Feeding mode	Herbivore	0.389	-0.043
	Invertivore	* 0.684	-0.367
	Invert/piscivore	0.446	0.293
Spawning type	Simple nester	0.131	* 0.759
	Broadcaster	* 0.731	-0.348
	Complex	0.197	0.062
Maximum size category (mm)	65-99	* 0.679	-0.373
	100-149	0.167	0.394
	150-199	0.486	-0.057
	200-250	0.136	* 0.724

Table 2.2. Continued.

(b)

Habitat	Axis 1 (R^2=37.9%) RESPONSE	Axis 2 (R^2=21.1%) TRANSPORT	Axis 3 (R^2=28.8%) SOURCE
Temperature	* 0.285	-0.045	* -0.457
Pool width	* 0.62	-0.155	* -0.553
Pool area	* 0.676	-0.166	* -0.538
Maximum depth	* 0.649	* 0.216	* -0.399
Residual depth	* 0.547	* 0.383	* -0.207
Dominant substrate	-0.168	-0.168	-0.012
Subdominant substrate	-0.18	-0.001	-0.008
Large woody debris	* 0.607	0.085	* 0.695
Undercut bank	0.199	* 0.646	0.046
Embeddedness	* 0.339	* -0.327	0.033

Table 2.3. Most parsimonious models from trait-environment AIC analyses at the (a) watershed and tributary scales and (b) reach scale. Multiple linear regressions elucidated which habitat indices (RESPONSE, TRANSPORT, or SOURCE) best predicted the value of each trait guild (COOLWATER or COLDWATER) at each scale. Sample size (N), Akaike weight of evidence (w_i), and parameter estimates for intercept and three multivariate habitat axes are reported. Significance levels ($\alpha = 0.05$) for each model are denoted as $p < 0.05$*, $p < 0.001$**, and $p < 0.0001$***.

(a)

Extent (N)	Trait axis (significance)	Adj-R^2	w_i	Parameter estimates			
				Inter-cept	Habitat Axis 1	Habitat axis 2	Habitat axis 3
Watershed	COOLWATER*	0.38	0.41	-0.03	---	---	-0.57
(22)	COLDWATER***	0.50	0.36	0.03	---	---	0.80
Murderers	COOLWATER***	0.22	0.96	-0.04	0.29	0.20	-0.18
(211)	COLDWATER*	0.04	0.45	0.12	---	-0.11	0.15
Black Canyon	COOLWATER***	0.43	0.57	0.30	0.62	---	-0.67
(124)	COLDWATER***	0.39	0.63	-1.17	0.58	---	-0.65
South Fork	COOLWATER***	0.45	0.54	-0.02	0.58	---	-0.11
(300)	COLDWATER*	0.02	0.43	0.11	-0.1	---	---

Table 2.3. Continued.

(b)

Reach (N)	Trait axis (significance)	Adj-R^2	w_i	Parameter estimates			
				Inter-cept	Habitat Axis 1	Habitat axis 2	Habitat axis 3
Murderers 1	COOLWATER	0.07	0.41	-0.05	---	0.22	---
(32)	COLDWATER	0.00	0.29	-0.42	---	0.08	---
Murderers 2	COOLWATER***	0.11	0.28	0.04	0.20	0.10	---
(116)	COLDWATER	0.02	0.41	-0.29	---	---	0.13
Murderers 3	COOLWATER***	0.30	0.61	-0.20	0.33	0.20	-0.19
(63)	COLDWATER*	0.05	0.34	0.41	---	0.19	---
Black Canyon 1	COOLWATER***	0.51	0.74	0.50	0.80	---	-0.99
(45)	COLDWATER***	0.36	0.70	1.31	0.65	---	-0.87
Black Canyon 2	COOLWATER***	0.53	0.74	0.39	0.77	---	-0.70
(47)	COLDWATER***	0.53	0.75	1.23	0.73	---	-0.67
Black Canyon 3	COOLWATER*	0.24	0.55	-0.47	---	0.42	---
(32)	COLDWATER*	0.24	0.55	0.40	---	0.41	---
South Fork 1	COOLWATER*	0.15	0.36	0.24	---	-0.42	-0.27
(38)	COLDWATER	0.07	0.43	-0.17	-0.12	---	---
South Fork 2	COOLWATER*	0.38	0.61	-0.03	0.51	---	---
(13)	COLDWATER	0.05	0.30	-0.09	-0.19	---	---
South Fork 3	COOLWATER*	0.11	0.34	0.10	0.30	---	---
(46)	COLDWATER	-0.01	0.27	-0.18	-0.08	---	---
South Fork 4	COOLWATER*	0.14	0.30	0.09	0.48	---	---
(32)	COLDWATER*	0.10	0.42	-0.25	---	0.57	---
South Fork 5	COOLWATER	0.06	0.30	-0.14	0.20	---	---
(21)	COLDWATER	0.06	0.41	-0.12	---	0.45	---
South Fork 6	COOLWATER*	0.08	0.42	0.04	0.31	---	-0.48
(73)	COLDWATER*	0.06	0.49	-0.12	-0.22	---	---
South Fork 7	COOLWATER	0.01	0.25	0.01	---	---	-0.19
(47)	COLDWATER*	0.20	0.43	0.37	-0.32	---	---

Figures

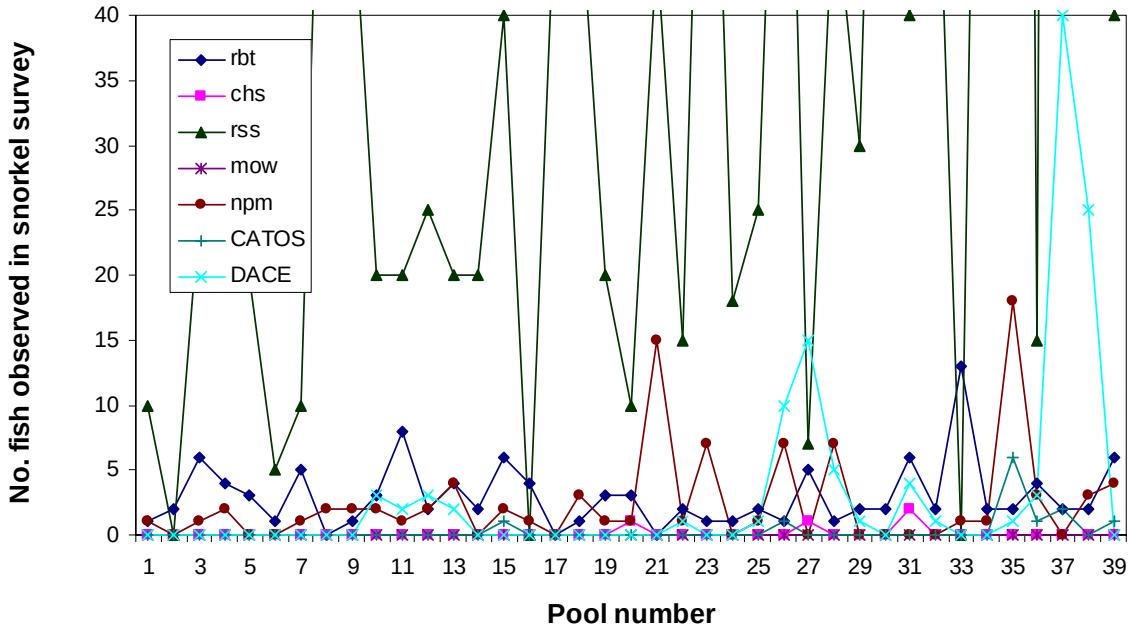

Figure 2.1. Distribution of the fish assemblage in the lowest reach Murderers Creek, from the July 2005 snorkel survey. Pool numbers are 1-39 from the mouth of the South Fork (left) towards the headwaters (right). Members of the fish assemblage here are redband trout (rbt), juvenile Chinook salmon (chs), redside shiners (rss), mountain whitefish (mow), northern pikeminnow (npm), the combination of three species of catostomids (CATOS) and two species of dace (DACE). Note that values for redside shiners (rss) exceed the y-axis scale of the graph, their highest abundance totaling 400 individuals in a single pool.

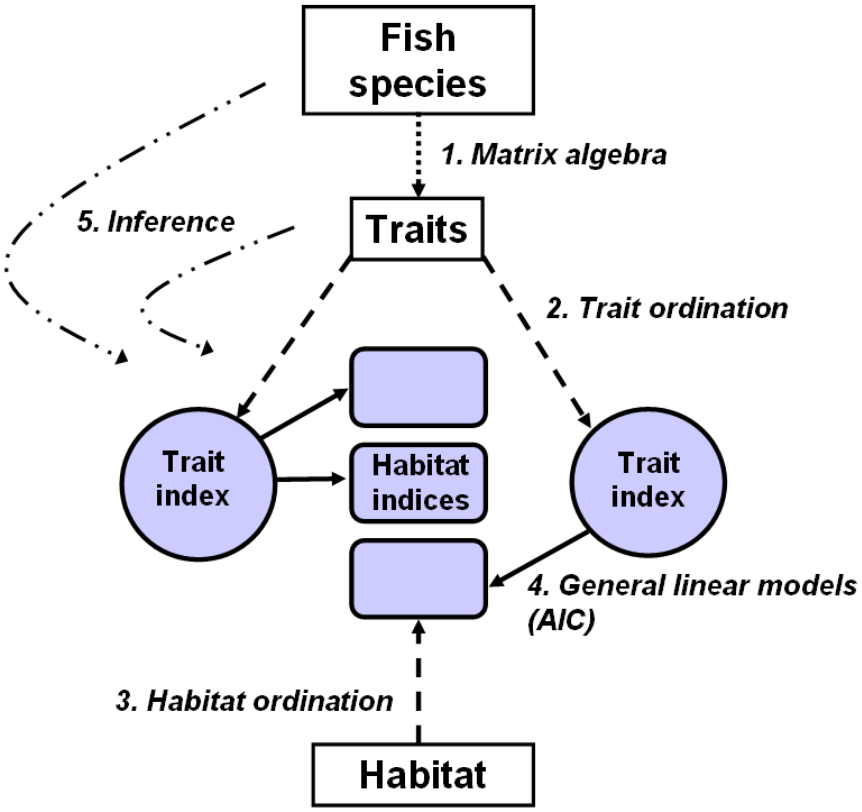

Figure 2.2. Conceptual diagram of modeling process, objectives 1 and 2. Flow of analysis proceeded as follows: (1) matrix algebra was used to convert fish species to traits, using published literature and data from the present study, information about (2) traits and (3) habitat was then condensed into indices using ordination (nonparametric multidimensional scaling, NMS), and (4) the indices were then related to one another using general linear models and Akaike's information criteria. The final step in the process (5) involves inferential reasoning about the nature of fish-habitat associations; note the chain of reasoning is longer for inferring species-habitat relationships, and shorter for inferring trait-habitat relationships. Models were created for the watershed, tributary, and reach scales.

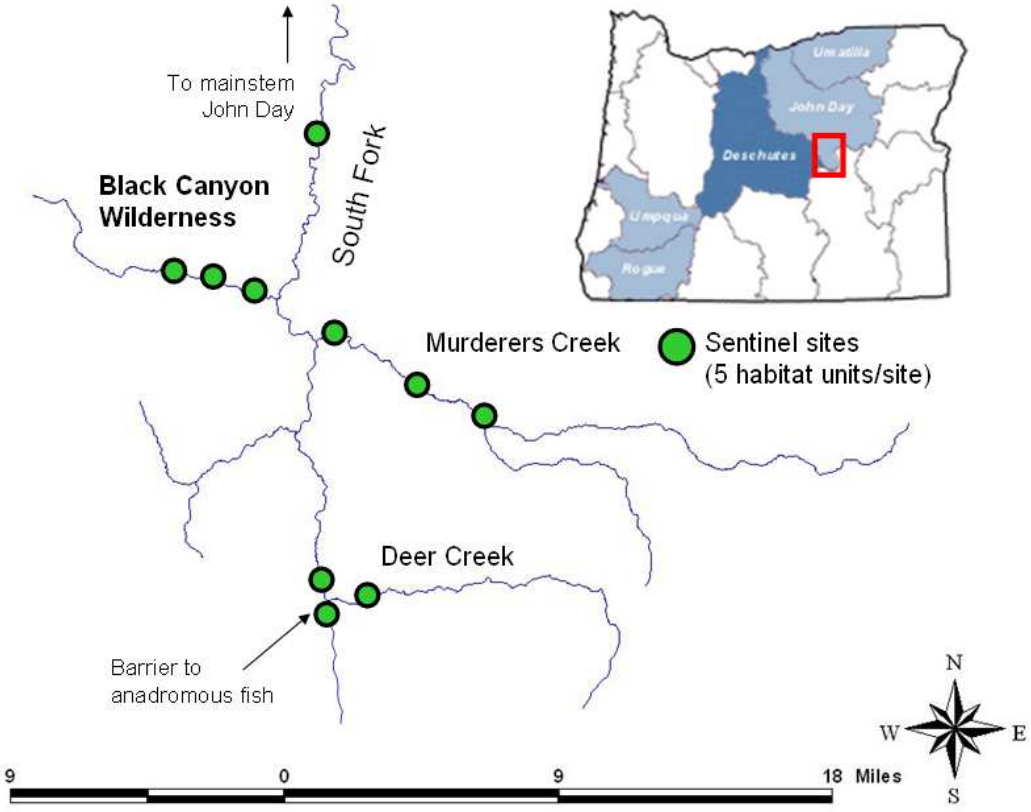

Figure 2.3. Location of anadromous fish-bearing portion of South Fork John Day River, northeastern Oregon. Shaded circles are locations of seasonal monitoring of *O. mykiss* growth and behavior in concurrent studies.

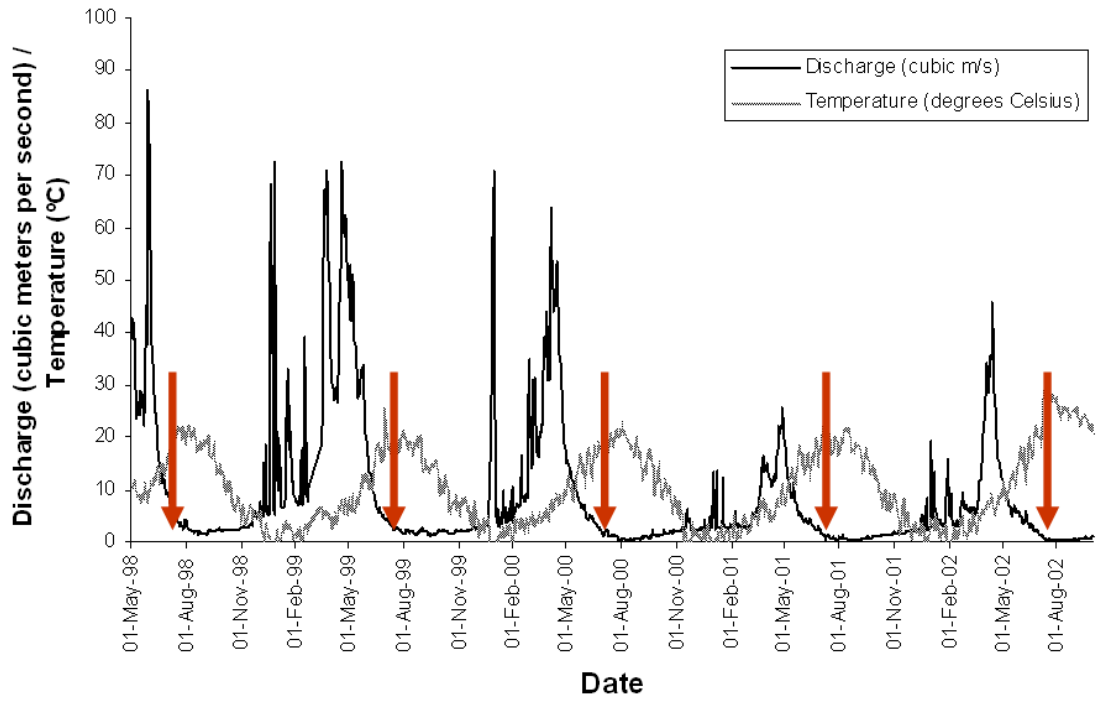

Figure 2.4. Five years (1998-2002) of average daily stream discharge and temperature at Murderers Creek mouth. Note that July-August of each year (indicated with arrows) marks the tail-end of declining stream discharge and approximate peak water temperatures. Due to agency funding cuts, continuous-time hydrographs and temperature data were not available for the period of study.

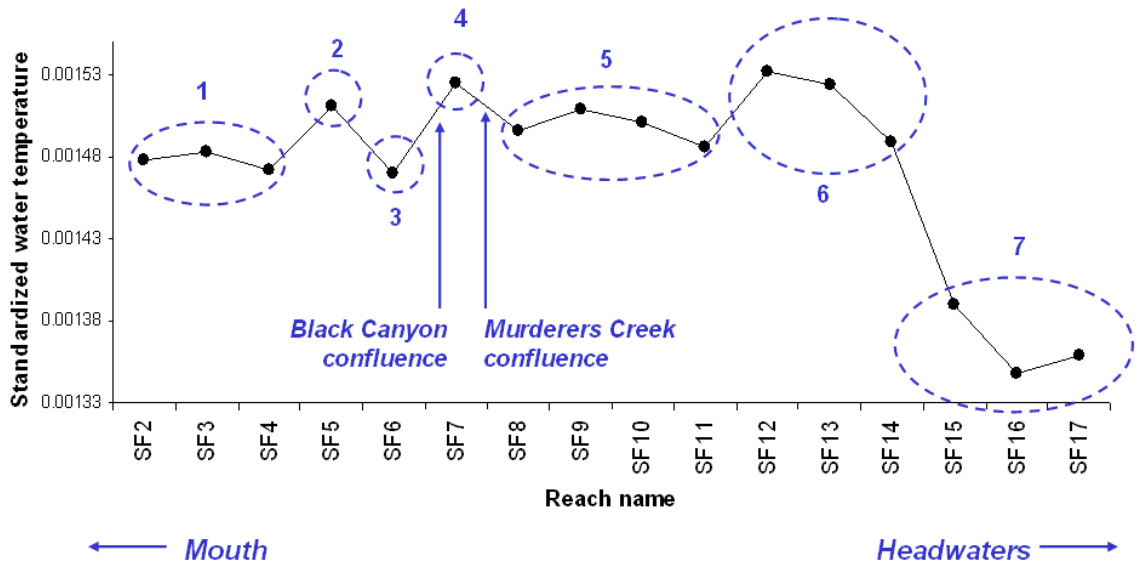

Figure 2.5. Longitudinal profile of standardized (from data matrix relativization), FLIR-derived stream temperature by reach in the mainstem South Fork John Day River, 2004. Dashed circles and associated numbers 1-7 indicate “meta-reach” designations based on adjacent river reaches with similar water temperatures.

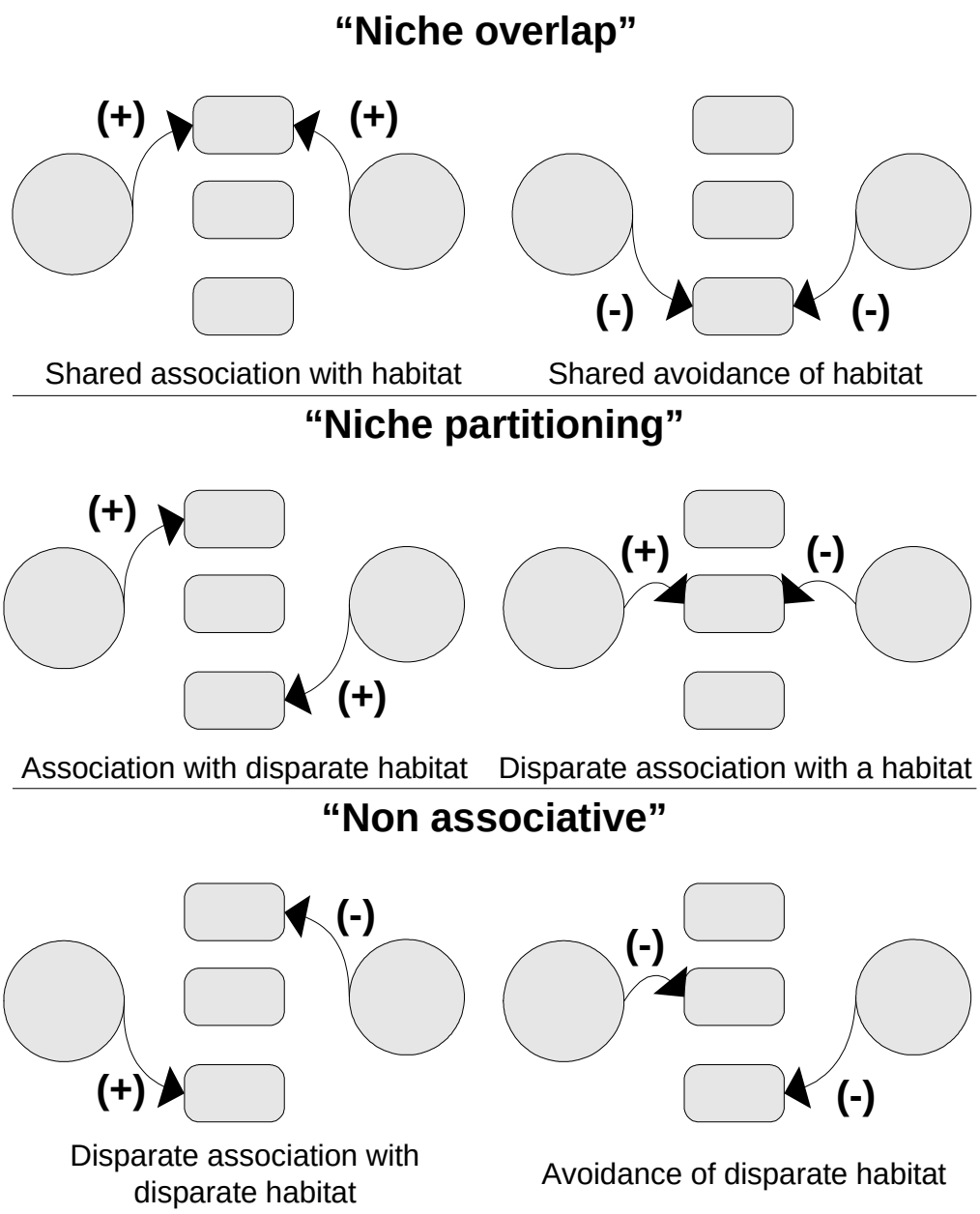

Figure 2.6. Classes of trait-environment models. Circles represent trait guilds and squares represent habitat types. See text for further description.

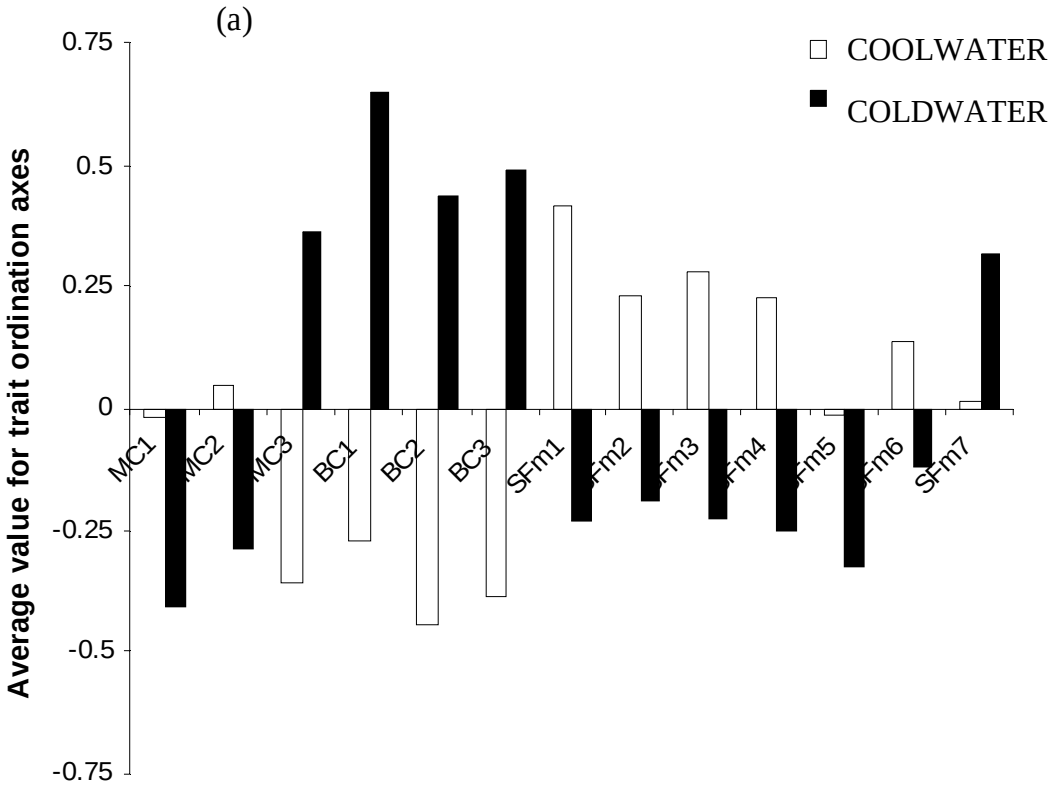

Figure 2.7. Longitudinal profiles of (a) trait ordination axes and (b) habitat ordination axes from NMS analyses.

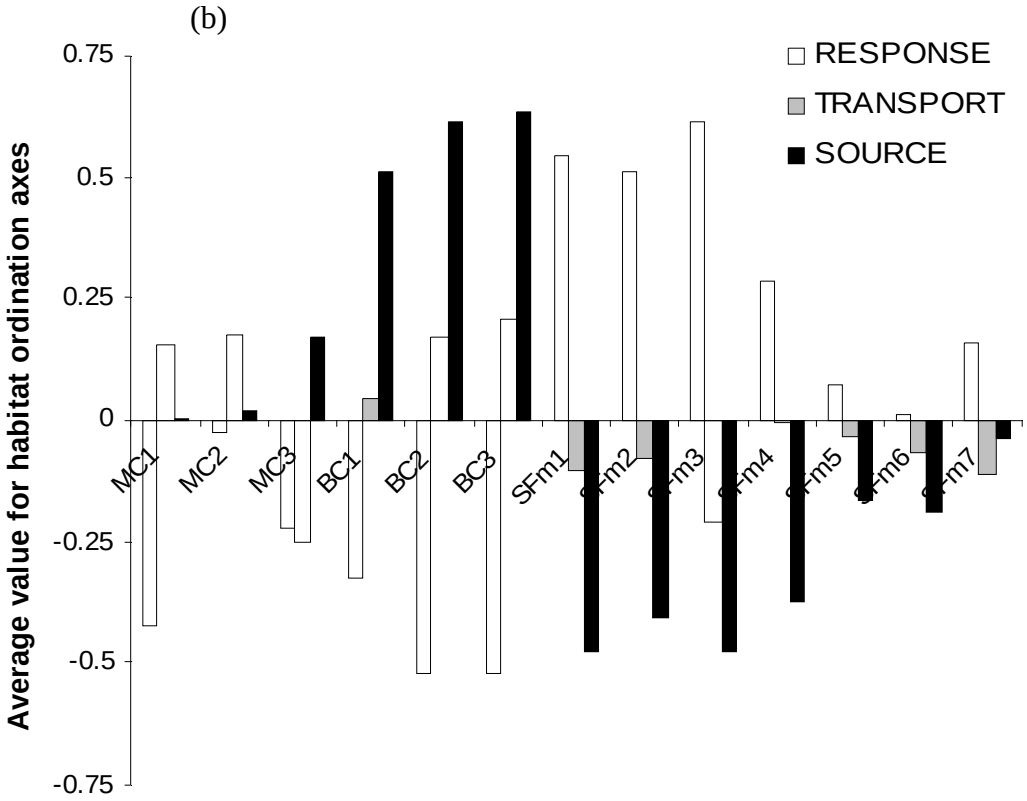

Figure 2.7. Continued.

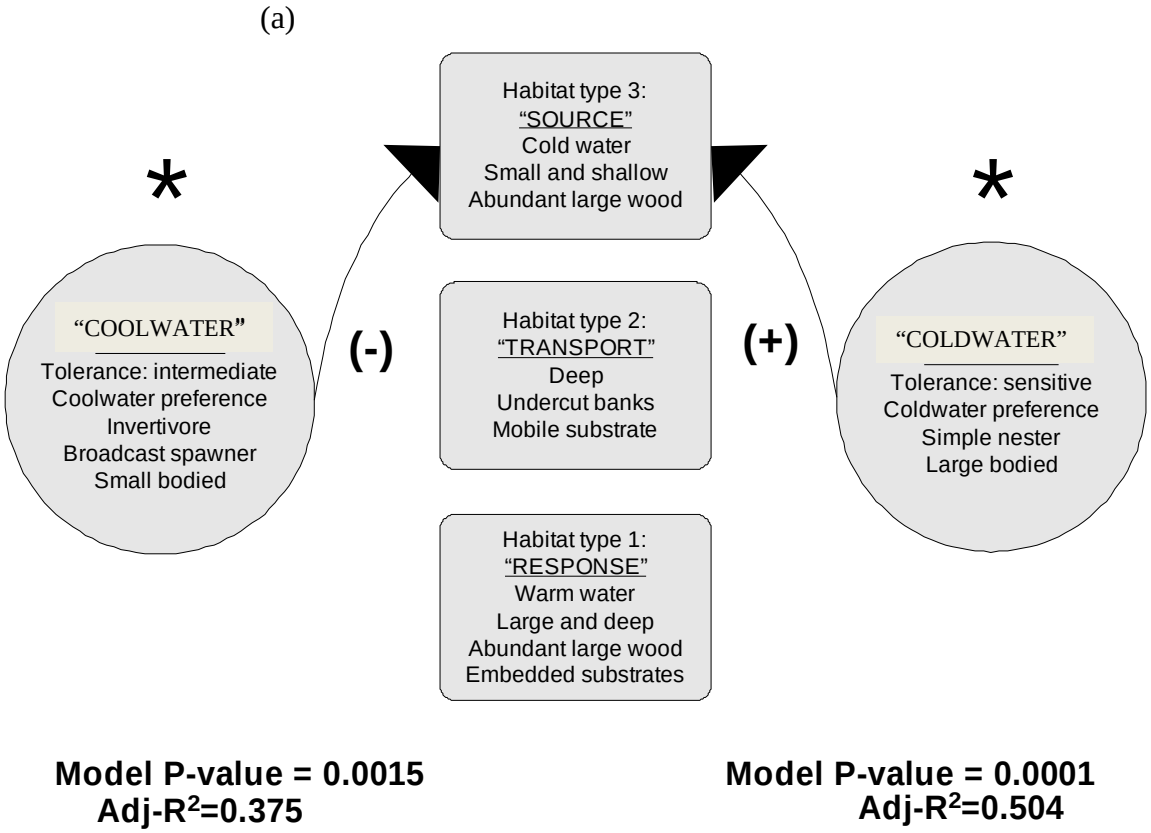

Figure 2.8. Conceptual diagrams trait-environment relationships at the (a) watershed and (b) tributary scales. Circles represent trait guilds (dependent variables derived from multivariate axes, Table 2.2a) while boxes represent habitat types (independent variables derived from multivariate axes, Table 2.2b). The sign of the relationship (+/-) between traits and environment is shown. See Table 2.3 for details and for reach-scale results.

(b)

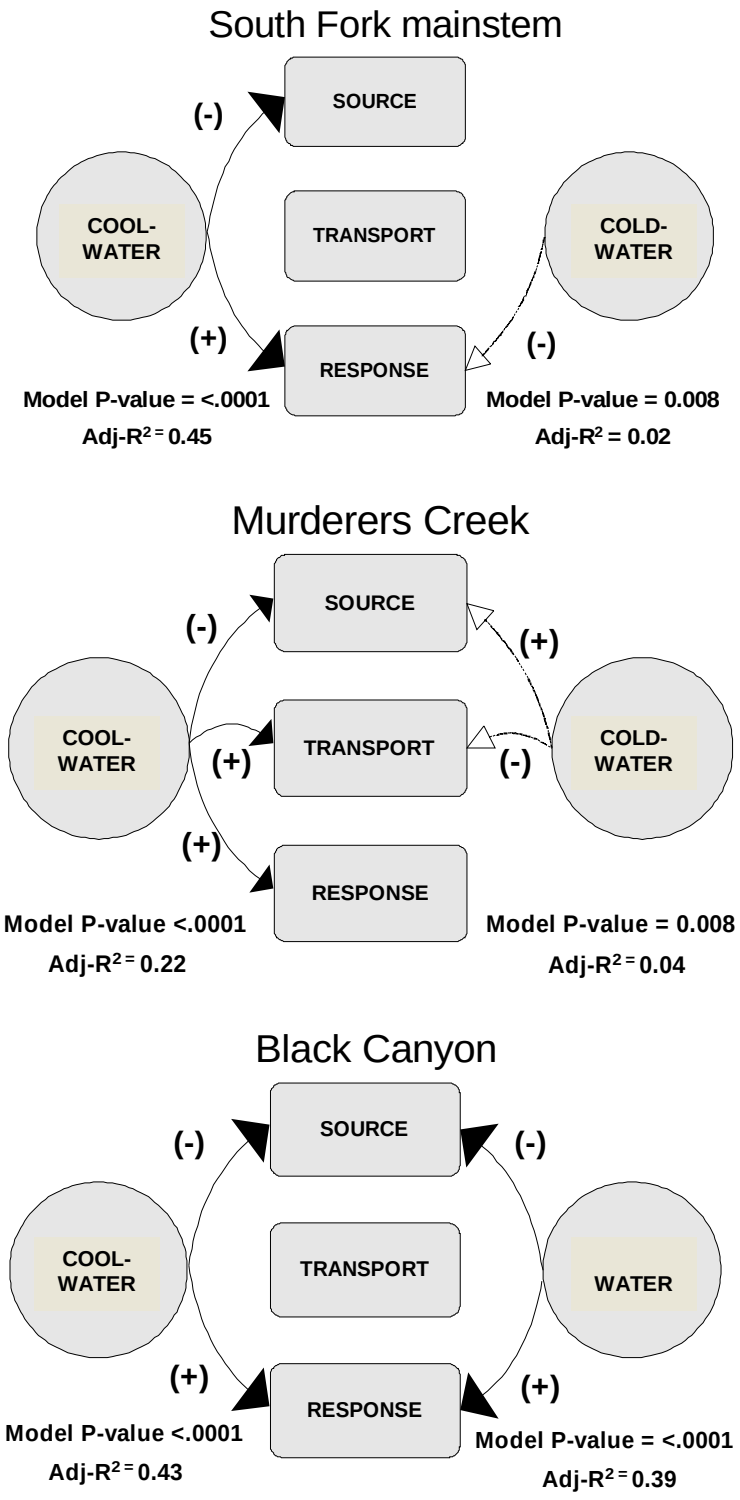

Figure 2.8. Continued.

Chapter 3

TOWARDS A ‘BEHAVIORSCAPE’ PERSPECTIVE OF A HIGH DESERT STREAM FISH: THE ROLE OF ECOLOGICAL CONTEXT IN REDBAND TROUT GROWTH, FORAGING, AND AGGRESSION

Abstract

Behavioral ecology can contribute valuable insights to aquatic conservation, but typically occurs at spatial scales too small to be relevant (e.g., microhabitats or aquaria). Landscape ecology can also offer insights, but typically occurs at very large spatial scales (e.g., watersheds to regions) and often glosses over mechanisms of statistical patterns. I describe a process for merging the disciplines of behavioral ecology and landscape ecology, and for conducting direct observations of fish foraging and aggressive behavior in natural environments in the South Fork John Day River in eastern Oregon. Using remotely-sensed geomorphic and stream temperature criteria, river sections were identified for monitoring fish distribution, fish behavior, environmental conditions, and invertebrate drift abundance. Underwater video observations suggested that two species in particular, redband trout *Oncorhynchus mykiss* and juvenile Chinook salmon *O. tshawytscha*, experienced intra- and interspecific interference competition and raised the question of whether competition for food was limiting salmonid growth. Redband trout exhibited a range of behaviors linked to foraging in the lower strata of pools, aggressive surface foraging, and territory defense; and these behaviors provided a multivariate framework describing components of the natural context of fish behavior in the system. A subsequent, manipulative field experiment revealed that food was indeed a limiting factor for fish growth and that redband trout foraging and aggression significantly increased with food supplementation in a stream with cold water and low discharge, but not in a stream with relatively warmer water and higher discharge. Fish movement among pools and out of tributaries was not significantly affected by food supplementation, but the experimental design was not ideal for testing hypotheses about local movement among habitats. These findings provide contextual knowledge about mechanisms driving observed species distributions and therefore have direct implications for research, monitoring, and restoration programs.

Introduction

> The myriad ways behavior can contribute to the conservation biology of fishes is limited only by our imagination and inventiveness.
>
> Shumway 1999, p. 195

> The trout is dark and obscure above, but behind this foil there are wondrous tints that reward the believing eye.
>
> John Burroughs, *Speckled Trout*

In the face of global declines in freshwater fish biodiversity (Lévêque et al. 2008), it is important for scientists working in the realm of theory to critically examine their contribution towards applied conservation efforts. The theoretical field of behavioral ecology has immense potential to contribute to fish conservation (Peckarsky 1981; Shumway 1999; Buchholz 2007), and behavior at the level of individual organisms can have impacts extending to the population level (Parker and Waite 1997; Anthony and Blumstein 2000), a common realm of interest for conservation biology. For example, studies of fish behavior can help predict the outcome of interactions between native and introduced species (Dubs and Corkum 1996), and this utility extends to a range of other taxa (Moore et al. 2008). Meanwhile, conservation efforts that fail to incorporate a nuanced understanding of how fish behave under natural conditions will likely prove unsuccessful (Shumway 1999). However, a large chasm has separated the theoretical field of behavioral ecology and the applied field of conservation biology for at least two decades, and researchers have yet to bridge the divide (Angeloni et al. 2008).

Perhaps one reason for our inability to integrate behavioral ecology and conservation are the vastly different scales at which the two disciplines occur. Behavioral ecology typically occurs at spatial scales too small (microhabitats or aquaria) to provide insights at the population or community level (Lima and Zollner 1996). Landscape

ecology (Forman and Godron 1986) and the “riverscape” perspective (Fausch et al. 2002) on the other hand, have made significant headway examining ecological phenomena at spatial scales relevant to conservation. While researchers employing a riverscape approach typically work larger spatial scales (watersheds to regions), their studies often gloss over mechanisms underlying statistical pattern. In many other cases, studies have occurred at spatial and/or temporal scales that are too small or too brief to gain real ecological insight into the relevant drivers of populations and community processes (Lawton 2000). Even highly intensive studies of animal communities such as the classic work by Lotrich (1973), who correlated production of the fish community with stream order, are typically only able to sample a small area relative to the total extent of an organism's habitat. Although providing much detail in terms of fish population parameters—growth, production, and community composition—Lotrich (1973) only sampled six pools and six riffles in an entire first- through third-order Kentucky stream network. Studies of fish behavior in particular have rarely occurred both in the field and at large enough spatial scales (however, see Power [1984] for a large-scale test of the ideal-free distribution). By combining the relative strengths of the two disciplines, we can begin to resolve a “behaviorscape” approach that can better contribute to conservation.

This study examines the behavioral ecology of a high desert stream fish assemblage in a wild, eastern Oregon stream network, drawing on the riverscape perspective and employing direct observations of fish in their natural environment. I organized the study into two parts: First, I employed a descriptive approach to reveal the behavioral landscape of the fish assemblage in an eastern Oregon, high desert stream network (Part I). I focused specifically on the redband trout *Oncorhynchus mykiss* in the South Fork John Day River because of their listed status under the Endangered Species Act (ESA), and due to interest by local and federal agencies in factors driving their declining population numbers. I determined the locations for behavioral observations using concurrent studies of landscape patterns of fish distribution and watershed conditions (Madriñán 2008), and redband trout migration and growth (Tattam 2006). The use of concurrent information about fish and habitat distributions and geomorphic context throughout the watershed to “embrace the ecological complexity of lotic systems

rather than try to force simplicity on them" (Fausch et al. 2002, p. 492), based on the premise that effective management strategies will be informed by studies recognizing complex, multi-scale ecological processes.

A multivariate approach to fish behavior was preferable over comparisons of single behaviors, as behavioral ecologists have gained an increasing appreciation for the interrelatedness of animal behavioral syndromes in recent years (e.g., Boinski 2005; Johnson and Sih 2007) and the approach capitalizes—rather than suffers from—the intercorrelated nature of ecological data (McCune and Grace 2002). For instance, Lind and Cresswell (2005) posit that in terms of antipredation behavior, we have reached the limits of what we can understand through the study of individual behaviors; that each behavior likely compensates for a gain or loss associated with another behavior. In fisheries and wildlife science, multivariate analyses have provided important insights regarding patterns of community structure and function (Paukert and Wittig 2002; Torgersen et al. 2006) and habitat characteristics (Capen 1980; White and Rahel 2008). However, although several multivariate approaches have their roots in studies of human behavior and sociology (Timm 1975), there has been scarce application of these approaches towards animal behavior.

While Part I of this study was strictly observational and not designed to test specific hypotheses, my observations led to several questions about the performance of salmonids in these habitats in response to resource availability. Therefore, Part II of this study addresses hypotheses about the effects of food availability on salmonid growth, behavior, and movement among local habitats. Food availability in summer is expected to affect not only growth rates of fish, but also the relative rates of foraging and aggressive (territorial) behavior. In several taxa including fish, the relative rates of behaviors associated with increased growth (i.e., foraging under predation risk and aggressive defense of feeding territories) are expected to correlate with increased rates of mortality, but it is unclear how these relative rates of behaviors change under different ecological contexts (Stamps 2007). In this portion of the study, I hypothesized that (a) food was a limiting factor for juvenile salmonid growth in late summer and (b) food supplementation would lead to reduced aggressive interactions and increased feeding

rates among salmonids, and (c) food supplementation would lead to increased rates of salmonid movement into local habitats.

Methods

Part I: The behavioral landscape of redband trout

General design

Using the classification scheme of geomorphically and thermally-distinct river reaches from concurrent studies in this basin (Madriñán 2008), I selected a series of sites with variable habitat characteristics and composition of the fish assemblage to monitor redband trout foraging and aggressive behaviors. The general idea was to observe *in situ* behavior of redband trout in sites where no experimental manipulations had occurred, under different ecological contexts (i.e., fish assemblage and physical habitat characteristics), and with minimal disturbance to the fish to ensure I was observing realistic behaviors. The range of behaviors that I observed was then examined under different ecological contexts. Specifically, multivariate axes of redband trout foraging and aggressive behavior were compared with measured habitat variables (e.g., water temperature, riparian cover, and habitat complexity) and abundances of members of the fish assemblage to assess the relative importance of each of these contextual features in determining how redband trout behave when foraging and defending territories.

Study area and fish assemblage

This research was conducted on the South Fork of the John Day River in eastern Oregon (Fig. 3.1), which sustains a population of redband trout *O. mykiss*, the focus of this study. The South Fork John Day is a stream impacted by cattle grazing, timber harvest, road building, and irrigation; but also containing within its watershed boundaries a wildlife refuge managed by the Oregon Department of Fish and Wildlife, Bureau of Land

Management holdings, the Ochoco and Malheur National Forests, the Black Canyon Wilderness Area, and several private ranches (Loy 2001). The John Day River is one of America's largest unimpounded rivers, and the South Fork maintains a Wild and Scenic designation. Other native fish species include Chinook salmon *O. tshawytscha*, mountain whitefish *Prosopium williamsoni*, northern pikeminnow *Ptychocheilus oregonensis*, longnose dace *Rhinichthys cataractae*, speckled dace *R. osculus*, chiselmouth *Acrocheilus alutaceus*, redside shiners *Richardsonius balteatus*, bridgelip suckers *Catostomus columbianus*, mountain suckers *C. platyrhynchus*, largescale suckers *C. macrocheilus*, lamprey *Lampetra* spp., and several species of sculpin *Cottus* spp.

I conducted this study at the basin and reach scales as described in a categorization of spatial hierarchy in streams (Frissel et al. 1986). In order to select sites for behavioral observations that were relevant in terms of the geomorphic and thermal environments of the fish assemblage, I used the classification system devised by Madriñán (2008), who designated reaches according to major changes in geomorphology: change from valley to canyon geomorphology, > 2% change in gradient, or major change in aspect or elevation; reaches were further partitioned if forward looking infrared (FLIR)-based water temperatures differed by > 3ºC, resulting in a total of 22 reaches.

In July and August of 2005 at the time of highest expected water temperatures and lowest expected stream flow (see Fig. 2.2), I visited 10 "clusters" of 5 contiguous pools distributed throughout the South Fork John Day watershed. Within the aforementioned reach designations, clusters were chosen using a stratified random sampling approach in reaches 1-3 of Murderer's Creek and Black Canyon Creek (Tattam 2006), and were otherwise chosen as follows: a lower mainstem South Fork due to occurrence of highest stream temperatures in the basin, the uppermost reaches of the mainstem South Fork because of their immediate adjacency above and below Izee Falls (a barrier to upstream fish migration), and the lower reach of Deer Creek because it was a site of fish habitat improvement projects intended to increase *O. mykiss* population size.

Observations of fish behavior

I used underwater video to document fish foraging and aggressive behavior in pools of the South Fork John Day and its tributaries. Pools were the habitat unit of primary interest in this study because they have been shown to be energetically favorable as compared to riffles (Rosenfeld and Boss 2001). Underwater video observations have been used to demonstrate a range of fish behaviors, including those associated with costs of swimming activity (Trudel and Boisclair 1996) and responses to predation (Healey and Reinhardt 1995). Direct observations of individuals in the wild have a long history in studies of other animal taxa such as primates (Washburn and Hamburg 1965) and birds (Altmann 1974), but few studies have taken full advantage of direct observations of fish in their natural environment (however, see the work of the late Japanese fish ecologist Shigeru Nakano, reviewed in Fausch [2000]).

In the central pool of each five-pool cluster and in one randomly selected pool of the cluster, a snorkeler first observed fish foraging and territorial behavior for five minutes to determine the area of concentrated salmonid activity (usually where the upstream riffle entered the head of the pool), and directed a submersible video camera toward the focal group of fishes. The first video observation always occurred in the downstream pool in order to avoid adversely affecting water clarity or altering fish behavior of the next study pool. Video observations were repeated for both morning and late afternoon time periods, within two hours of dawn and dusk near the expected time of peak fish foraging. The camera recorded fish behavior for 20 minutes in the absence of the experimenter, after which the camera was withdrawn, and the procedure was repeated in the upstream pool.

While viewing video tapes in the laboratory, I disregarded the first five minutes of each video sequence to account for fish recovery of their natural territories after snorkeler disturbance and for fish acclimation to the unmanned video camera. Two other observers and I watched each video sequence three times: first an initial scan, alternating between 1x-4x film speed, for a broad impression of what species were present and their general behavior; second to document the numbers of each species appearing in the video

frame by pausing the tape every 1:00 min and counting fish appearing on the video screen by species or as “unidentified” if species could not be determined; and third to document rates of foraging and territorial aggression of redband trout. Foraging events were categorized as surface feeding, water column feeding, feeding on the benthos, or capturing and rejecting potential food items. Aggressive or territorial events were classified as chasing, charging, or nipping; these events were categorized by the species initiating and receiving the aggression. After each aggressive interaction, the video tape was rewound to the beginning of the event so that the observer could determine if other foraging or aggression had occurred while the first event was being viewed. Videos were scored by three separate people to indirectly test for observer bias; however, observers did not record overlapping data from identical video sequences, allowing me to test only for extreme differences in observer records as compared to other categorical variables.

Fish assemblage-habitat variables

I defined ‘fish assemblage-habitat’ variables as fish abundance by species in the pool, determined from snorkel surveys (Thurow 1994; Mullner et al. 1998) in pools at mid-day of each sample event; locational variables such as the stream and reach where the site was located; time of day (morning or late afternoon); which observer scored behavioral events from videos; and information from habitat surveys conducted after fish observations were complete.

Habitat information included pool geometry: pool width, length, area, maximum thalweg depth, and volume. I also measured several features providing refuge and cover habitat important for multiple age classes and species of fish (Li et al. 1994; Reinhardt and Healey 1997; White and Rahel 2008): undercut banks, large woody debris, overhanging riparian vegetation, substrate size and embeddedness, and water temperature. I measured undercut banks in two ways: first by visually estimating the percent of shoreline length having banks undercut ≥ 40 cm and next by measuring the total area of undercut bank. As proxy of large woody debris input from the riparian zone,

I recorded the number of pieces of wood having stem diameter ≥ 10 cm in contact with the pool and measured the aerial coverage of large wood within 1 m of the stream's surface. (However, it should be noted that large wood in this system is relatively small compared to other systems, in which stem diameters ≥ 50 cm are typically considered large.) I estimated the aerial coverage of riparian vegetation within 1 m of the stream's surface. I visually estimated the size classes of dominant vs. subdominant substrates on a ranked scale (sand/silt/clay, small gravel, large gravel, cobble, boulder, or bedrock), ranked the degree of substrate embeddedness based on degree of difficulty freeing substrate from the stream bottom by hand (1-4 with increasing resistance), and estimated the percent of the benthic surface covered in fine sediments. Stream thalweg temperatures were assessed to 0.5 °C accuracy via hand-held thermometer readings immediately prior to video recordings. Using a hand-held GPS, I recorded the UTM (5-15 m accuracy) of each channel unit for later referencing in a geographic information system (GIS) database.

As an indicator of relative food availability by tributary reaches, I conducted similar procedures as N. Weber and others (unpublished data), who developed protocols for evaluating food resources for salmonids in the South Fork John Day River. In August and September 2005, I measured invertebrate drift abundance and density using 24-hour sets of 500-µm drift nets placed near the stream bottom at 3-8 points per reach in Black Canyon, at 3 points in Deer Creek, and 1-4 points in the lower two reaches of Murderers Creek. In the laboratory, larval aquatic invertebrates greater than 2 mm in length (this size prey composing the vast majority of salmonid diet in this system as per N. Weber, unpublished data) were counted. Estimates of invertebrate abundance were conducted at the reach scale and did not correspond with individual pools. Therefore, average invertebrate density was compared only among tributary reaches. Invertebrate drift densities were generally similar in the tributary reaches were I examined them, with the exception of one strong outlier in the uppermost reach of Black Canyon (Fig. 3.2). The average value of drift density (no. invertebrates/100m stream/second) in the uppermost reach of Black Canyon was 4.71, and in all other measured reaches ranged from 0.59 to 0.91. The large average invertebrate drift density in upper Black Canyon was the result of

a single large measurement at 11.4 invertebrates/100m/s; values of the two other measurements in that location were similar to those of other portions of the South Fork watershed: 1.04 and 1.25, indicating that for the most part, invertebrate drift densities were comparable among tributaries.

Data analysis

I used a multivariate approach to describe the repertoire of redband trout foraging and aggressive behavior. Studies of single behaviors in isolation from the variety of behaviors employed by individuals are not likely to yield useful ecological information (Lind and Cresswell 2005). Rather, I was interested in both foraging and territorial behavior exhibited by redband trout in context of the social and environmental conditions of the watershed. Therefore, I employed nonmetric multidimensional scaling (NMS) (Kruskal 1964; Mather 1976) to describe the relationship between fish foraging and aggression. NMS is an ideal ordination technique for ecological data for several reasons, including no assumption of normality or linear relationships among variables (McCune and Grace 2002).

Because a large majority (80.2 percent) of aggressive events directed towards and initiated by redband trout (both among and between other fish species) occurred in the form of charging bluffs by fish—described as a rapid approach towards another fish with no subsequent chase or contact—and because one of the three video observers did not feel comfortable delineating aggression types, I grouped all three types of aggressive events (charge, chase, nip) into one category “aggression” even though previous studies have shown that these behaviors represent a range of associated energetic costs (McNicol and Noakes 1984). However, in the present study, chases and nips represented only 13.8 and 6.0 percent of redband trout aggressive interactions, respectively. These percentages are derived from a subset of 167 aggressive interactions where I felt confident in observers' designations of aggression type.

I was interested in the proportional differences of various behaviors and therefore used Sørensen's distance measure in the NMS analysis to describe those relationships. In order to explain foraging and aggressive behaviors relative to one another, the behavior dataset was relativized by behavior totals. Foraging and aggressive events were scaled to the average number of redband trout visible in the video frame (e.g., no. surface feeds/fish/min). In NMS, a random starting configuration was used with 40 runs with the real data and 50 runs with randomized data for a Monte Carlo test of significance. Dimensionality was chosen by stepping down from a 6-dimensional solution and examining the tradeoffs between cumulative variance explained by the axes (R^2), stress, instability, and interpretability of axes. The original sample size was 40 video observations before excluding videos with no redband trout present in the video frame, no redband trout feeding or aggressive interactions during the video segment, or multivariate outliers $\geq$ 2.0 standard deviations (Sørensen's distance).

Fish assemblage-habitat variables on continuous scales were transformed to natural logarithms while variables on ranked (ordinal) scales were not; all continuous and ordinal variables were compared with NMS axes using Pearson correlations. To test for group differences in behavior related to categorical fish assemblage-habitat variables, I conducted multiple response permutation procedure (MRPP) (Mielke and Berry 2001), using ranked-transformed scaling and Sørensen's distance measure to match interpretations from the NMS analysis. Multivariate analyses (NMS and MRPP) and Pearson's correlations were performed using PC-ORD v.5.19 beta (McCune and Mefford, n.d.), software specifically designed for analysis of ecological data.

Part II: Experimental manipulations of food availability

General design and setup

Observations of fish behavior in 2005 led to several questions about the effect of food resources on redband trout growth, movement, and behavior. I first needed to establish that food was a limiting factor for salmonid growth in this system in order to demonstrate

that changing this particular feature of the fish's 'ecological context' could have consequences for fitness. Next, I was interested in whether changing the ecological context (in this case, food availability) would significantly alter the relative rates of redband trout foraging and aggression, and if so under what conditions. This is an important and unanswered question in the field of ethology, and specifically for *O. mykiss*: to what degree are patterns in foraging behavior fixed versus plastic under different ecological contexts (Wilson and Stevens 2005)? Finally, although the study was not specifically designed to test for movement among habitat units, the way in which I conducted the experiment allowed me to examine at least anecdotal evidence for this effect. My overall strategy was to supplement food resources at a number of sites in two tributaries and compare the growth, behavior, and movement of redband trout (and Chinook in the case of growth and movement) in treatment and control sites.

In July and August of 2006, I conducted experiments in two representative tributaries in the South Fork John Day watershed: Black Canyon and Deer Creek (Fig. 3.1). These two streams are similar in fish densities, habitat characteristics, and thermal regime; but differ in regard to fish species composition and discharge. Deer Creek contains only redband trout and potentially sculpin (*Cottus* spp.), while Black Canyon harbors redband trout, juvenile Chinook salmon, dace, and sculpin. Black Canyon has substantially higher discharge than Deer Creek, especially during late-summer base flows because Black Canyon is mainly spring-fed and remains relatively constant flow year round. Discharge in Black Canyon ranged from 2.47 to 2.96 m^3/s at the beginning and end of the experiment; while discharge in Deer Creek ranged from 1.35 to 0.61 m^3/s at the beginning and end of the experiment, respectively. Water temperatures were slightly warmer in Black Canyon than in Deer Creek during the experiments, with maximum and minimum stream temperatures of 20.0 and 10.4°C in Black Canyon and 19.3 and 9.9°C in Deer Creek. For both streams the seven-day maximum average water temperature centered on August 6, and was 19.1°C in Black Canyon and 17.0°C in Deer Creek. Invertebrate densities were similar among all sites and time periods, with a slight trend of increasing drift density in both streams towards the end of the experiment (Fig. 3.3). Drift densities expressed as milligrams dry weight of invertebrates per cubic meter of stream

water were approximately 15 mg/m^3 at the beginning of the experiment and ranged from approximately 25-30 mg/m^3 at the end of the experiment.

In each of the two streams, eight experimental sites were chosen to represent either "full monitoring" sites, where I measured fish growth, behavior, and movement as a response to food supplementation; or "behavior monitoring" sites where I measured only fish behavior (Fig. 3.4). Full monitoring sites were clusters of three adjacent pools, while behavior monitoring sites were individual pools. In each stream, two of the four full monitoring sites were randomly selected as treatments (sites of food supplementation) while the two remaining sites were designated as controls (no food supplementation). Each experimental site was located at least 50 m (stream distance) from other sites to avoid confounding effects of nearby treatments. Prior to the beginning of the experiment, I installed stationary passive integrated transponder (PIT) antennas (powered by solar panels) below the lowest site in each stream for monitoring downstream emigration of fish PIT-tagged in this experiment and potential upstream immigration of fish PIT-tagged in concurrent studies for the duration of the experiment. Next, I temporarily installed block nets above and below each full monitoring and behavior monitoring site to prevent local movements of fish during the time of sampling; and in the case of full monitoring sites, block nets were installed between each pool. I employed electrofishing and snorkel-seining (Tattam 2006) to assess fish distribution. All salmonids captured via electrofishing and snorkel-seining were PIT-tagged, measured for fork length, weighed, and promptly returned to the location where they were caught. After these procedures, all block nets were removed so that fish were free to migrate during the course of the experiment. After the experiments, block nets were re-installed and fish sampling was repeated to assess changes in fish growth and movement. At the end of the experiments, I compared the initial and final numbers and biomass of salmonids in each treatment and control site.

Food supplementation

In treatment sites, I installed automatic feeders (spring-operated conveyor belts) in the riffle immediately upstream of the pool in behavior monitoring sites, and upstream of the central pool in full monitoring sites. Freeze-dried krill *Euphasia pacifica* served as a surrogate for natural invertebrate drift. Because prior observations of foraging revealed that salmonids were feeding primarily in the water column, I soaked the krill with stream water 20 minutes prior to each feeding event so that food was neutrally-buoyant and drifted in the water column rather than floating on the stream's surface. Krill were delivered in amounts equal to five percent of initial fish biomass per day. Daily rations of food of this magnitude have been used in previous feeding studies in natural streams (Mason 1976; Boss and Richardson 2002; Boughton et al. 2007) and account for rations for optimal fish growth. The timing of food delivery was divided between two daily sessions: 2 hrs centered at dawn and 2 hrs centered at dusk, occurring on a daily basis for each treatment site until termination of the experiment. Control sites were visited at the same frequency as treatment sites to account for fish behavioral response to human presence. Feeding occurred for a period of approximately two and a half weeks, beginning shortly after the initial mark-recapture runs and ending just prior to the final recapture runs in both streams (July 28 – August 16 in Deer Creek and July 31 – August 18 in Black Canyon).

Evaluation of fish growth, behavior, and movement

I monitored fish growth rates as a response to food supplementation via comparing fish biomass of individually PIT-tagged fish in treatment and control sites. At the beginning and end of the experiment, I measured fork length to the nearest 1 mm and estimated biomass with a field balance to the nearest 0.1 g. Instantaneous growth rates (Ricker 1979) were compared between treatment and control sites and between streams, and were calculated as:

$100*([\ln(W_{t2})-\ln(W_{t1})]/\text{day})$,

where W_{t1} and W_{t2} were the weights (g) of fish marked and recaptured in the central pool of full monitoring sites at the beginning and end of the experiment, respectively.

Steelhead trout foraging and aggressive behavior in the field experiment was documented in a similar manner as previously described in this paper; with the exception that in this experiment, video cameras were deployed the evening prior to observations and were remotely-operated from the stream bank in an attempt to further minimize disruption of fish behavior. For the duration of the experiment, two underwater video cameras were utilized to capture feeding and aggression behavior in the center pool at all sites. Visitations with video cameras were scheduled so that every site was filmed an equal number of times, but the order in which sites were filmed was randomized, with each site filmed once every four days on average. Video recordings in the focal feeding area occurred in 20 min segments centered within the 2 hr dawn and dusk feeding periods. Multivariate behavioral scores from films in this experiment were compared with the previous NMS behavioral analysis, and among treatments and streams (see Data analysis). Only after the final experimental feedings and video observations of fish behavior were complete did I re-install block nets, just prior to re-sampling of fish distributions.

I evaluated the degree of fish movement from the start to end of the experiment among individual pools and between treatment and control sites. Permanent block nets typically employed in experiments in natural streams can produce artificial responses in fish growth and drift densities (Zimmerman and Vondracek 2006); therefore, I removed block nets immediately after the initial mark-recapture event and fish were allowed to freely migrate among sites during the course of the experiment. Individually marked (PIT-tagged) fish and snorkel estimates allowed comparisons of fish densities among pools from the start to end of the experiment. To monitor potential longer-distance migrations of fish out of both experimental streams, stationary PIT antennae at the downstream end of each stream record fish migrating towards the mainstem South Fork or lower reaches of the respective tributary.

Data analysis

I evaluated the effect of food supplementation on instantaneous growth rates using analysis of variance (ANOVA) and a randomized block design (Zar 1984) with two treatments (feeding and no feeding) and two fixed effect blocks (Black Canyon and Deer Creek), as responses were expected to vary with the different habitat characteristics and fish species compositions of the two streams. A two-sample t-test with equal variances (Steel et al. 1997) was used to determine if growth rates differed by species.

The behavioral response of redband trout to food supplementation was examined by fitting multivariate scores of the 35 new videos to the existing NMS ordination (Part I) and testing for multivariate differences due to treatment, stream, and type of experimental site (full monitoring or behavior monitoring) using MRPP (Sørensen distance). New NMS scores were derived using a prediction algorithm (McCune and Grace 2002), holding the original ordination stable and finding the lowest-stress positions for new points along the three original axes, simultaneously. If new scores fit the original ordination poorly (i.e., extended beyond original axes scores ≥ 5 percent), I removed those points from the analysis to avoid extrapolation beyond the original model.

Fish movement among experimental pools in response to feeding treatment was examined via a two-way contingency table and frequency analysis, using Fisher's Exact Test due to the small number of recaptured fish (i.e., less than 10 times the number of cells in the contingency table, as per Legendre and Legendre [1998]). We tested the null hypothesis that fish in treatment versus control sites were making similar movements among experimental pools; the three potential movement response categories were (1) fish were recaptured at the end of the experiment in the pool of their original capture, (2) fish moved into the center pool of a three-pool sequence from an upstream or downstream pool, or (3) fish moved out of the center pool of a three-pool sequence from an upstream or downstream pool. I performed the same statistical procedure, with the exception of using Pearson's Chi-square Statistic due to the larger sample size, to test

whether PIT-tagged fish appeared to be migrating out of the experimental streams as a response to feeding treatment, using two categories of response: (1) detected or (2) not detected at the downstream PIT antennae.

The ANOVA, t-test, and frequency analyses (Fisher's Exact and Pearson's Chi-square tests) were performed using the SAS software package (SAS, 2004), while multivariate analyses of fish behavior (NMS and MRPP) were performed in PC-ORD (McCune and Mefford, n.d.).

Results

Part I: The behavioral landscape of redband trout

Foraging and aggressive behaviors

As mentioned in the Methods, the territorial behaviors of charging, chasing, and nipping composed 80.2, 13.8, and 6.0 percent, respectively, of redband trout aggression in a representative subset of 167 redband trout encounters in the non-manipulated sites in 2005. Most redband trout aggression was intraspecific. Of the 174 total recorded aggressive events for redband trout, 83.3 percent of events were intraspecific while the remaining 16.7 percent were interspecific. In interspecific aggressive events, redband trout initiated interactions in over half (58.6 percent) of the events and were the recipients of aggression in 41.4 percent of the events. Most interspecific aggression by redband trout was directed towards juvenile Chinook salmon (41.2 percent), followed by redside shiners (35.3 percent), unidentified species (17.6 percent), and dace (5.9 percent). Most aggression towards redband trout was initiated by catostomids (41.7 percent), followed by unidentified species (33.3 percent), redside shiners (16.7 percent), and northern pikeminnow (8.3 percent). The aggression that I observed that was initiated by catostomids towards redband trout differed slightly from aggression by other species in that catostomids did not seem to maintain or attempt to establish constant feeding territories but rather, catostomids appeared to freely range along the stream bottom while

scraping algae, and if redband trout became too close, the catostomids charged and even nipped at redband trout, who subsequently avoided the attacker. Redband trout were not observed initiating any aggressive interactions towards northern pikeminnow (although the reverse was true), and juvenile Chinook salmon were not observed initiating any aggressive interactions towards redband trout (although again, the reverse was true).

The ordination of fish behavior revealed three multivariate axes (Table 3.1a) that were highly significant ($p = 0.004$) and which explained a large portion of the variance (cumulative $R^2 = 0.84$). The final sample size in the NMS analysis was 25 videos, after excluding 14 videos where redband trout were rare or absent in the video frame (thus yielding zero foraging or aggressive interactions) and one strong multivariate outlier with standard deviation = 2.4 (Sørensen distance). Stress for the final solution was low (10.5), while final instability was relatively high (0.08) after 500 iterations towards a solution. Each axis explained roughly the same proportion of variance in the behavioral dataset ($R^2 = 0.31$, 0.23, and 0.30 for axes 1-3, respectively). I considered correlations with the NMS axes with Pearson's $r \geq 0.20$ as ecologically significant, and thus used only those variables in my final interpretation of those axes.

The three behavioral axes (Table 3.1a) appeared to conform to current paradigms of animal foraging and aggressive behavior in terms of tradeoffs between growth and mortality risk, with behaviors linked to higher growth rates (e.g., increased foraging rate or aggression toward competitors) often negatively correlated with survival (e.g., via attraction of aerial predators or injuries from fighting, respectively) (Stamps 2007). Axis 1 was termed “low strata foraging,” as this behavior was described by foraging in the water column and benthic zone—but not on the surface—and infrequent initiation of interspecific aggression, coupled with only moderately frequent intraspecific aggression. Axis 2 was termed “aggressive surface foraging,” as this behavior was described by foraging on the surface (where, incidentally, fish are more likely to attract aerial predators) and frequent intra- and interspecific aggression. Axis 3 was termed “territory maintenance,” as this behavior was described by infrequent feeding in all strata, and by infrequent initiation of interspecific aggression coupled with only moderately frequent

intraspecific aggression. Both axes 1 and 2 (low strata and aggressive surface foraging) consisted of rejecting food items, while axis 3 (territory maintenance) was not.

Relationships with fish assemblage-habitat variables

Redband trout behavioral axes were correlated with ordinal, fish assemblage-habitat variables (Table 3.1b). Again, I considered correlations with Pearson's $r \geq 0.20$ as ecologically significant. Axis 1 (low strata foraging) was correlated with the abundance of the fish assemblage as follows: positively with speckled dace and northern pikeminnow, and negatively with conspecifics (redband trout) and juvenile Chinook salmon. Low strata foraging was also positively correlated with dominant substrate size, riparian overhang, and pool size (length, width, area, and volume); and negatively correlated with percent fines and percent and of undercut banks. Axis 2 (aggressive surface foraging) was positively correlated with abundance of only one member of the fish assemblage—speckled dace—and positively correlated with habitat variables percent and area of undercut banks. Axis 3 (territory maintenance) was negatively correlated with the abundance of redside shiner, speckled dace, and juvenile Chinook salmon. Territory maintenance was correlated with habitat variables as follows: positively with subdominant substrate size, degree of embeddedness, and negatively correlated with pool size (maximum depth and volume) and water temperature.

Tests of group differences among categorical variables revealed that redband trout behavior differed by both stream reach and observer ($p < 0.001$), but not by tributary or time of day ($p > 0.05$). Videos from Murderers Creek reach 2 and South Fork above Izee Falls were not included in the analysis because only one video was available from each reach, while MRPP requires more than one data point in each category in order to test for group differences. Differences in fish behavior by tributary as measured by effect size were large ($A = 0.57$) while differences in fish behavior recorded by individual recorders were relatively small ($A = 0.19$). The large differences in fish behavior by stream reach were primarily associated with their position along NMS axis 1 (low strata foraging) and

axis 3 (territorial maintenance) (Fig. 3.5). Differences in fish behavior in Deer Creek were especially pronounced (Sørensen distance = 0.41) and corresponded with high values of both low strata foraging and territory maintenance. Pronounced differences in fish behavior were also noted in the upper mainstem South Fork below Izee Falls (Sørensen distance = 0.34) and corresponded with relatively lower values of territory defense. Differences among other reaches were comparatively minor as indicated by their Sørensen distance values: upper Black Canyon (0.16), lower Black Canyon (0.14), middle Black Canyon (0.14), lower South Fork (0.054), and upper Murderers Creek (0.091).

Part II: Experimental manipulations of food availability

Fish growth

At the end of the feeding experiment in 2006, I recaptured 44 PIT-tagged fish in the central pools of all sites with full monitoring (growth plus behavior monitoring), out of the 493 total marked fish in all pools in both time periods. ANOVA revealed that food supplementation had a significant positive effect on fish growth in both streams ($F_{1,10}$ = 34.32, MSE = 0.05, p = 0.0002). Instantaneous growth rates (± standard error) of fish recaptured in treatment sites were 0.96 (± 0.11) versus 0.11 (± 0.07) in controls sites (standard errors for means were different because of an imbalance in the experimental data, with unequal sample sizes in treatment and control sites). ANOVA revealed no evidence for an interaction between stream and treatment (p = 0.32), indicating that recaptured fish were not growing differently between Black Canyon and Deer Creek in response to food supplementation.

Additionally, I conducted a post-hoc analysis to discover whether redband trout and juvenile Chinook salmon grew at different rates in response to food supplementation. Because the previous ANOVA revealed no difference in growth rates among streams, I consolidated data from treatment sites in both streams (n = 13 and 8 recaptured redband trout and Chinook, respectively) and found no significant difference between the two

species (t = 1.52, p = 0.15). However, this finding of no statistical difference could likely be explained by the small number of fish recaptured in treatment sites.

Fish behavior

Of the 35 new video scores, only four matched my designation of 'poor fit' by exceeding the 5 percent extrapolation range, and therefore a majority of the new scores (n = 31) could be compared with the original NMS ordination. MRPP revealed that although behavior was not statistically different between treatment and control sites at the $\alpha = 0.05$ level in both streams combined, a trend was present (A = 0.03, p = 0.06). Because redband trout behavior was significantly different between the two streams (A = 0.03; p = 0.04), I conducted additional MRPP analyses in each stream independently. In Black Canyon, there were no significant behavioral differences due to treatment (A = 0.02, p = 0.18) while in Deer Creek, behavior was significantly different between treatments (A = 0.08, p = 0.03), a pattern that was most notable in the first two NMS axes: redband trout in sites with food supplementation tended to exhibit more low strata and aggressive surface foraging than redband trout in control sites (Fig. 3.6).

Fish movement

Of the 63 fish that were marked at the beginning and recaptured at the end of the experiment in all experiment pools (including and in addition to the aforementioned 44 recaptured fish from central pools in fully monitored sites only), 50 were redband trout and 13 were juvenile Chinook salmon. In only one case did I record movement of juvenile Chinook salmon—one Chinook salmon in a treatment site moved from a downstream pool into a center pool where food was being delivered. Therefore, I analyzed the effects of food supplementation on the movement patterns of redband trout only. In only one case did an individual redband trout move from one cluster of pools to another—from a treatment site into a control site—so I excluded that individual fish from

the analysis, resulting in a sample size of n = 49 redband trout. Fisher's Exact Test revealed that food supplementation had no significant effect on redband trout movements among experimental pools ($p = 0.84$). In general, there were few movements observed among redband trout during the course of the experiment. Of the total 49 fish in the analysis, only nine movements were noted: four of the 29 redband trout in treatment sites moved towards the center pool while one redband trout moved away from the center pool; as compared to four of 21 redband trout in control sites that moved towards the center pool, while none moved away from the center pool.

Of the 493 fish marked in both streams and both time periods of the experiment, only 18 appeared to migrate downstream as evidenced by their detection at PIT antennae at the lower end of experimental reaches. Both redband trout and juvenile Chinook salmon were detected at antennae, so I included both species in the analysis. Pearson's Chi-square Test revealed no significant relationship between detection at the PIT antennae and feeding treatment ($\chi^2 = 0.62$, d.f. = 1, $p = 0.43$), indicating that downstream migration was not affected by treatment.

Discussion

The behaviorscape of redband trout

If we want to understand the interrelated nature of fish behavior in context of the range of environmental and social conditions that fish encounter in the wild, then an approach that allows us to view the entire landscape of fish behavior—the "behaviorscape"—from a high vantage point is the most prudent first step. The landscape metaphor has been applied to evolutionary fitness (Wright 1932), landscape ecology (Forman and Godron 1986), riverscapes (Fausch et al. 2002), viewscapes (Bradley et al. 2005), and soundscapes (Smith 1994). Can we extend this metaphor to animal behavior? Doing so would involve employing novel techniques for monitoring behavior at numerous sites in a fish's natural environment, versus over-scrutinizing single behaviors in constricted situations such as aquaria or laboratory tanks.

In the South Fork John Day watershed, redband trout exhibited three primary types of foraging and aggressive behavior: low strata foraging, aggressive surface foraging, and territory maintenance (Table 3.1a) corresponding to the current paradigm of animal behavior in response to food abundance, competition, predation risk, and energy maximization. Fish behavioral ecologists established early on, for example, that aggression and territory maintenance of individual fish not only provide the benefit of more productive foraging locations, but are directly related to their ability to avoid predators (Symons 1974). Juvenile coho salmon *O. kisutch* have been shown to prefer pools with ample instream cover for refuge from predators, yet within those pools select foraging locations in the open where prey is perhaps more detectable (Giannico and Healey 1999). Reinhardt et al. (2001) attributed decreased growth rates of masu salmon *O. masou* fry to the presence of predaceous Japanese huchen *Huchen perryi*, via indirect effects on foraging behavior. Guppies *Poecilia reticulata* have been shown to assess relative patch quality as a function of the gain expected from food resources and the risk of predation (Abrahams and Dill 1989). And sometimes fish may allocate time and energy defending territories, an activity with no immediate reward in terms of energy return, but which secures more optimal foraging locations and potentially higher net energy returns (Grant and Godin 1997).

In the present study, redband trout engaged in low strata foraging behavior via active feeding in the water column and especially benthic zone where fish are less likely to be observed by aerial predators than at the surface, and at the same time defended territories from conspecifics while avoiding initiation of risky interactions with heterospecifics. Low strata foraging occurred in pools with lower densities of conspecifics and juvenile Chinook, perhaps due to the increased individual predation risk posed to fish aggregated at lower densities (Parish 1999). This behavior was also associated with higher densities of speckled dace and northern pikeminnow—with speckled dace potentially attracted to sites where redband trout were more actively foraging, and redband trout were in a more risk-averse manner in the presence of northern pikeminnow, a known competitor and predator (Zimmerman and Ward 1999).

Pools where low strata foraging was prevalent were larger in terms of length, width, area, and volume; but notably lacked deep water and undercut banks, likely imposing a greater predation risk for fish seeking visual isolation from predators (Utne et al. 1993). Contrary to my expectations, habitats where low strata foraging occurred had large substrates free of fine sediments and were shaded by riparian overhang—characteristics typically associated with visual isolation from both water column competitors and aerial predators (Keenleyside 1979; Rosenfeld and Boss 2001; Pusey and Arthington 2003). The most explicable correlate of low strata foraging, however, was the lack of deep water foraging areas and undercut banks (Table 3.1b), an interpretation corroborated by the strong negative association between this mode of behavior and juvenile Chinook salmon abundance which are known to prefer deeper water habitats and slower water velocities (Everest and Chapman 1972).

Redband trout engaged in aggressive surface foraging via actively feeding on the stream surface which as mentioned above, may pose increased predation risk from aerial predators. This mode of behavior was also described by abundant aggressive interactions between both conspecifics and heterospecifics, an expensive strategy due to the high energetic costs (Trudel and Boisclair 1996; Rosenfeld and Boss 2001) and predation risk (Pusey and Arthington 2003) of increased activity. Aggressive surface foraging occurred in habitats with abundant undercut banks, which in previous studies have been linked to higher abundances and presumably survival of young salmonids—attributed to increased refuge from predators (Bayley and Li 2008; White and Rahel 2008). The contrast between low strata and aggressive surface foraging strategies was most interpretable in terms of forager access to refugia in habitats where fish were more actively feeding on the stream surface. If fish are more likely to engage in risky foraging behavior in the presence of refuge, it follows that land management activities that reduce such refuge—such as intensive cattle grazing that occurs frequently in western U.S. riparian areas (May and Somes 1982; Beschta et al. 1998)—will serve to decrease foraging opportunities and perhaps lead to lower fitness of the population via reduced individual growth.

While I did not systematically document direct predation on fish during the course of this study, field observations confirmed the presence of several known predators of

fish including aforementioned northern pikeminnow, great blue heron *Ardea herodias*, common merganser *Mergus merganser*, osprey *Pandion haliaetus*, golden eagle *Aquila chrysaetos*, river otter *Lutra canadensis*, mink *Mustela vison*, black bear *Ursus americanus*, and anglers *Homo sapiens*. On numerous occasions I observed avian predators with unidentified fish in talons, and one occasion the field crew observed a garter snake *Thamnophis* sp. that had captured a young-of-the-year redband trout. Furthermore, I frequently observed what appeared to be scars on the backs of salmonids in areas where belted kingfisher *Ceryle alcyon* were common, an observation also noted by Bayley and Li (2008) in nearby streams. With redband trout under the constant watch of these predators yet still needing to conserve and replenish energy reserves for the near future and coming winter, it is not a large inferential leap to presume their behaviors are constrained and even defined by the relative tradeoffs between growth and mortality risk, as has been shown in several animal taxa (Stamps 2007) including the focal species of the present study, *O. mykiss* (Wilson and Stevens 2005)

The third behavioral strategy that I observed in redband trout was that of territory maintenance, where fish were notably passive in terms of foraging but actively defended and/or attempted to acquire territories from conspecifics (via intraspecific aggression), meanwhile strongly avoiding initiation of aggressive bouts with heterospecifics. Although I did not explicitly measure territory size, rates of aggressive interaction provided a useful proxy; it has long been established that aggressiveness in juvenile salmonids—and specifically *O. mykiss*—is positively correlated with territory size (Slaney and Northcote 1974). The territory maintenance strategy also differed from both low strata and aggressive surface foraging in that redband trout were less likely to reject food items, potentially because the overall decreased time spent foraging imposed limits on how selective fish could be in terms of nutritive quality of their prey. Territory maintenance occurred in pools with fewer redside shiners and juvenile Chinook salmon, in habitats with larger substrates tightly embedded into the stream bottom, and in small and shallow pools. However, the most notable difference between pools where redband trout engaged in territory maintenance versus the two foraging strategies was related to water temperature: territory maintenance, in part described infrequent foraging, occurred

in colder water habitats. Metabolic activity and food digestion rates of fish and other ectotherms are known to be directly related to body temperature (Elliot 1982) and so foragers selecting habitats with colder temperatures may experience less demand for energy intake. The strategy employed by redband trout in this study of decreased foraging rates in colder water habitats can therefore be potentially explained as a tradeoff between energy intake and expenditure.

Of all the categorical fish assemblage-habitat variables, the location of habitats in the watershed as indicated by stream reach had the largest influence on redband trout behavior (Fig. 3.5). The reach scale was also the most important unit of observation in a concurrent study of *O. mykiss* growth, survival, and emigration (Tattam 2006) and a concurrent study of *O. mykiss* habitat relationships (Madriñán 2008). Most notably, fish in the lower reaches of Deer Creek exhibited strong territory maintenance and low strata foraging behavioral strategies, which may represent the unique history of this tributary—Deer Creek harbored no anadromous populations of *O. mykiss* prior to modification by land managers, due to a natural, steep-gradient barrier to migration near the mouth of the tributary. In recent decades, habitat improvements targeted towards restoring anadromous *O. mykiss* populations have included removing the barrier with dynamite and facilitating deeper-water habitat via the creation of plunge pools created by artificial log structures (K-dams). While the intent of these management activities may have been to increase the size of anadromous *O. mykiss* populations by linking to source populations in the mainstem South Fork and increasing the area or volume of habitats in the tributary, other habitat characteristics of the tributary are likely to hinder management expectations. Namely, field observations indicated that the benthic zone of Deer Creek was highly armored with hard clay soils, and there were subsequently fewer interstitial spaces that salmonids are known to use as behavioral refuge from predators (Valdimarsson and Metcalfe 1998). In the present study, this observation was corroborated by the correlation between substrate embeddedness and the territory maintenance behavioral strategy (Pearson's r = 0.54) frequently employed by redband trout in Deer Creek (Fig. 3.5).

Behavioral strategies in Deer Creek were in marked contrast to those in the upper mainstem South Fork, a stream reach very near the Deer Creek reach (Fig. 3.1) yet

unique in terms of habitat characteristics and fish species composition. The upper mainstem South Fork sites are immediately below a barrier to anadromous fish migration, have a more diverse fish community, and unlike Deer Creek have historically sustained wild populations of anadromous *O. mykiss*. In these locations, redband trout exhibited far less territory maintenance than in Deer Creek (Fig. 3.5), potentially allowing more time and energy for food intake. And again, just as territory maintenance was correlated with degree of embeddedness, the relative scarcity of this behavioral strategy was associated with substrates that were not embedded, and therefore contained interstitial spaces that juvenile salmonids are known use as refuge from predators (Valdimarsson and Metcalfe 1998). So again, behavioral strategies of redband trout in this system seem to shift more towards foraging when opportunities for refuge exist.

While time of day and tributary were not significantly correlated with behavior, redband trout behavioral strategies differed among observers of the video records. Because this was only an indirect test of observer bias, I could not determine whether behavioral strategies differed according to the way in which observers recorded data, or whether behavioral strategies of redband trout were in fact different among the videos assigned to each observer. However, although observer was a statistically significant variable ($p < 0.001$), the effect size was relatively small ($A = 0.19$) and was overpowered by the strong effect size and significance of stream reach ($A = 0.57$, $p = 8.0$ e-7). Nevertheless, future research addressing differences among how observers record behavior, more intensive training of observers, or studies that employ a single observer to record behavior from all videos could perhaps provide more methodological consistency.

My designation of all aggressive behaviors (charge, chase, and nip) as a single category has obvious implications for interpreting these results. These behavioral nuances likely represent a spectrum of activities that will be employed differently among various life history stages or even species of fish, or in context of the particular demands from the environment—with each behavior having its own associated cost, risk, and potential gain. For example, McNicol and Noakes (1984) discovered that juvenile brook charr *Salvelinus fontinalis* balanced the high energetic cost of defending territories by switching to tactics requiring less energy, such as lateral displays. Investigating interactions among coho

salmon *O. kisutch* and steelhead *O. mykiss*, Young (2003) demonstrated that larger individual fish and coho were more likely to chase potential competitors, while smaller individuals and steelhead were more likely to passively display. By combining all types of aggression into a single category in the present study, I have potentially overlooked some interesting facets of redband trout behavior. Because all observers of the video tapes were not comfortable delineating types of aggression, my data do not allow me to examine these questions at present. However, in the subset of records where observers were confident in their designation of aggression types, the rate of energetically-costly behaviors (chasing and nipping) was low (combined rate of 19.8 percent) compared to that of the most common form of aggression, charging (80.2 percent), and so the decision to aggregate categories was not likely to drastically effect my interpretations. And finally, one advantage of this method is that the videos provide a permanent record, and the tapes can be re-assessed in the future as these and other interesting research questions arise.

Because the above descriptions of redband trout foraging and aggressive behavior was based on observational studies—or "mensurative experiments" as termed by Altmann (1974)—I considered these findings an exercise in pattern description, an important part of the scientific process often overlooked in studies of natural communities (Lawton 2000). My intention was to provide the environmental and social context of components of redband trout behavior, so that subsequent experimental manipulations were not conducted in a naïve manner that ignored the prevalent behaviors of the organism under study. These findings led to several questions about the nature of resource availability in the South Fork John Day watershed, especially since for the most part food availability was relatively uniform throughout the watershed (Fig. 3.2) and therefore was not a changing feature of the behaviorscape. Specifically, I noted that behavioral strategies involving different rates of foraging and aggression were correlated with several environmental conditions but under relatively similar invertebrate drift densities, but at the same time prevailing foraging theory predicts that these strategies will also be strongly influenced by resource availability (Stephens and Krebs 1986). The following section is a discussion of the effects of manipulations of food supplementation on redband trout foraging behavior in natural streams.

The effects of supplementing food resources

I found that in the late summer period, food was indeed a limiting resource of salmonid growth the South Fork tributaries. On average, instantaneous growth rates of redband trout and juvenile Chinook salmon in sites of food supplementation were 0.96, versus the background rate of 0.11, nearly an order of magnitude difference. Low background growth rates of *O. mykiss* in summer were also reported in nearby Murderers Creek: fish grew at rates approximately 0.1 to 0.2 percent of body length per day (relative growth rate) as opposed to springtime growth rates of nearly 0.5 percent body length per day (Tattam 2006). As in the present study, Boughton et al. (2007) found that supplementing food resources for *O. mykiss* in a natural stream in California drastically increased fish growth; though in their case the change spanned a larger range of instantaneous growth rates—from 0.038 to 2.28 in controls and treatments, respectively. Growth rates of cutthroat trout *O. clarki* also increased with food supplementation in Pacific coastal streams—from background levels of 0.022 to treatment levels of 1.72 percent body weight per day (Boss and Richardson 2002).

Clearly, growth rates of salmonids in the present and other river systems are limited by availability of food, at least during some seasons. Of course salmonid growth is affected by a range of other factors, most notably temperature (Elliot 1982) and activity rates (Trudel and Boisclair 1996; Vøllestand and Quinn 2006), but food has been demonstrated as an overriding factor within the range of environmental conditions salmonids typically inhabit (e.g., Boughton et al. 2007). Increased growth of individuals has the potential to translate into increased productivity at the population and community levels (Lotrich 1973). Therefore, conservation practices that aim to boost food resources have the potential to increase productivity of the population of interest. Because salmonids rely more heavily on terrestrial than aquatic invertebrates during the late summer-autumn season (Wipfli 1997; Nakano and Murakami 2001), such conservation practices might include managing riparian forests in a way that increases production of both terrestrial and aquatic invertebrates (Deal 2007). The similar levels of background

food availability in both streams—with a trend towards a slight increase in invertebrate density towards the end of the experiments (Fig. 3.3)—were apparently not sufficient to support the kind of growth rates I observed in treatment sites in this experiment, nor in springtime as determined by concurrent studies in the watershed (Tattam 2006). However, increased growth rates of individuals in late-summer autumn do not always translate into increased survival later on (Boughton et al. 2007), and coupled with a lack of refuge habitat that can lead to severe winter mortality of juvenile salmonids (Cunjak 1996) and several other density-dependent factors (Ward et al. 2007), individual growth during one season may in some cases be a poor correlate of population fitness as a whole.

In order to glean further insights regarding the effects of food supplementation on salmonids, I monitored the behavioral response of redband trout in context of the aforementioned behaviorscape. I found it was feasible to predict new behavioral scores from the original NMS ordination, a finding and strategy contrary to a common critique of multivariate analyses as being a merely descriptive rather than predictive approach (Peters 1991). A vast majority (31 of 35) of behavioral scores from the manipulative experiment were within 5 percent of original NMS axes scores, indicating the efficacy of the statistical method and substantiating the ecological realism (as per Levins 1966) of the experiment itself—food supplementation did not lead to behaviors that were outside the context of the behavioral repertoire of redband trout in this system. In fact, food supplementation had only a minor effect on behavior when both Deer Creek and Black Canyon were considered together.

There was an overall difference in fish behavior in both treatment and control sites in both streams, which led to my examination of each stream independently and subsequent finding of a treatment effect in Deer Creek alone, with behavior in sites of food supplementation tending towards more foraging and aggression in that stream (Fig. 3.6). That there was a significant effect on behavior in Deer Creek alone is likely a result of disparate habitat characteristics (i.e., discharge and water temperature) between the two streams. Black Canyon had higher average discharge over the duration of the experiment (2.72 m^3/s) than Deer Creek (0.98 m^3/s) and because foraging and aggressive activities are expected to be more energetically costly with higher water velocities

(McNicol and Noakes 1984), it is likely that behavior in Black Canyon did not significantly change due to the higher costs associated with altering behavior in that stream. Additionally, higher current velocities can be associated with higher invertebrate drift rates and subsequently high consumption rates among salmonids (Nislow et al. 1999), which could potentially explain why fish in the higher-velocity Black Canyon Creek appeared less concerned with altering their foraging behavior. However, our examination of invertebrate drift in the basin indicated that for the most part, food availability was similar in both streams (Fig. 3.3), potentially ruling out this explanation. Black Canyon was also slightly warmer than Deer Creek at the time of experiments, another factor known to increase energetic demands for foraging ectotherms (Elliot 1982), and would likewise be expected to temper a drastic behavioral responses to a modified environment.

In Deer Creek where I observed a significant shift in redband trout behavior due to supplemental feeding, the most notable effect was an increase in both aggressive surface and low strata foraging (NMS axes 1 and 2) (Fig. 3.6). These two behavioral strategies involved high rates of feeding—increased water column feeding in the case of low strata foraging and increased surface feeding in the case of aggressive surface foraging (Table 3.1a). The two names of behavioral axes 1 and 2 may seem mutually exclusive, but this is only an artifact of imperfect labeling of the axes—high scores are possible on both axes because different variables can contribute to a cumulative high score. Although it was not surprising that feeding rates increased with food supplementation—as growth rates in treatment sites were substantially higher than in control sites—other studies of food supplementation in natural streams demonstrating increased growth rates have not documented concurrent increases in foraging rates (Mason 1976; Dill et al. 1981; Boss and Richardson 2002; Boughton et al. 2007). Although establishing a link between foraging rates and growth rates may at first glance seem trivial, this is an important connection to make because growth rates could also be explained via energetic savings due to lower metabolic demands in colder water (Elliot 1982) or via innate differences in metabolic rate among fish (Yamamoto et al. 1998). As in Deer Creek, fish in Black Canyon treatment sites also grew faster than those in control

sites, yet redband trout behavior was not significantly affected by food supplementation ($p = -0.18$). I attribute this finding to either to shifts in redband trout behavior in Black Canyon that were necessarily subtle enough—due to the energetic constraints described earlier—to yield a negative result, or to the fact the higher discharge and corresponding current velocities in Black Canyon more effectively delivered food to foraging areas, preempting the need for fish to substantially alter their behavior in order to capitalize on an increased food supply.

The most evident change in behavior in Deer Creek treatment sites was an increase in aggressive surface foraging (Fig. 3.6), which involved not only increased rates of surface feeding but an increase in all modes of aggressive behavior—intraspecific aggression, initiation of interspecific aggression, and recipient of interspecific aggression (Table 3.1a). Because Deer Creek harbors only conspecific *O. mykiss* and no other observed fish species, high scores on this behavioral axis are necessarily driven by surface feeding rates and intraspecific aggression. This finding corresponds with that of other studies demonstrating either an increase in aggression with increasing growth rates (Lahti et al. 2001) or an increase in territory size with increasing food ration (McNicol and Noakes 1984). However, several other studies have found either no change in territory size or aggression with food supplementation (Chapman 1962; Imre et al. 2004), a negative correlation between food ration and territory size (Dill et al. 1981; Mason 1976; Keeley 2000), or a negative correlation between growth rate and antagonistic behavior (Vøllestand and Quinn 2006). These varied behavioral responses to food supplementation are likely linked to the different environmental contexts in which foragers find themselves (Ward et al. 2007).

In the case of Deer Creek in the present study, the increase in aggression could be explained by intense competition for food as demonstrated by the higher growth rates of fish in treatment sites and low baseline food availability. Another potential explanation for increased aggression is the way in which I delivered food—brief pulses of larger amounts of food at dawn at dusk. Recent theories of resources pulses predict that shorter and more intense pulses will have more dramatic effects than longer and more diffuse pulses (Holt 2008), especially in aquatic ecosystems where effects may transmit more

rapidly than in terrestrial systems (Nowlin et al. 2008). And specifically for fish, competitive interactions are less likely when food is distributed more evenly over a longer time period (Milinski and Parker 1991; Bryant and Grant 1995).

While interpreting these analyses, the question arose as to how stable were the behaviors over time—both through the course of the experiment and between years. Two lines of reasoning support the idea that behaviors were typically stable enough to employ as a robust indicator of redband trout performance. First, regarding short-term stability of behavior, a plot of redband trout aggression rates (no. interactions/fish/min) in treatment sites over time into the second week of the experiment revealed a humped-bell shaped curve, with aggression peaking at around 7 days in response to supplemental feeding, then decreasing (Fig. 3.7). However, there was for the most part far more aggression in the sites where were fed than in control sites, So in that sense behavior did change over time, but the response to treatment was stable. And as mentioned earlier, the NMS technique that I used to compare behaviors demonstrated that the relative rates of foraging and aggression were similar among both years. In 2005 I created the original ordination from sites throughout the basin, which was then used as a baseline for subsequent measurements of behavior under experimental conditions. If the behaviors were wildly different among years, or if my perturbations of feeding had rendered behavior far outside its typical range, then I would have discovered this by my new scores (which were projected onto the original ordination) being outside the range of ‘normal’ behavior by 5% of the axis length.

In general, salmonids moved infrequently during the course of the experiment. Only one of 13 marked and re-captured juvenile Chinook salmon was observed moving—this fish moved into a treatment pool from an adjacent downstream pool. Juvenile Chinook salmon are known to use small streams for rearing prior to their outward migration to sea (Myers et al. 1998) and establish feeding territories in those streams (Everest and Chapman 1972). Even if juvenile Chinook salmon do in fact select habitat according to food availability, the present experiment likely occurred too late in the season to capture the window of time whence they were making those “decisions,” as their migration into the South Fork John Day River and tributaries typically peaks in July

(ODFW, unpublished data). Likewise, I also found no significant effect of food supplementation on redband trout movement—only nine of 49 marked and recaptured redband trout appeared to move among the habitats, and those movements appeared to be similar among treatment and control sites. A concurrent study using radio tags also found that *O. mykiss* movement among local habitats in summer was limited (Madriñán 2008). However, the negative finding could also be explained by either missing the window of time in which redband trout select habitat; lack of adequate sample size; or failure to account for varying competitor densities, a factor known to affect habitat selection (Fretwell and Lucas 1970; Fretwell 1972). Because habitat selection has important consequences for salmonid fitness which may cascade up to the population (Rosenfeld and Boss 2001; Wissmar and Craig 2004), I considered the issue of local movements among habitats as a response to food availability and competitor densities unresolved and addressed the question in a subsequent experiment.

Concluding remarks

In this study I investigated the diversity of foraging and aggressive behaviors of salmonids in a high desert stream ecosystem, using a riverscape perspective and employing observational techniques intended to minimize the influence of the observer. I found that redband trout *O. mykiss* employed a range of foraging behaviors that could be described in terms of energy optimization and degree of risk from competitors and potentially predators, and were linked to habitat features that allowed or denied foragers access to refuge. Food supplementation increased salmonid growth rates as expected and shifted redband trout behavior towards more feeding and aggression in a stream with lower discharge and colder water temperatures. Management activities that alter the availability of invertebrate input to the stream (such as timber harvest, wildfire suppression, and livestock grazing) are likely to influence the growth and behavior of salmonids in natural situations, and the present study provides contextual background for what kinds of changes could be expected. The results from this study indicate that a multivariate approach that recognizes rather than ignores the correlated nature of

different foraging behaviors is a feasible and useful method and can provide ecological context for future observations and experiments.

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Tables

Table 3.1. Composition of and Pearson correlations between each NMS axis and (a) redband trout behavioral variables and (b) ordinal fish assemblage-habitat variables. Pearson's $r \geq 0.20$ were used in interpreting ecological significance of axes and are indicated with an asterisk.

(a)

		Axis 1 Low strata foraging	Axis 2 Aggressive surface foraging	Axis 3 Territory maintenance
Category	*Event*			
Redband trout foraging	Water column feeding	* 0.36	* -0.22	* -0.39
	Surface feeding	0.14	* 0.59	-0.04
	Benthic feeding	* 0.65	0.10	-0.05
	Reject food item	* 0.37	* 0.34	* -0.23
Redband trout aggression	Intraspecific	* 0.21	* 0.83	* 0.22
	Interspecific (aggressor)	* -0.34	* 0.45	* -0.58
	Interspecific (recipient)	0.02	* 0.41	-0.19

Table 3.1. Continued.

(b)

		Axis 1 Low strata foraging	Axis 2 Aggressive surface foraging	Axis 3 Territory maintenance
Category	*Variable*			
Fish abundance	Redband trout	* -0.37	-0.16	-0.19
	Redside shiner	0.18	0.04	* -0.32
	Speckled dace	* 0.35	* 0.27	* -0.24
	Northern pikeminnow	* 0.20	-0.09	-0.14
	Juvenile Chinook salmon	* -0.63	-0.15	* -0.39
Habitat complexity	Dominant substrate size	* 0.38	-0.05	0.10
	Subdominant substrate size	0.17	0.01	* 0.35
	Percent fines	* -0.51	0.11	0.10
	Level embedded	-0.16	-0.08	* 0.54
	Percent undercut	* -0.46	* 0.22	0.18
	Area undercut	* -0.26	* 0.30	0.17
	No. large woody debris	-0.06	-0.03	0.16
	Area large woody debris	-0.14	-0.05	0.09
	Area riparian overhang	* 0.50	0.11	0.01
Pool geometry	Length	* 0.45	0.18	-0.18
	Maximum depth	0.05	0.11	* -0.20
	Width	* 0.44	-0.05	0.09
	Area	* 0.50	0.12	-0.09
	Volume	* 0.35	0.09	* -0.26
Temperature	Stream water temp.	0.16	0.07	* -0.30

Figures

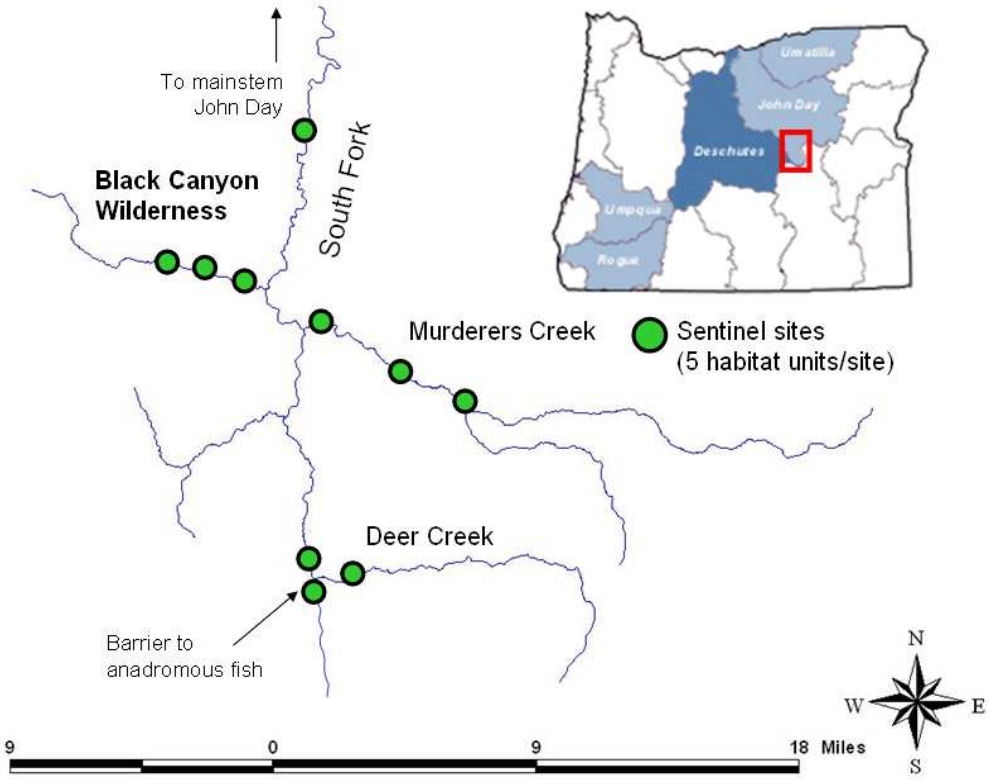

Figure 3.1. The South Fork John Day River and its major tributaries, eastern Oregon. Shaded circles represent 'sentinel sites'—clusters of five pools each used for monitoring redband trout growth, migration, and behavior.

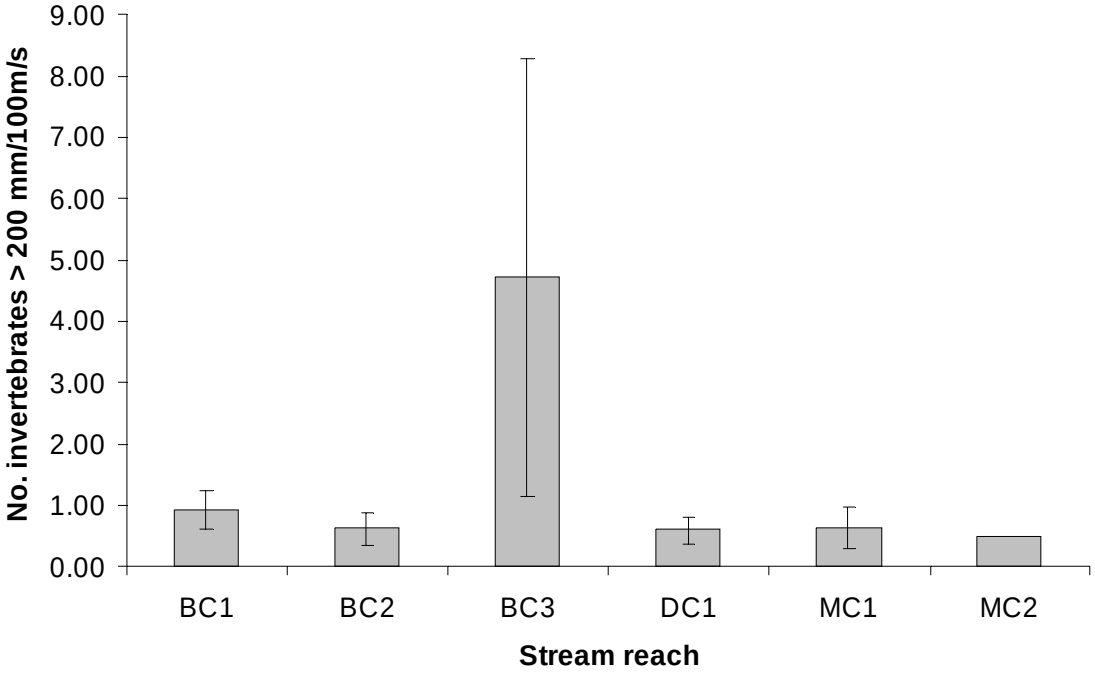

Figure 3.2. Average invertebrate density by tributary reach (Black Canyon = BC, Deer Creek = DC, Murderers Creek = MC) in August and September 2005. Error bars represent ± one standard error. The large value and variation in Black Canyon reach 3 are driven by a single data point (see text). Murderers Creek reach 2 was composed of only one data point.

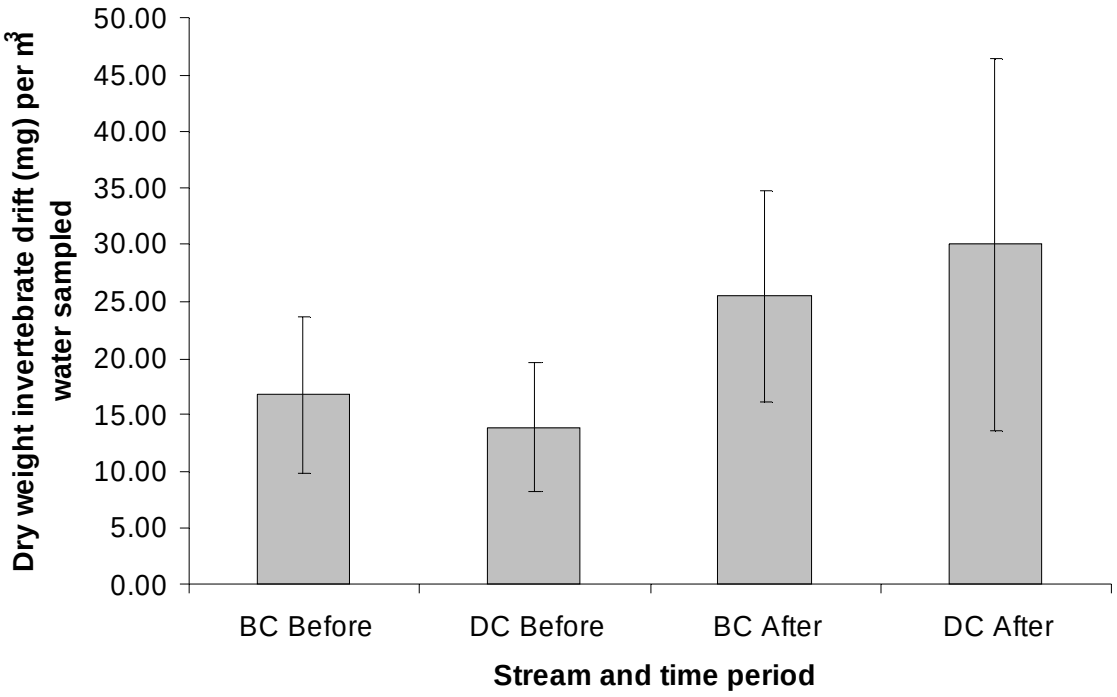

Figure 3.3. Average invertebrate drift density by stream and time period (Black Canyon = BC, Deer Creek = DC) before and after the 2006 experiment. Error bars represent ± one standard error.

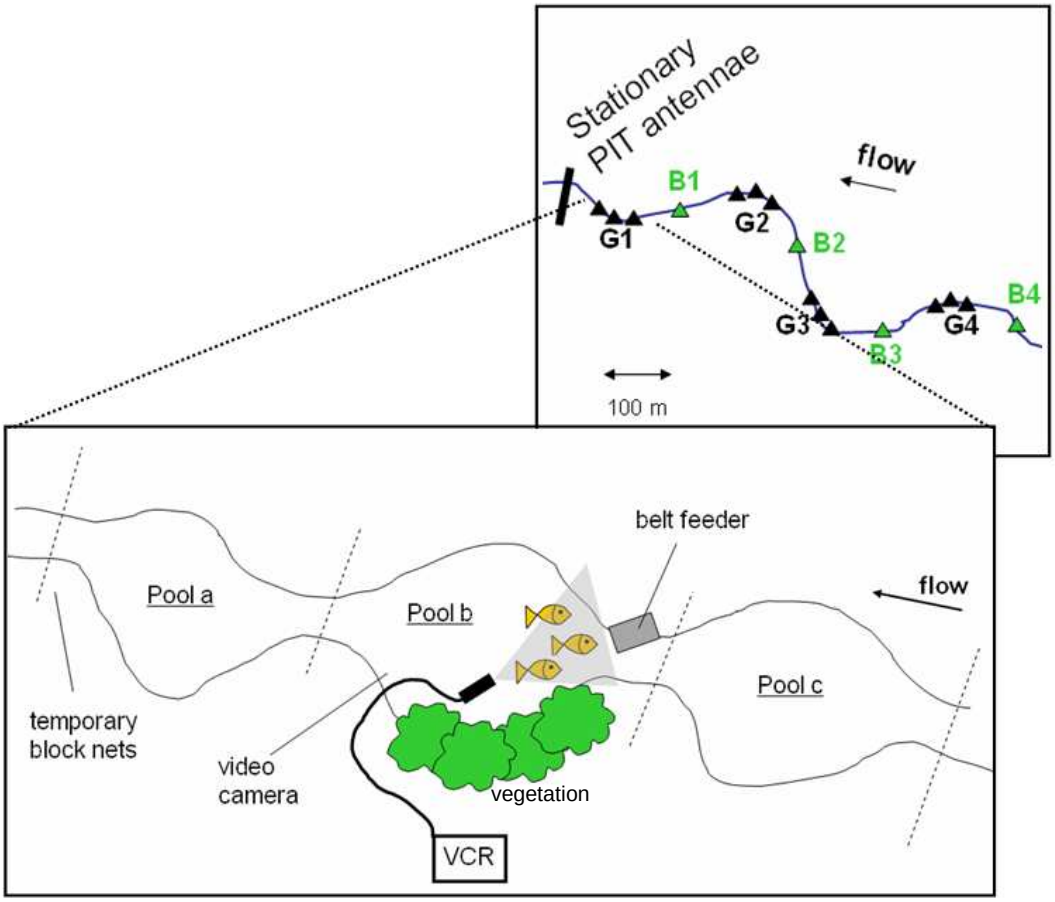

Figure 3.4. Diagram of 2006 experimental sites. Top diagram represents arrangement of full monitoring sites (G1-4, solid triangles) and behavior monitoring sites (B1-4, shaded triangles), with treatments in both streams randomized among sites. Lower inset represents arrangements of pools, temporary block nets, video equipment, and food delivery system in full monitoring sites.

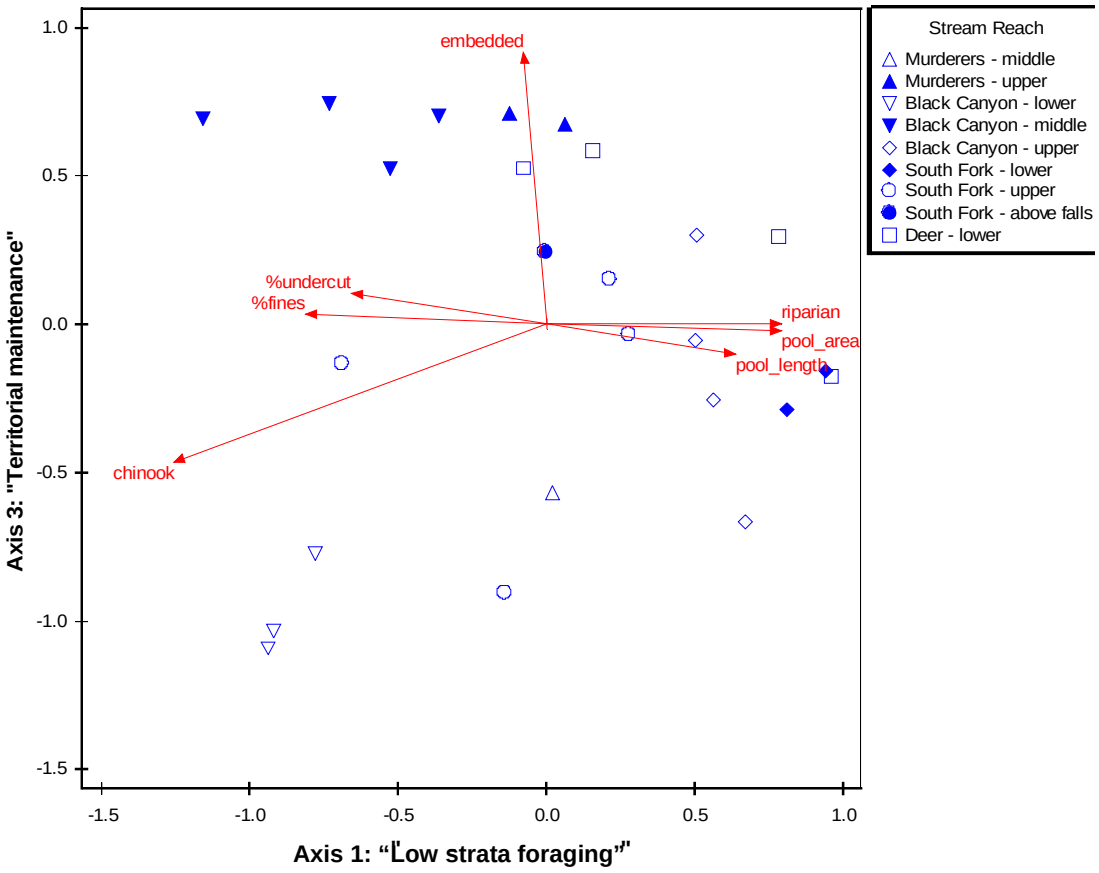

Figure 3.5. Biplot of NMS axes 1 and 2 for the 2005 mensurative experiment. Points represent videos in redband trout behavioral space, categorized by stream reach. Arrowhead vectors represent relationships with quantitative fish assemblage-habitat variables correlated with NMS axes (Pearson's r > 0.20). The degree of embeddedness was strongly correlated with axis 2 (territory maintenance), while other variables shown were correlated with axis 1 (low strata foraging).

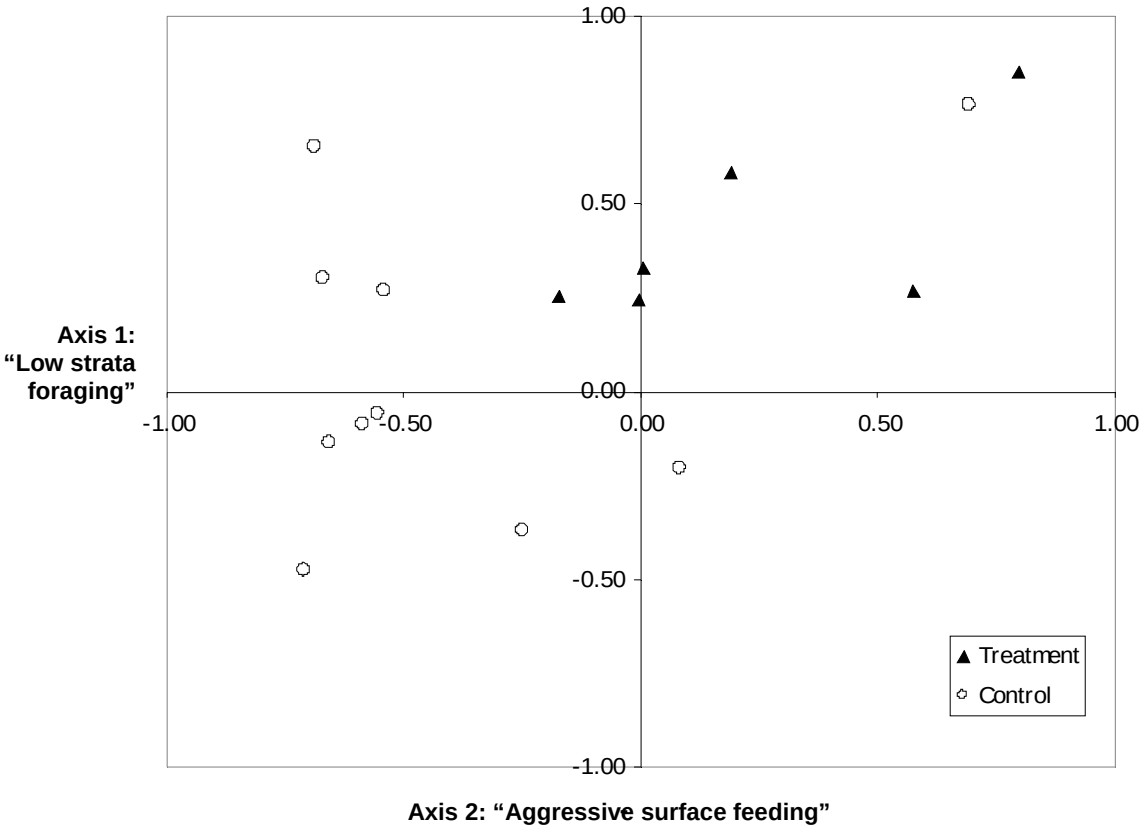

Figure 3.6. Ordination of NMS axes 1 and 2 scores from 2006 experimental manipulation of food resources in Deer Creek. Points represent videos in redband trout behavior space, delineated as treatments (black triangles) and controls (open circles). Redband trout in treatment sites tended to exhibit more 'low strata foraging' and 'aggressive surface foraging.'

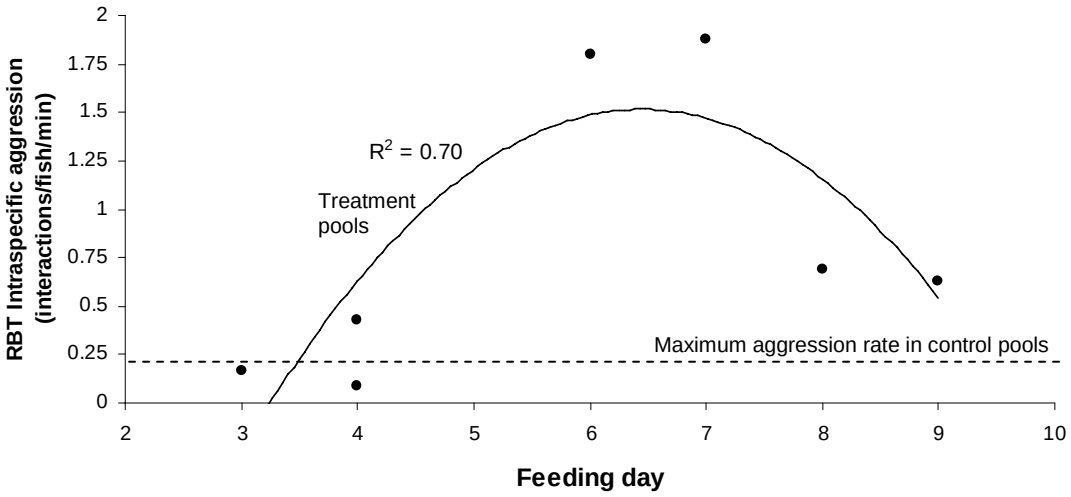

Fig 3.7. Redband trout (RBT) intraspecific aggression rates in treatment sites as a function of the number of days that fish have been fed. A second order polynomial curve is fit to the data, indicating that intraspecific aggression increases to a certain point (~ day 7), then decreases. Dashed line represents the maximum aggression rate (0.22 bouts/fish/min) in comparable control pools.

Chapter 4

ISOLEG THEORY MEETS A WILDERNESS STREAM: EFFECTS OF LOCAL POPULATION ABUNDANCE ON FISH HABITAT SELECTION AND BEHAVIOR

Abstract

Many current approaches to modeling fish habitat associations do not account for distinct versus shared habitat preferences, thus ignoring the potential role that biotic interactions—such as competition—may play in structuring fish assemblages. This study addressed the question of whether habitat selection and behavior of two sympatric fish species of management concern, redband trout *Oncorhynchus mykiss* and juvenile Chinook salmon *O. tshawytscha*, are affected by intra- and interspecific local population densities. A particularly useful framework for addressing the above question is isoleg theory (Rosenzweig 1979, 1981), a model describing habitat selection and other behaviors of dominant and subordinate species as a function of competitor densities. At a series of 20 sites (16 sites from a single stream in summer 2007, four sites from two streams in summer 2006) with independently varying densities of both species, I created artificially 'good' habitat by supplementing food resources in treatment sites and observed habitat selection and behavioral responses via snorkel surveys and underwater video. Using an information-theoretic approach, I discovered that both intra- and interspecific competitor biomass appeared to affect redband trout habitat selection: migration into 'good' habitats decreased with increasing biomass of redband trout as expected; while contrary to my expectations, redband trout migration into quality patches increased with increasing biomass of Chinook, which I attribute to either habitat effects or heterospecific attraction. Habitat selection by Chinook was not significantly influenced by biomass of either species, suggesting their distributions were affected by factors other than competition for space or resources in late summer, that habitat selection by Chinook occurred earlier in the season, or that the failure to complete a response surface design led to a poor model for this species. Framing questions in the context of existing habitat selection theory in a natural stream has the three-fold advantage of advancing ecological theory through the application of an empirical test, addressing questions of management concern regarding mechanisms of fish distributions, and contributing to natural history by revealing interactions within the fish assemblage that have been either ignored or applied in systems (e.g., aquaria) that bear little or no resemblance to natural systems.

Introduction

> We can now define a habitat distribution which will provide a reference for the study of dispersive populations. This is the ideal free distribution.
>
> Fretwell 1972, p. 83

> The rich eat where they wish; the poor eat where they can.
>
> Rosenzweig 1979, p. 285

Evidence from observational studies suggests that in the South Fork John Day River of eastern Oregon, congeneric redband trout *Oncorhynchus mykiss* and juvenile Chinook salmon *O. tshawytscha* are selecting dissimilar riparian and geomorphic features at the habitat unit scale, with Chinook found in sites having abundant large woody debris and redband trout found in sites having a broader range of habitat characteristics (White, unpublished data). These and similar observations are corroborated by past research on salmonids in the Pacific Northwest, which suggests that different species of salmonids occupy different niche space (as per Hutchinson 1957) via separation in timing of reproduction (e.g., Everest and Chapman 1972) or differences in morphology that allow them to capitalize on dissimilar types of habitat (e.g., current velocities as per Bisson et al. 1988). However, when longitudinal profiles of *O. mykiss* and *O. tshawytscha* in the South Fork John Day are examined at a larger scale of resolution (i.e., the river reach) the occurrence of the two species appears to be positively correlated in many instances (Fig. 4.1), suggesting that their distributions may in fact be driven by a shared preference for habitat characteristics. Furthermore, landscape-scale models of fish-habitat associations indicate that redband trout are distributed somewhat uniformly throughout the South Fork John Day watershed, even though habitat conditions and stream water temperatures (both recognized as important for this species) are relatively heterogeneous (Madriñán 2008), implying that although redband trout have known preferences for certain types of habitat, intraspecific competition may be pushing some conspecifics into suboptimal habitat. These previous modeling approaches do not elucidate whether observed patterns are the

result of distinct vs. shared niche preference (as per McGill et al. 2006), or whether intraspecific competition among individual *Oncorhynchus* spp. are affecting their distributions, thus ignoring the potential role that biotic interactions—such as competition—may play in structuring fish assemblages.

Prevailing wisdom suggests that these and other closely-related salmonid species that have coexisted for tens to hundreds of thousands of years in the Pacific Northwest have developed subtle differences in the way they use the environment, and thus interactions between species are minimized. However, an equally plausible scenario is that these and other salmonid species exist on a continuum of interactive to selective segregation (as per Brian 1956, cited in Nilsson 1967). Interactive segregation implies that species use the environment in different ways due to the effects of competition or other biotic interactions occurring in present-day, ecological timescales; whereas selective segregation implies that species' use of the environment has diverged through evolutionary time so that they have evolved distinct modes of using the environment. And although temporal differences in important life history stages do exist between *O. mykiss* and *O. tshawytscha*—for example, spring versus fall spawning of each species respectively; and although in the South Fork watershed they are temporally-separated for the majority of any given year—with *O. tshawytscha* juveniles using the South Fork and its tributaries as rearing areas from June through November only in a given year—there is still the potential that these species can be placed farther on the side of interactive segregation than previously suspected. Previous observations in the field and via video analysis of interaction rates suggest this may be the case. This study addresses the question of whether habitat selection and foraging and aggressive behaviors of the two species are affected by the presence and abundance of intra- and interspecific fish densities.

A particularly useful framework for addressing the above questions is isoleg theory (Rosenzweig 1979, 1981), a graphical model which describes habitat selection and other behaviors of dominant and subordinate species as a function of competitor density space (Pimm et al. 1985; Abramsky et al. 1990; Young 2004; Berec et al. 2006). The model has its roots in ideal free distribution theory (Fretwell and Lucas 1970; Fretwell

1972) but accounts for potential interactions among multiple species. The basic idea behind isoleg theory is that given two species, one of which is dominant, there will be various competitor densities at which dominants and subordinates are expected to be distributed in poor and high quality habitats. The isoleg approach differs from the classical approach of comparing habitat selection or other measures of performance (e.g., growth and feeding habits) of potential competitors in allopatric and sympatric populations—best exemplified by Werner and Hall's (1976) classic study of niche shifts in sunfish *Lepomis* spp. stocked in artificial ponds—in that isoleg studies typically examine niche shifts along a gradient of competitor densities. This latter scenario represents realistic conditions which species actually encounter in the wild. Furthermore, complete removal of fish from natural streams is impractical due to difficulty catching them and the numerous hiding places available, rendering it nearly impossible to examine niche shifts in allopatric and sympatric habitats that are adjacent to one another and therefore representing similar environmental conditions. Nonetheless, it may still be useful to test theories of habitat selection in the wild. Although ideal free distribution and isoleg theory originated several decades ago and have been repeatedly tested in several systems, the complex relationship among habitat selection, competition, and behavior are still poorly understood for fish—partly because many studies have not applied these theories in natural field settings (Ward et al. 2007). Finally, many studies employing ideal free distribution and related theories test the effects of competitor densities on habitat selection alone, and do not account for effects on fish behavior (i.e., foraging and aggression). Insights on fish behavior in different ecological contexts can increase the utility of fisheries science to conservation and management (Buchholz 2007).

Figure 4.2 is a graphical representation of isoleg theory modified from Pimm et al. (1985). Isolegs for subordinate fish (solid lines) and dominant fish (dashed line) represent transition points along the range of competitor densities where fish move from good to poor quality habitat patches. K_s and K_d represent carrying capacity for the subordinate species (in this case, juvenile Chinook salmon) and dominant species (redband trout), respectively. Subordinate species are expected to exclusively occupy high quality patches only under the conditions of low densities of conspecifics and

dominants (section A). Subordinates occupy both poor and high quality patches at moderate densities of conspecifics and/or dominants (section B). At higher levels of dominants, all subordinates are located in poor quality habitat (sections C and D). Dominants are expected to occupy quality habitat at only low to intermediate densities of conspecifics (sections A, B, and C) with some dominants moving into poor quality habitat at high densities of conspecifics (section D). The low angle of the dashed isoleg for dominants indicates the minor influence of subordinates on habitat selection by the dominant species, with subordinate densities in poor habitat only slightly decreasing the expected profitability in those patches by dominants. Isolegs can also represent behaviors other than habitat selection (such as feeding or aggression rates) as a function of competitor density space, and yield insights into mechanisms driving competitive interactions. My approach was to use isoleg theory as a conceptual tool for discovering how two species respond to each other's relative abundance, and to use multiple linear regression and model selection techniques to determine (a) selection of 'good habitat' (explained later) and (b) foraging and aggression as a response to all potential combinations of intraspecific fish densities, interspecific fish densities, and the interaction terms. Confirming the validity of isoleg theory as diagrammed in Figure 4.2 was the essential goal of this study.

The natural conditions of the South Fork John Day River and dynamics between redband trout and Chinook are an ideal situation to test isoleg theory. From the perspective of fisheries biologists, streams represent to a certain extent continuous input systems where resource input rates are minimally affected by the abundance of foragers (as per Parker and Stuart 1976), at least at the habitat unit scale (i.e., an adjacent pool and riffle). This is especially true for systems where fish forage on insects drifting down into a pool from an upstream riffle. Another reason that streams (especially small ones) are ideal for testing habitat selection theories is that organisms are confined to an area where they can be more easily observed than in other types of environments such as lakes, large rivers, estuaries, or ocean habitats. Much of the aquatic-related research testing the ideal free distribution and related theories has been either observational, with no manipulations of habitat quality applied (e.g., Power 1984; Morita et al. 2004; Haugen et al. 2006), thus

potentially overlooking causal mechanisms of habitat selection; or has been conducted in laboratory aquaria or other conditions not representing natural conditions (e.g., Utne et al. 1993; Young 2004; Berec et al. 2006), thus diminishing the external validity (as per Altmann 1974) of the results. One notable exception to the latter case is the work of Fraser and Cerri (1982) who combined findings from experiments in a "seminatural artificial stream" (i.e., first-order stream channels constructed adjacent to a second-order stream) and field observations to describe mechanisms of two minnow species habitat use in response to refuge and predation risk. However, testing habitat selection theories in natural streams may reveal more realistic patterns. Finally, many stream fish are ideal organisms for testing habitat selection theories because they are mobile enough to assess patch quality on a regular basis (Gowan and Fausch 2002), which allows them to perceive and respond to differences in their potential food intake rates.

In this study, I first tested the null hypothesis that habitat selection and behavior were unrelated to fish abundance. This would mean that for both redband trout and juvenile Chinook salmon, patterns of habitat selection and behavior do not correspond to the relative abundances of intra- and interspecific competitors. Failure to reject this null hypothesis would indicate that salmonids do not select habitat based on densities of other members of the fish assemblage. I then address intraspecific effects on habitat selection and behavior: habitat selection and behavior of redband trout were expected to be influenced by density of conspecifics; likewise for Chinook salmon. This is essentially the ideal free distribution—the abundance of conspecifics alone decreases habitat quality and thus drives habitat selection and behavior. Examining behavior in response to conspecific densities in natural habitats permits mechanistic understanding of processes driving intraspecific competition, information important for both ecological theory and management (Ward 2007). I expected that foraging rates would decrease while aggression rates would increase in the presence of high densities of conspecifics. Finally, I expected habitat selection and behavior would be affected by interspecific competition. In the case of redband trout, I expect only intraspecific competition would be important—their behavior and habitat selection affected by conspecifics only. In the case of Chinook, however, I expect their habitat selection and behavior to be influenced by conspecific

abundance, but more importantly by interspecific competition because Chinook are presumed to be competitively inferior to *O. mykiss* regarding their dominance ranking (Kelsey et al. 2002). Thus competition would be asymmetric, with redband trout as the dominant and Chinook as the subordinate species.

Methods

Conceptual approach

Isoleg theory tests whether the selection of or performance in a good habitat patch *X* or a poor habitat patch *Y* by species *A* or *B* is a function of competitor density, abundance, or biomass (after Rosenzweig 1979):

$Z_{X,Y} = \mathrm{f}(A, B)$ (eqn 1)

where *Z* is some measure of organism performance, such as habitat selection or behavior. The model assumes 'good' and 'poor' patches exist and can be selected by organisms, a condition that I imposed by supplementing food resources in so-called good habitat patches. Late-summer food availability is potentially a limiting factor for fish growth in this system as salmonid growth is very slow during this period (Tattam 2006), and so food resources are therefore a good indicator of habitat quality. Pools were the habitat unit of primary interest in this study because they have been shown to be energetically favorable as compared to riffles (Rosenfeld and Boss 2001). Testing the isoleg concept involved evaluating whether competitor densities in a series of three pools enclosed by block nets affected the choice of good habitat by each species, in addition to rates of foraging and aggressive interactions. If habitat selection or behavior by salmonids in this system is affected by conspecific or heterospecific fish densities, then I would expect a model in the form equation 1 to be statistically significant and explain the greater portion of variance in the data. Measures of performance (the response, *Z*) in the case of this experiment were habitat selection (i.e., an increase or decrease in biomass in 'good' habitat patch *X*) and foraging and aggressive behavior—the latter measure derived from

trout foraging observations in 2005 and a subsequent multivariate analysis describing relative rates of redband trout foraging and aggression throughout the South Fork watershed (Table 1).

Study sites and organisms

The South Fork John Day in eastern Oregon (Fig. 4.3) harbors, among other fish species, a population of redband trout and is the location of summer-autumn rearing of juvenile spring Chinook. Prior to their outward migration to sea, juvenile Chinook salmon use small streams for rearing (Myers et al. 1998) where they establish feeding territories (Everest and Chapman 1972). Black Canyon was the location of 18 of 20 experimental sites and was chosen based on the relative absence of other fish species there. Except for two species of dace, speckled dace *Rhinichthys osculus* and longnose dace *R. cataractae*, the presence of other fish species in Black Canyon was either rare or fish occurred in the benthic zone (i.e., sculpin *Cottus* spp.) and did not appear to compete with salmonids. The watershed boundaries of Black Canyon Creek define the Black Canyon Wilderness Area in the Ochoco National Forest, a roadless area with relatively pristine conditions and minimal livestock grazing. Deer Creek, where two of the 20 experimental sites were located, harbors only redband trout and potentially *Cottus* spp. The portion of Deer Creek examined in this study is administered by Bureau of Land Management, bordering Malheur National Forest, and although heavily forested its riparian vegetation experiences more livestock grazing than does Black Canyon.

Both Black Canyon and Deer Creek have cold water and high gradient relative to other streams in the South Fork drainage and have similar habitat characteristics, with the exception that Black Canyon is spring-fed and maintains higher discharge levels in late summer (average 2.72 m^3/s in late summer 2006, 2.59 m^3/s in 2007) than Deer Creek (average 0.98 m^3/s in late summer 2006). Maximum and minimum water temperatures in Deer Creek 2006 were 19.3 and 9.9ºC in Deer Creek 2006 and 22.4 and 11.0ºC in Black Canyon 2007 during experiments, determined from Onset submersible data loggers

recording at 15 min intervals and distributed throughout river reaches where experiments were conducted. Previous observations indicated that pool size and the percentage of undercut bank were important habitat characteristics for fish in this system. In Black Canyon, average maximum thalweg depth (± standard deviation) was 0.62 m (± 0.13), average width of pools was 3.74 m (± 0.13), and average percent of shoreline having undercut banks > 40 cm was variable at 10.02% (± 16.04). In Deer Creek, average maximum thalweg depth (± standard deviation) was 0.51 m (± 0.19), average width of pools was 3.76 m (± 1.15), and average percent of shoreline having undercut banks > 40 cm was again variable at 8.88% (± 17.0). Based on multiple 24-hour sets of 500-μm drift nets scheduled through the course of the experiment and throughout the extent of the river reach studied, invertebrate drift densities expressed as milligrams dry weight of invertebrates per cubic meter of stream water were on average (± standard error) 19.3 mg/m^3 (± 6.6) in Deer Creek 2006 and 84.3 mg/m^3 (± 15.1) in Black Canyon 2007.

Experimental design

In order to select sites, I conducted snorkel surveys (Thurow 1994; Mullner et al. 1998) of pools throughout the lowest river reach of Black Canyon where redband trout and juvenile Chinook salmon are known to coexist and chose sites to complete a response surface grid—with independently varying densities of both species (Inouye 2001). With the exception of two sites, I used naturally-occurring fish densities present in the streams. A response surface design has several advantages over additive and substitutive designs typically used in ecological experiments, including the ability to distinguishing among alternative models of organism distribution which I employed in this experiment via model selection techniques. Because of the ubiquitous redband trout distributions and the relatively heterogeneous Chinook distributions, it was necessary to augment natural fish densities by removing redband trout and adding Chinook to and from adjacent stream sections. These additions and removals simulated the natural, seasonal chronology of habitat selection by fish in the system, with redband trout having prior residence over Chinook. Redband trout are present in the South Fork year-round (Tattam 2006) while

peak immigration of juvenile Chinook into South Fork tributaries occurring July-August (ODFW, unpublished data). For the most part, I succeeded in representing a range of biomass values for both species, with the exception of missing zero values for redband trout (Fig. 4.4). There were no sites where redband trout were absent, and attempts to remove them using electrofishing and seining yielded only slight reductions in their abundance. Therefore, the subsequent models describe habitat selection and behavior by fish as a function of only non-zero values of redband trout biomass. Although I failed to locate sites with zero abundance of redband trout, their presence is typically ubiquitous throughout the South Fork John Day watershed (Madriñán 2008) and therefore models represent the realistic range of fish densities expected to occur in this system. However, missing zero and low-abundance values of redband trout in this experiment have potentially masked the effect of redband trout on juvenile Chinook salmon habitat selection and behavior, and I therefore temper my interpretations with this in mind. In contrast, Chinook distributions spanned a broader range of biomass values—they were absent in three of the 20 sites—but their distribution was not as evenly distributed as that of redband trout. In experimental sites, I maintained the natural size asymmetry between the two species in this system, with size of Chinook more homogeneous and smaller than redband trout.

In 2007, the 16 experimental sites consisted of three-pool sequences arranged in the manner diagrammed in Figure 4.5. Block nets were first installed at the downstream and upstream ends of each site, and after a ~1 hr acclimation period I conducted snorkel surveys of each pool within the site, with each fish species recorded in 5 mm length categories. Biomass of salmonids and dace (the latter also observed feeding on drifting invertebrates) was calculated by first applying calibration coefficients developed by comparing snorkel surveys with mark-recapture population estimates (Bayley et al. unpublished data):

$$Ni = Si/Ei \quad \text{(eqn 2)}$$

where Ni is the estimated population size, Si is the number of fish observed via snorkeling, and Ei is the snorkel efficiency coefficient for each species and size category

i. Snorkel efficiency coefficients (*E*) were 0.32, 0.25, and 0.45 for redband trout < 101 mm, 101-150 mm, and > 150 mm total length, respectively. Snorkel coefficients for Chinook and dace were 0.50 and 0.16, respectively. I then calculated total fish biomass for experimental sites using length-weight regression curves developed for each species from 2006 data in this system. Fish biomass was used as a measure of fish abundance in response and predictor variables in the isoleg model in order to account for varying sizes of fish and their expected differential response to treatments based on size asymmetry (Young 2004; Berec et al. 2006). The time period of treatment (two to four days) was not long enough to see a measurable increase in fish size, so changes in fish biomass represent fish movement rather than growth. Redband trout and dace biomass was best described by the following power relationships:

$W_{O.\ mykiss} = (L_{O.\ mykiss})^{2.86}$ and (eqn 3)

$W_{\text{dace}} = (L_{\text{dace}})^{2.83}$, (eqn 4)

where W is weight in grams and L is median length in the size category in mm. Chinook biomass was best described by the linear equation:

$W_{O.\ tshawytscha} = 0.25 \cdot L_{O.\ tshawytscha} - 13.41$. (eqn 5)

Immediately after snorkel surveys and calculations of fish biomass, I began adding freeze-dried krill *Euphasia pacifica* to the center pool of each site using automatic belt feeders. Amounts of food totaled 3% per day (delivered from mid-morning to late afternoon) of estimated fish biomass of all salmonids and dace in the three-pool sequence. This amount of krill ensured there was always an abundance of food in the center pool, regardless of potential fish immigration from the upstream or downstream pool. Thus, the center pool of each three-pool sequence served as 'good' habitat (patch *X*, equation 1) while the upstream and downstream pools served as 'poor' habitat (patch *Y*, equation 1). Daily rations of food of similar magnitude have been used in previous feeding studies in natural streams (Mason 1976; Boss and Richardson 2002; Boughton et al. 2007) and account for rations for optimal fish growth.

The next morning and every afternoon and morning thereafter for the period that each site was in operation, I conducted 20-minute video observations of fish foraging and aggressive behavior in 11 out of 16 sites in 2007. All video records from the 2007 experiment were processed by a single observer to maintain methodological consistency—the rates of redband trout intra- and interspecific aggression (charging, chasing, and nipping) and foraging interactions were recorded (Table 4.1) and scaled to the average number of redband trout present in the video frame. In each site of video analysis, recording occurred in all three pools of the sequence, but in the laboratory the uppermost or lowermost pool was randomly selected for processing of behavioral scores. Each experimental site ran for two to four days based on our finding (via repeated snorkel surveys) that fish migration among the three pools would equilibrate after this time period; and also based on findings from prior supplemental feeding experiments with *O. mykiss* in the John Day River system (Hiram W. Li, unpublished data). After termination of each experimental site, I conducted a final snorkel survey of fish distribution, removed block nets, and measured habitat characteristics as described below. At any given time, two to four experimental sites were in operation because I wanted to conduct the experiment in a brief amount of time to control for potential seasonal changes in fish migration and environmental conditions, and because this was the number of sites that could be maintained simultaneously by a crew of three to four people in the field.

In order to increase the sample size to n = 20 sites and to capture a broader range of fish densities to complete the response surface design, I used data from four sites from a previous experiment in 2006 that was designed to test the effects of food addition on salmonid growth and behavior. Procedures were similar between the two years except that in the previous year, 2006, fish were fed for approximately 2.5 weeks, no block nets were used after initial surveys of fish distribution, krill were pre-soaked so that they would be neutrally-buoyant in the water column and delivered at 5% of fish biomass (versus 3% in 2007), and krill addition was pulsed at dawn and dusk (versus distributed evenly from mid-morning to late-afternoon in 2007). Two of the four sites in 2006 were located in Deer Creek, a nearby stream that harbors only redband trout; while the other two sites from that year were in Black Canyon where the two species are sympatric.

Despite these differences, data from the two years were compatible with the isoleg analysis because the fundamental conditions were met for testing the theory in both years: (a) 'good' and 'poor' habitat patches existed, (b) fish were free to migrate among and select the different habitat patches, and (c) sites represented independently varying densities of both species (with zero Chinook in the two Deer Creek sites). Because in the isoleg analysis I used biomass as a measure of fish abundance, I needed to remove the effect of fish growth due to prolonged feeding (approximately 2.5 weeks) in the 2006 treatment sites. Therefore, from the final pool biomass estimates from the 2006 sites I subtracted the biomass that fish were expected to gain based on average instantaneous growth rates (mean ± standard error) of 0.96% (± 0.11) body weight per day for both redband trout and Chinook. While models of habitat selection incorporated data from both years, behavioral responses (foraging rates and aggression) were examined using videos from 2007 only because of differences in the manner in which fish were fed.

Data analysis

For the two species of salmonids, habitat selection was evaluated in a model selection context (Burnham and Anderson 2002), where the response variable *Z* for a multiple regression model was the change in biomass in the center pool (site of food addition) of species *i* as a function of the candidate variables: intra- and interspecific competitor biomass *A* and *B* (equation 1) and the interaction term *A*B*. In order to assess appropriate sample size, I conducted an *a priori* power analysis for a multiple regression model with three independent variables; based on an expected R^2 between 0.40 and 0.50 (determined from a pilot study), I found that a sample size of 20 was more than adequate to achieve power = 0.80 (Fig. 4.6). Independent variables were natural log-transformed (ln[x + 1]) in order to meet the assumption of normality. Models were ranked according to their Akaike (1973) value and adjusted for small sample sizes (AIC_c), with lower values indicating a more parsimonious model (Burnham and Anderson 2002), and by their Akaike weight (w_i) indicating the weight of evidence for the model given the data (Buckland et al. 1997).

The behavioral response of redband trout to food supplementation was examined by fitting multivariate scores of the videos to an existing nonmetric multidimensional scaling (NMS) ordination (Kruskal 1964; Mather 1976) of redband trout behavior across a range of environmental conditions and fish species densities in the South Fork John Day watershed (Table 4.1). New NMS scores were derived using a prediction algorithm (McCune and Grace 2002), holding the original ordination stable and finding the lowest-stress positions for new points along the three original axes, simultaneously. If new scores fit the original ordination poorly (i.e., extended beyond original axes scores ≥ 5 %), I removed those points from the analysis to avoid extrapolation beyond the original model. In order to test whether redband trout behavioral responses were affected by intra- or interspecific fish density, I conducted model selection procedures in a similar manner as for habitat selection. Response variables were the three behavioral axes from NMS analyses (Table 4.1), and the predictor variables were identical to those of the habitat selection analysis: the natural-log transformed estimates of redband trout and Chinook biomass in each experimental site.

Multiple regressions, model selection, and power analysis were performed using the SAS software package (SAS, 2004). Multivariate analysis (NMS) was performed using PC-ORD v.5.19 beta (McCune and Mefford, n.d.), software specifically designed for multivariate analysis of ecological data.

Results

Habitat selection

Model selection of multiple linear regression models indicated that habitat selection of redband trout was best described by the dependent variables redband trout and Chinook biomass of the three-pool sequences (Table 4.2a). The multiple linear regression describing the top model was as follows:

$$\Delta RST = 154.89 - 25.73 \ln(RST+1) + 8.68 \ln(CHS+1), \quad \text{(eqn 6)}$$

where ΔRST is percent change in redband trout biomass in enriched habitat and RST and CHS are the natural log-transformed values of redband trout and Chinook biomass in grams, respectively ($n = 20$, $p < 0.0001$, $R^2 = 0.67$. $w_i = 0.61$). The next best model describing redband trout habitat selection—similar to the top model but including the interaction term—had Akaike weight substantially lower than that of the best model ($w_i = 0.39$), indicating the top model most likely described habitat selection given the data. Regardless of whether the interaction term is included, biomass of both species appeared to affect habitat selection by redband trout. In the top-ranking model, conspecific biomass was negatively correlated with selection of the enriched patch as expected (Fig. 4.7a), indicated that intraspecific competitor densities impose a limit on the abundance of redband trout that will migrate to an enriched site. This finding demonstrates existence of the rightmost isoleg for redband trout in Figure 4.2. The finding is also evidence for the positive slope of the dominant isoleg, with Chinook biomass positively correlated with selection of the rich patch by redband trout (Fig. 4.7b).

To see if I could improve upon the above model for redband trout habitat selection (having $R^2 = 0.67$), I conducted post-hoc multiple linear regressions in a similar manner, but included physical habitat variables known to affect redband trout habitat selection and foraging and aggressive behavior as candidate variables along with intraspecific competitor densities. Physical habitat such as cover and refuge has long been known to interact with competitor densities and food abundance to affect habitat selection (as per Paul Errington's 1930s work on bobwhite quail, cited in Schorger 1966). Inclusion of the following habitat characteristics did not improve the model as measured by percent variance explained (R^2 of leading the strongest model that included the habitat variable), and no models formed significant relationships ($p < 0.05$): area of undercut banks ($R^2 = 0.41$), percent of stream bottom with embedded substrates ($R^2 = 0.40$), maximum thalweg depth ($R^2 = 0.51$), and pool volume ($R^2 = 0.40$). Therefore, the model including the negative intraspecific effects of conspecific redband trout and positive heterospecific effect of juvenile Chinook salmon was the most probable explanation for redband trout habitat selection.

All of the candidate models describing habitat selection by Chinook were poor (Table 4.2b), as determined by the small amount of variance explained by even the most parsimonious of available models ($R^2 = 0.14$), and that model was not significant at the $\alpha = 0.05$ level ($p = 0.24$). Therefore, I did not proceed with interpreting models of habitat selection for this species. Juvenile Chinook salmon appeared to move very infrequently during the course of the experiment, potentially for reasons addressed in the Discussion. Whereas the median percent change of biomass in enriched sites for redband trout was +16.1%, the median percent change of juvenile Chinook was -5.3% in enriched sites. The weak movement signal by juvenile Chinook salmon also has important implications for the interpretation of the positive slope of the redband trout's isoleg (Fig. 4.2). Because Chinook were stationary and the isoleg slope remained positive, a new explanation is required other than the one provided by Pimm et al (1985), who reasoned that increased densities of subordinates would further decrease the value of 'poor' patches for dominants, thus making the 'poor' habitat even more so. Field observations indicated that speckled dace often foraged in a similar manner and in similar locations in the water column as redband trout, and hence they were also potential competitors in this system. Therefore, I ran similar models testing for the affect of speckled dace biomass on redband trout habitat selection, and the effect of redband trout biomass on speckled dace habitat selection. The strongest model predicting redband trout habitat selection did not include speckled dace as a predictor; in fact the weight of evidence for this set of models included only the intraspecific effect redband trout on their own habitat selection ($w_i = 0.59$), similar to models previously reported. The strongest model predicting habitat selection by speckled dace did include biomass of redband trout and carried a slight majority of weight of evidence ($w_i = 0.54$), but the model was not statistically significant ($p = 0.30$), either because of the small number of sites where speckled dace occurred ($n = 10$) and hence low statistical power, or because there truly was no effect of redband trout abundance on habitat selection by dace.

Behavior

In addition to examining habitat selection, I used the logic of isoleg theory to determine whether fish densities of both species affected redband trout foraging and aggression. A multivariate framework from a previous NMS analysis of baseline redband trout behaviors from throughout the South Fork watershed was used to generate new scores from videos in the present analysis, and those new scores were used as the response variable in the same way that habitat selection from the previous analysis (equation 1) was used as the response variable in the analysis above. Of the 22 new videos considered for this experiment, one video could not be processed due to poor placement of the camera and subsequent poor visibility. Out of the remaining videos, only one exceeded the 5% extrapolation limit from the 2005 NMS calibration scores, meaning that the vast majority (20 of 21) of behavioral responses to isoleg treatments were within the range of natural redband trout behavior previously observed in the watershed. Model selection revealed that while NMS axis 1 (low strata foraging) did not yield a good model (highest $R^2 = 0.11$, $p = 0.15$), NMS axes 2 (aggressive surface foraging) and axis 3 (territory maintenance) yielded relatively good models ($R^2 \geq 0.41$ and $p < 0.05$ for both models, Table 4.3). In the best-fitting models, multiple linear regressions describing redband trout behavior where as follows:

$$\text{Axis 2} = 22.79 - 3.09 \ln(\text{RST}+1) - 4.10 \ln(\text{CHS}+1) + 0.55 * \ln([\text{RST}+1]*[\text{CHS}+1]), \text{ and} \quad \text{(eqn 7)}$$

$$\text{Axis 3} = -3.24 + 0.43*\ln(\text{RST}+1), \quad \text{(eqn 8)}$$

where axes 2 and 3 are the NMS behavioral scores for aggressive surface foraging and territory maintenance by redband trout, respectively (Table 4.1). Aggressive surface foraging by redband trout (axis 2) decreased with both increasing conspecific biomass (Fig. 4.8a) and Chinook biomass (Fig. 4.8b). Territory maintenance by redband trout (axis 3) decreased with increasing conspecific biomass (Fig. 4.8c). These results indicated that indeed, behavior of redband trout was affected by both intra- and interspecific fish densities, with a general trend of decreasing foraging and aggression with higher densities of conspecific and heterospecifics.

Additionally, I conducted post-hoc analyses on the potential effects of habitat variables on redband trout behavior in the same manner as for habitat selection above. While habitat variables (undercut banks, embeddedness, maximum thalweg depth, and pool volume) did not seem to affect habitat selection, their addition to models of fish behavior did increase the explanatory value of the models in almost all cases. Because these were post-hoc analyses I do not place a large amount of confidence in this interpretation, but I did note that simply adding pool volume to the original model describing axis 2 (aggressive surface foraging) increased the explanatory value by 15% ($R^2 = 0.58$ versus the previous $R^2 = 0.43$) and the model was highly significant ($p = 0.004$), with a positive relationship between aggressive surface foraging and pool volume. I also noted that simply adding undercut bank to the model describing axis 3 (territory maintenance) increased the explanatory value by 17% ($R^2 = 0.58$ versus the previous $R^2 = 0.41$) and the model was also highly significant ($p = 0.001$), with a negative relationship between territory maintenance and area of undercut bank.

Although this analysis was based on evaluating changing values of fish biomass in enriched sites as a function of competitor densities, I was also interested in the contribution of the different size classes to changes in biomass, as territory size is known to scale allometrically with fish size in salmonids (Keeley and Grant 1995; Grant et al. 1998; Keeley 2000). By plotting the average change in redband trout abundance (Fig. 4.9a) and biomass (Fig. 4.9b) in enriched patches by size class, it became evident that the smallest redband trout (< 65 mm body length) were excluded from enriched patches, while all larger size classes appeared to increase in enriched sites, with the exception of redband trout 150-200 mm in length (Fig 4.9a). The changes in abundance of redband trout < 200 mm body length translated into only minor contributions of biomass when compared to the contribution by larger fish in the 200-250 mm size class (Fig. 4.9b), so although the change in abundance among fish > 65 mm was relatively even, changes in abundance of the largest size classes of fish had a large influence on the total fish biomass as a response to treatment. And since larger fish have larger territories (Keeley 2000), it is likely that this size class of fish contributed most to the limit on carrying capacity in this experiment.

Discussion

Effects of fish density on habitat selection

I found that at least in late-summer, habitat selection of enriched patches by redband trout was negatively affected by conspecific densities, but not by juvenile Chinook salmon. This finding of density-dependent population regulation or self-thinning as a response to conspecific competitors and resource availability is not novel (i.e., Errington 1948; Fretwell and Lucas 1970; Fretwell 1972), but the results from this experiment employed a modeling approach that allowed me to examine to what degree competitors affect habitat selection, and potentially what value of competitor biomass at which fish will begin selecting a "poorer" (i.e., low food abundance) patch. At lower densities, redband trout were more likely to select enriched patches, a finding that demonstrates a measurable limit to which managers can expect to increase carrying capacity or productivity of salmonid habitats (Mobrand et al. 1997).. The effects of high densities of competitors on fish performance have been demonstrated in a number of ways in previous studies, such as increased likelihood of emigration (Imre et al. 2004) or in the case of interspecific competition, the negative impacts of dominant species on subordinates (Pimm et al. 1985; Abramsky et al. 1990; Morita et al. 2004). This finding also suggests that models of habitat selection not accounting for competitors may be misrepresenting the kinds of habitat the species prefers, that in many cases individuals of a given species will be found in suboptimal habitat, especially if populations are near carrying capacity.

The model selection approach employed in the present study revealed that juvenile Chinook biomass also influenced habitat selection by redband trout (Table 4.2). The effect of Chinook on redband trout was in the direction expected, but probably for different reasons than posed by Pimm et al. (1980), who attributed the positive slope of the dominants' isoleg to the diminished quality of 'poor' habitat due to high densities of subordinate species excluded to poor habitats. In the present experiment, food treatments did not induce juvenile Chinook salmon to migrate among habitats, and therefore the positive-sloping dominant isoleg could not be a function of decreased profitability in 'poor' patches due to heterospecifics. Rather, I attribute this pattern to one of two causes.

First, redband trout response to feeding was potentially more pronounced in larger, deeper pools (with subsequently slower water velocities) which juvenile Chinook are known to prefer (Everest and Chapman 1972), and it therefore may have been easier for redband trout to detect and/or capture prey in the slower water velocities typically associated with these types of pools. However, my post-hoc analysis that included pool depth and other refuge characteristics that juvenile Chinook salmon are known to prefer did not improve upon the original models describing habitat selection as a function of the fish assemblage. Also, Gowan (2007) demonstrated that closely-related *O. clarki* use water velocity as a positive cue in recognizing quality foraging locations, a finding that seems to rule out this first explanation. Additionally, pool depths were not markedly different between pools in Black Canyon with juvenile Chinook salmon present and absent—with average maximum thalweg depths (± standard deviation) of 0.65 m (± 0.14) in pools where Chinook were present, versus 0.58 m (± 0.09) where they were absent. A second explanation for the heightened response of redband trout to feeding treatment with increasing Chinook biomass was that redband trout were attracted to sites where Chinook were vigorously feeding on krill, via attraction of heightened activity or perhaps pheromones. Salmonids have been shown to use foraging activity of conspecifics as a cue to monitor patch quality (Gowan 2007), a phenomenon also demonstrated in guppies (Reader et al. 2003) and a diversity of other animals (Parish 1999), so it does not seem unreasonable that cues from congeneric heterospecifics could provide similar cues about patch quality. While ecologists typically study negative interactions such as competition, there is rapidly advancing evidence that many organisms, including fish, use social information as a cue for habitat quality (Danchin et al. 2004). A third potential mechanism is one of the 'behavioral competitive refuge' potentially afforded to smaller redband trout in groups of Chinook. Tinus and Reeves (2001) demonstrated that smaller juvenile steelhead *O. mykiss* shoal among redside shiners *R. balteatus* to avoid negative competitor interactions between larger conspecifics, and this behavior could potentially extend to other species as well. My observations indicated that indeed, smaller redband trout of similar size classes occupied similar places in the pool as juvenile Chinook—in the deeper, scoured areas near the longitudinal center of the pool—whereas larger redband trout occupied foraging positions in shallower water near the head of the pool.

The additional finding that larger fish contribute most to changes in biomass in enriched sites has direct management implications for size-structured fish populations—such as those of the South Fork John Day (Madriñán 2008)—because stream reaches inhabited by larger fish may be less likely to respond to restoration in terms of fish production. The greater biomass of large fish, even if only moderate in abundance—more profoundly imposes a territorial limit on the amount of production that can be expected. This finding also emphasizes that biomass is a key parameter to measure changes or status of fish populations: if fish abundance had been measured alone, I would have been far less able to detect the changes in habitat selection.

Because juvenile Chinook did not respond to treatments or competitor densities in any significant manner, I was not able to explain how this species selects habitat. In the nearby Middle Fork John Day and Wenaha Rivers, mechanisms driving differential distributions of the fish community (including redband trout and Chinook) could only be inferred from observational data and were therefore left unexplained (Torgersen et al. 2006). Because the mechanism of habitat selection for juvenile Chinook salmon remains ambiguous in the present study as well, I consider this a logical next step for future research. Based on the ambiguous findings of the present and previous studies, it would be interesting to test whether these two species are involved in a shared or distinct niche community organization (Rosenzweig 1985), where the two species prefer similar or disparate habitat, respectively; or perhaps whether they exist in a centrifugal community organization (Rosenzweig and Abramsky 1986), where species have shared primary habitat preference but distinct secondary preferences. An approach that examines habitat selection earlier in the season (i.e., late June) when juvenile Chinook begin migrating into tributaries for rearing and/or in places such as the North Fork John Day where the asymmetry between the two species' distributions is reversed (thereby completing a full response surface grid), would be ideal approaches.

Effects of fish density on foraging and aggressive behavior

The present study improves upon most previous isoleg research in that I not only account for the effect of competitor densities on habitat selection, but also on behavior (i.e., foraging and aggression) in a natural field setting. Two notable exceptions are the early field study by Pimm et al. (1985), who documented decreased foraging rates of subordinate hummingbirds *Archilochus alexandri* and *Eugenes fulgens* as a response to higher densities of dominants *Lampornis clemenciae*, and another field study by Abramsky et al. (1990), who documented similar patterns of activity density in two species of gerbils *Gerbillus* spp. Additionally, the study was conducted in a natural field setting—using remotely-operated underwater video cameras—where I attempted to minimize disturbance by the observers on the organisms under study. Early research on the bioenergetics and behavior of rainbow trout *O. mykiss* indicated that feeding rates did not necessarily decrease with higher competitor densities, although fish at higher densities experienced decreased efficiency of converting food resources into growth (Li 1973). In contrast, the present study demonstrated that foraging rates of redband trout decreased with increasing competitors, especially conspecifics, a finding corroborated in a study on juvenile sea-trout *Salmo trutta* in the wild (Elliot 2001). In addition to the foraging rate response, previous theoretical and empirical work suggests that niche breadth should increase with increasing pressure from competition (Venne and Magnan 1995; Doebeli and Diekmann 2000; McLaughlin 2001; Svänback and Eklöv 2003). Although I did not have the statistical power to test this hypothesis, a cursory look seemed to corroborate the theory, with more dispersed behavioral scores at higher competitor densities.

These relationships may not necessarily be linear as the models in my study assume. Pimm et al. (1985) found that feeding activity of subordinate hummingbirds decreased in a significantly convex manner with increasing density of dominants. And although I did not design the experiment in a manner amenable to testing for significant curvature in the models (due to lack of power), each of the models describing redband trout behavior as a function of fish density appears to be convex, with the most apparent example being the relationship between redband trout territory maintenance as a function

of conspecifics (Fig 4.8c). Territory maintenance (lack of foraging and interspecific aggression) in redband trout appears to increase quickly in the presence of a few conspecifics, but as competitors are added the rate of increase slows. This pattern (if real) may represent the need for fish to maintain some level of foraging even in highly competitive and therefore stressful conditions, in addition to the need to continually initiate aggression at even low levels in order to maintain territories.

Aggression, often linked to the establishment of territories or territory defense, is known to change as a function of many factors, including competitor densities (Grant and Godin 1997). In the present study, redband trout aggression typically decreased with higher competitor densities. Higher densities of both conspecifics and Chinook were associated with decreasing aggressive surface foraging in redband trout, a behavior primarily described by high rates of surface feeding and intraspecific aggression. However, visual inspection of the scatterplot of aggressive surface foraging by redband trout as a function of Chinook biomass reveals that the relationship is perhaps driven by two data points having very high values for both Chinook biomass and the behavioral response (Fig. 4.8b), so even though the full model (the one including all parameters) appears valid as assessed by its explanatory power, statistical significance, and by visual examination of a plot of residuals against fits, the causal link is perhaps tenuous. A cleaner relationship was noted in the higher densities of conspecifics that were associated with increasing territory maintenance by redband trout (Fig. 4.8c), a behavior primarily described by low rates of water column feeding and interspecific aggression. In salmonids, territory size has been shown to decrease with increasing competitor densities (Keeley 2000). In a study of brown trout *Salmo trutta* stocked in natural streams, Brännäs et al. 2004) found that aggression was a more important strategy at low and intermediate fish densities but became increasingly infrequent with higher densities.

Several early laboratory studies of fish aggression also report this pattern of increasing aggression to certain threshold levels, then decreasing with higher densities (as cited in Li and Brocksen 1977), findings that are explained via submissive fish burying themselves in the substrate to avoid harmful interactions at high competitor densities. One of the above authors suggests that in a natural stream, these submissive individuals

would have migrated to other, less-imposing habitat: “These individuals could not cope with the stress; in an open system, such as a natural stream, these individuals would have been displaced downstream” (Li 1973, p. 77). Likewise, my results suggest that in a natural stream, redband trout switch behavioral tactics at much higher competitor density values than for habitat selection. Fish in this system are apparently not willing to withstand suboptimal foraging and aggressive situations, or for some other reason are displaced from enriched patches. So although fish may not be ‘perfect foragers’ that can always readily and accurately assess nearby habitat quality (Gowan 2007), it appears that they may have at least enough knowledge of nearby habitats to make decisions regarding which habitat to select that will likely maximize their fitness.

Another pattern I noted but was not able to test for (due to lack of power), was the apparent trend of decreased aggression in pools of food supplementation (Fig. 4.8). In all cases, redband trout in sites of food addition appeared to be less aggressive—in context of competitor densities—than their counterparts in pools upstream and downstream of the feeder. This potential pattern is in direct opposition to the statistically significant pattern of higher aggression in sites of food supplementation from the experiment in 2006, where I fed fish in pulses at dawn and dusk rather than throughout the day as in the present study. Empirical evidence and ecological theory suggest that shorter and more intense resource pulses will have more dramatic effects than longer and more diffuse pulses (Normile 1998; Holt 2008), especially in aquatic ecosystems where effects may transmit more rapidly than in terrestrial systems (Nowlin et al. 2008). And specifically for fish, competitive interactions are less likely with an even food distribution (Milinski and Parker 1991; Bryant and Grant 1995) such as in the feeding regime employed in the present study. During the 2007 experiment, I noted what appeared to be an outbreak of tent caterpillars (fall webworm, *Hyphantria* sp.) in riparian red alder *Alnus rubra*. Much of the alder leaves had become defoliated, and because the caterpillars’ tents were often hanging over the stream, it was possible that caterpillars were also supplementing food resources for fish in this system, but in a pulsed fashion due to the infrequent nature of their input. Repeated trials of tossing caterpillars into the stream always resulted in redband trout immediately coming to the surface and consuming them. And in two out of

the ten drift samples I collected through the course of the experiment, the caterpillars were present and composed 1.21% and 0.44% of the total invertebrate biomass of their respective samples. This small bit of natural history has relevance to current paradigms in ecology regarding resources pulses, but also for redband trout in the South Fork John Day if indeed the manner in which food comes to fish affects their behavior.

These trends in the data that point towards potentially interesting patterns that I can only speculate about now—such as nonlinear responses of behavior to competitor densities, increasing niche breadth with more intense competition, and reduced aggression in pools where food was distributed evenly over a long time period—demonstrate the powerful utility of isoleg theory and the use of response surface designs in determining intra- and interspecific interactions. Although my sample size was adequate for testing *a priori* hypotheses about the effect of competitors on habitat selection and behavior, future experiments with larger sample sizes will likely yield even more interesting results. Young (2004) employed a response surface design and large sample size of 115 density combinations and various sizes of coho and redband trout to determine the relationship among asymmetric competition, habitat selection, and niche overlap; but the experiments were conducted in flow tanks and so extrapolating findings to natural systems is tenuous at best. Combining these types of large sample sizes with experiments in natural streams where interpretations are likely to afford greater realism than artificial conditions will likely provide information that is more useful to conservation (Peters 1991).

By conducting post-hoc analyses in an effort to improve the explanatory power of models describing redband trout habitat selection, I found that the inclusion of habitat variables did not improve the original models based on the fish assemblage alone. This implies that biotic interactions were more important in determining how redband trout selected habitat, at least at the spatial scale of observation in this study. However, a post-hoc analysis of habitat variables *did* appear to affect foraging and aggressive behavior, as determined via their substantial improvement of models upon their inclusion as candidate variables. Most notably, aggressive surface foraging in redband trout—a behavior described as high surface feeding and aggression rates—increased with pool volume

while decreasing with intra- and interspecific fish densities. This provided at least circumstantial evidence that space is a limiting resource for foraging in this system, with the mechanism for limitation being behaviorally mediated. Larger pool volumes appeared to ameliorate the effects of increased competition via permitting higher feeding rates. Another significant improvement on the behavioral models came in the form of including undercut banks in explaining territory defense—a behavior described by low rates of foraging and moderate levels of aggression. The relationship was inverse, so with more undercut banks available, redband trout tended to forage more frequently, compete with conspecifics less frequently, and engage heterospecifics (i.e., juvenile Chinook salmon) in interspecific bouts more often. A possible mechanism for this finding is that undercut banks contributed to habitat complexity and hence a higher number of available microhabitats in the pools, which are known to increase foraging opportunities for salmonids in a given amount of space (Gowan 2007). The increased number of microhabitats would then serve to minimize competitive interactions among conspecifics (Keenlyside 1979), and perhaps stimulate territorial behavior against heterospecific juvenile Chinook salmon who are expected to seek slower water velocities at the microhabitat scale (Everest and Chapman 1972).

Comment on the potential interactive segregation of redband trout and Chinook salmon

Nilsson (1967) lists the characteristics of interactive selection—the state of coexistence where innate use of the environment has not yet become evolutionarily fixed among species—as follows: (1) occurs most severely among closely-related species, (2) species are segregated into different food niches or habitats although coexistence may be apparent, (3) potential displacement of exclusion of one or more species, (4) segregation is behaviorally mediated via attraction or avoidance stimuli, (5) degree of competition varies with food supply—with less intense competition in the presence of superabundant resources, and (6) the niche space of a given species is reduced in the presence of another species. Although salmonids in the Pacific Northwest are commonly perceived as having coexisted for such long periods of time that they have evolved different, innate means of

exploiting the environment, the findings from the present research, concurrent studies in the watershed, and a reexamination of evidence from past studies may serve to temper this commonly-held wisdom. In other words, perhaps the nature of interaction between salmonids in this watershed can be placed a bit farther towards the interactive versus the selective segregation end of the spectrum.

To address Nilsson's (1967) criteria for interactive selection point-by-point: (1) *O. mykiss* and *O. tshawytscha* are closely-related genera of Pacific salmonid (Benhke 2002); (2) although the two salmonids often co-occur at the reach scale, distinct habitat preferences have been demonstrated (Everest and Chapman 1972); (3) *O. tshawytscha* in the present study did not move into (i.e., were potentially excluded from) habitats with superabundant food, perhaps because of the ubiquitous presence of *O. mykiss* in all experimental sites; (4) a behavioral effect was observed in the present study as a response to heterospecifics fish density—with *O. mykiss* surface foraging rates and aggression rates decreasing with higher *O. tshawytscha* densities, and *O. mykiss* may have been attracted to increased *O. tshawytscha* feeding rates (5) aggression among/between salmonids appeared to decrease with food addition in the present study; and (6) as stated earlier, *O. tshawytscha* may have been prevented from migrating into food-enriched sites by *O. mykiss*, though this latter finding is ambiguous at the present time. Although I do not have conclusive evidence on all of these points (with evidence for criteria 5 and 6 especially needing further corroboration), these findings and the finding of others point to the possibility that the fundamental niche space *O. mykiss* and *O. tshawytscha* overlaps more than we have presumed in the past.

Implications for theory and management

Several approaches have been applied in an attempt to infer competition among stream fishes from distributional data alone, such as the "regression method," where density of a species is regressed against that of its potential competitors (e.g., Townsend and Crowl 1991; Fausch et al. 1994) or the "isodar method," (Morris 1988) which evaluates the

degree of competition in multiple habitat types, also adopting logic of the ideal free distribution (see Morita et al. 2004 for recent fisheries applications of both strategies). Although these methods can be useful in data-limited situations and are a good starting point, findings are admittedly subject to multiple interpretations—neither method can distinguish between distinct habitat preference and biotic drivers of habitat selection because of the observational nature of the data collected. In contrast, experimental manipulations such as those in the present study can lend greater confidence to interpretations of field data, and arrive more closely at causal mechanisms of species distributions.

Findings from the present study demonstrate that it is possible to make accurate *a priori* predictions about the outcomes of competitive interactions, at least for the short-term, even though some authors maintain that natural systems are too complicated to do so (e.g., Sloman and Armstrong 2002). One reason why behaviors associated with competition may have been difficult to predict in previous studies is that single behaviors are often evaluated using univariate statistical approaches, whereas behavioral ecologists now understand that organisms balance the relative costs and benefits of different behaviors (e.g., foraging, predator avoidance, shoaling, and territory defense) based on the net increase in fitness among the different strategies (e.g., Boinski 2005; Johnson and Sih 2007). In the present study, I adopted a multivariate perspective of fish behavior that accounted for multiple behaviors employed by redband trout in this system, thereby accounting for a range of strategies and arriving at a more nuanced understanding of the organism. A nuanced examination of the ecological context of relative rates of different behaviors among foraging organisms is likely to yield interesting findings regarding the adaptive value of those behaviors, one of the ultimate goals of behavioral ecology as a discipline (Parker 2006).

Furthermore, mathematical theory is infrequently tested in field settings (Sagoff 2003), which threatens to turn ecology into a discipline that has little concern whether its findings correspond to reality (Porter 1995). Continuing the tradition of framing questions of ecological theory in the field (as per Power 1984; Pimm et al. 1985; Nakano and Murakami 2001; Haugen et al. 2006; as selective examples) will likely keep ecology

grounded as a discipline that can contribute to conservation and management, and findings from field studies can then be re-incorporated into mathematical models of competitive interactions, which are typically short on empirical data (Abrams 2001). Specifically, the findings from this study have important implications when considering restoration efforts designed to increase salmonid carrying capacity or productivity (Mobrand et al. 1997)—the results suggest that there is a measurable limit to the density of organisms that can occupy habitats in the late-summer period in the South Fork John Day watershed, and that traditional habitat selection models should account for potential biotic interactions when assigning "habitat preferences" to species.

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Tables

Table 4.1. Pearson correlations between multivariate axes (nonmetric multidimensional scaling, NMS) and behavioral variables measured in summer of 2005. Pearson's $r \geq 0.20$ were used in interpreting ecological significance of axes and are indicated with an asterisk.

		Axis 1 "Low strata foraging"	Axis 2 "Aggressive surface foraging"	Axis 3 "Territory maintenance"
Category	*Event*			
Foraging	Water column feeding	* 0.36	* -0.22	* -0.39
	Surface feeding	0.14	* 0.59	-0.04
	Benthic feeding	* 0.65	0.10	-0.05
	Reject food item	* 0.37	* 0.34	* -0.23
Aggression	Intraspecific	* 0.21	* 0.83	* 0.22
	Interspecific (aggressor)	* -0.34	* 0.45	* -0.58
	Interspecific (recipient)	0.02	* 0.41	-0.19

Table 4.2. Results of AIC models for habitat selection for (a) redband trout (RST) and (b) juvenile Chinook salmon (CHS).

a. Habitat selection by redband trout *O. mykiss* (RST).

K	R-Square	Variables	AIC_c	Δ_i	w_i
2	0.67	RST, CHS	124.43	0.00	0.61
3	0.70	RST, CHS, RST*CHS	125.31	0.88	0.39
1	0.34	RST	136.09	11.66	0.00
1	0.27	CHS	138.02	13.59	0.00

b. Habitat selection by juvenile Chinook salmon *O. tshawytscha* (CHS).

K	R-Square	Variables	AICc	Δi	w_i
1	0.14	CHS	85.20	0.00	0.56
1	0.03	RST	86.67	1.47	0.27
2	0.15	RST, CHS	87.91	2.71	0.15
3	0.16	RST, CHS, RST*CHS	91.46	6.26	0.02

Table 4.3. AIC results for redband trout *O. mykiss* behavior as a function of conspecific (RST) and juvenile Chinook salmon *O. tshawytscha* (CHS) biomass: (a) low strata foraging did not yield a good model (best p = 0.15), while (b) aggressive surface foraging and (c) territory maintenance were significantly related to fish biomass (p > 0.05). Models are ranked according to AIC_c value, with lower values representing a more parsimonious model. See text for model parameters.

a. Low strata foraging (see axis 1, Table 4.1).

K	R-Square	Variables	AIC_c	Δ_i	w_i
1	0.11	CHS	-39.31	0.00	0.55
1	0.04	RST	-37.68	1.62	0.24
2	0.11	RST, CHS	-36.89	2.41	0.16
3	0.12	RST, CHS, RST*CHS	-34.32	4.99	0.05

b. Aggressive surface foraging (see axis 2, Table 4.1).

K	R-Square	Variables	AIC_c	Δ_i	w_i
3	0.43	RST, CHS, RST*CHS	-29.12	0.00	0.63
1	0.15	RST	-26.38	2.74	0.16
1	0.13	CHS	-25.87	3.25	0.12
2	0.20	RST, CHS	-25.07	4.05	0.08

c. Territory maintenance (see axis 3, Table 4.1).

K	R-Square	Variables	AIC_c	Δ_i	w_i
1	0.41	RST	-41.03	0.00	0.65
2	0.43	RST, CHS	-39.07	1.96	0.24
3	0.46	RST, CHS, RST*CHS	-37.44	3.59	0.11
1	0.02	CHS	-30.88	10.15	0.00

Figures

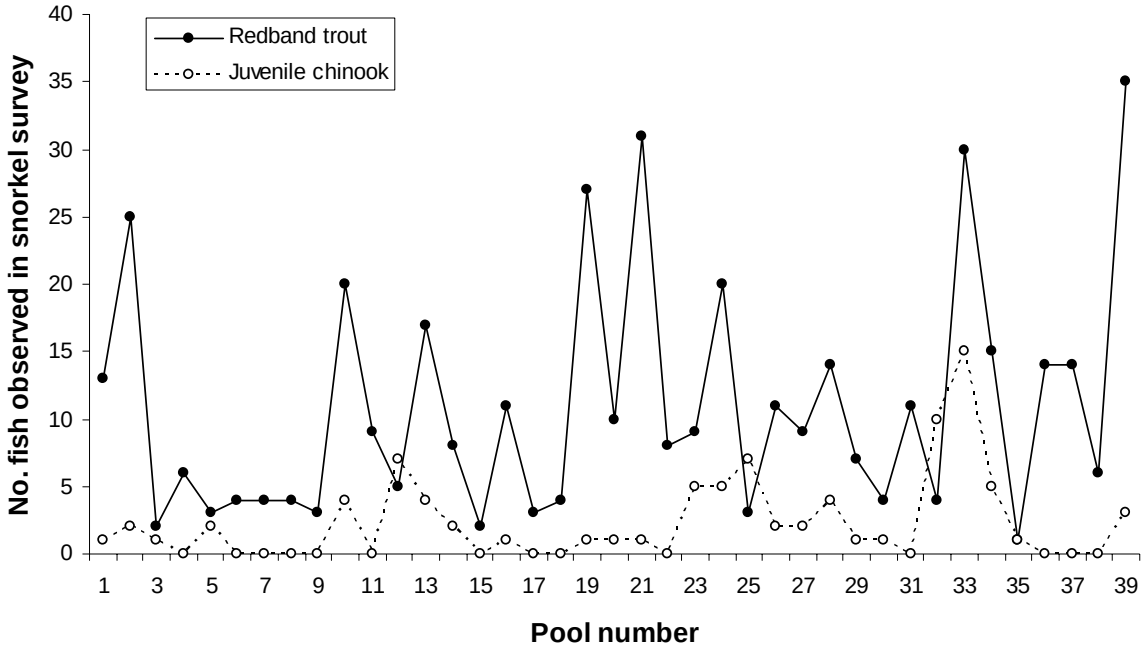

Figure 4.1. Distribution of redband trout *Oncorhynchus mykiss* and juvenile Chinook salmon *O. tshawytscha* in the lowest geomorphic reach of Black Canyon Creek, from a July 2005 snorkel survey. Pool 1 (left) is nearest the mouth at the confluence of the South Fork John Day; pool 39 is the upstream most pool in this river reach.

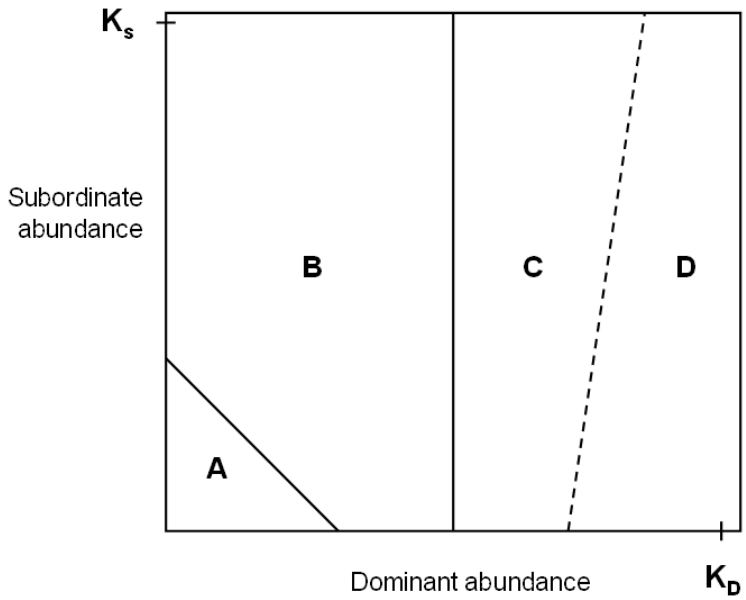

Figure 4.2. A graphical representation of isoleg theory. Isolegs for subordinate (solid lines) and dominant species (dashed line) represent transition points where fish move from good to poor quality habitat patches. K_s and K_d represent carrying capacity for the subordinate species and dominant species, respectively. See text for further details. Adapted from Pimm et al. (1985).

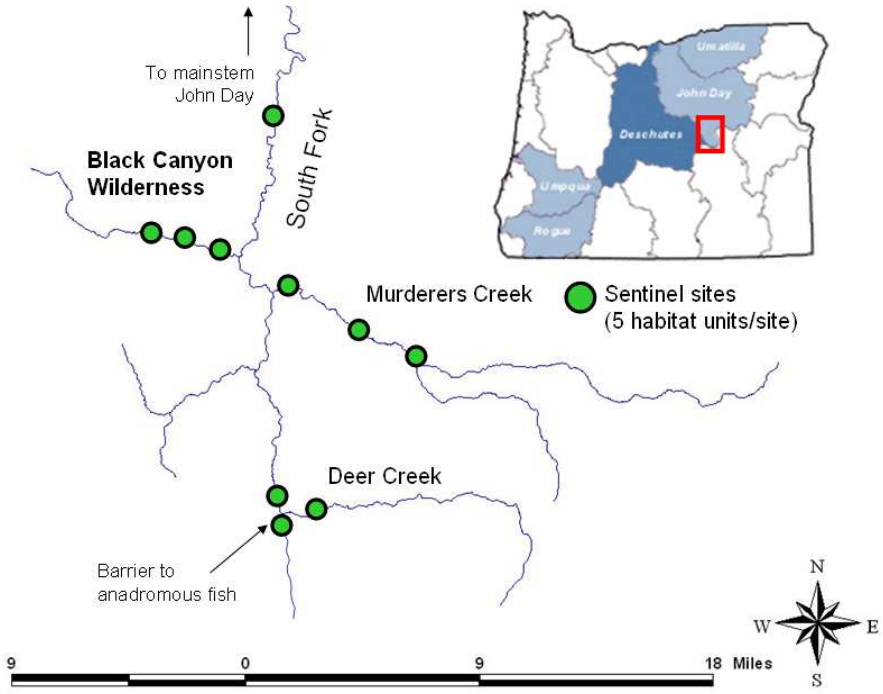

Figure 4.3. The South Fork John Day River and its major tributaries, eastern Oregon. Shades circles are sites of fish behavior monitoring in 2005.

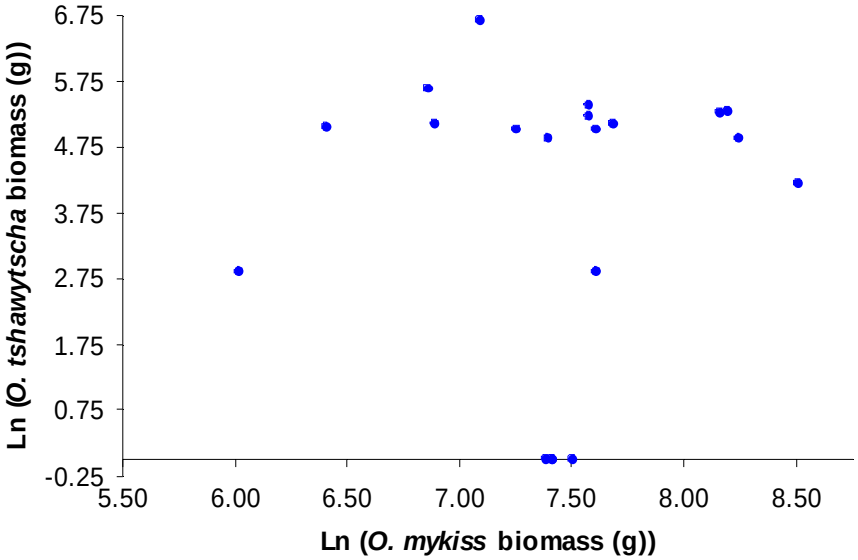

Figure 4.4. Final response surface of fish biomass values. Values are natural log-transformed fish biomass (g) from all three pools in each experimental site. Note that three points are at y = 0, sites where Chinook were not present.

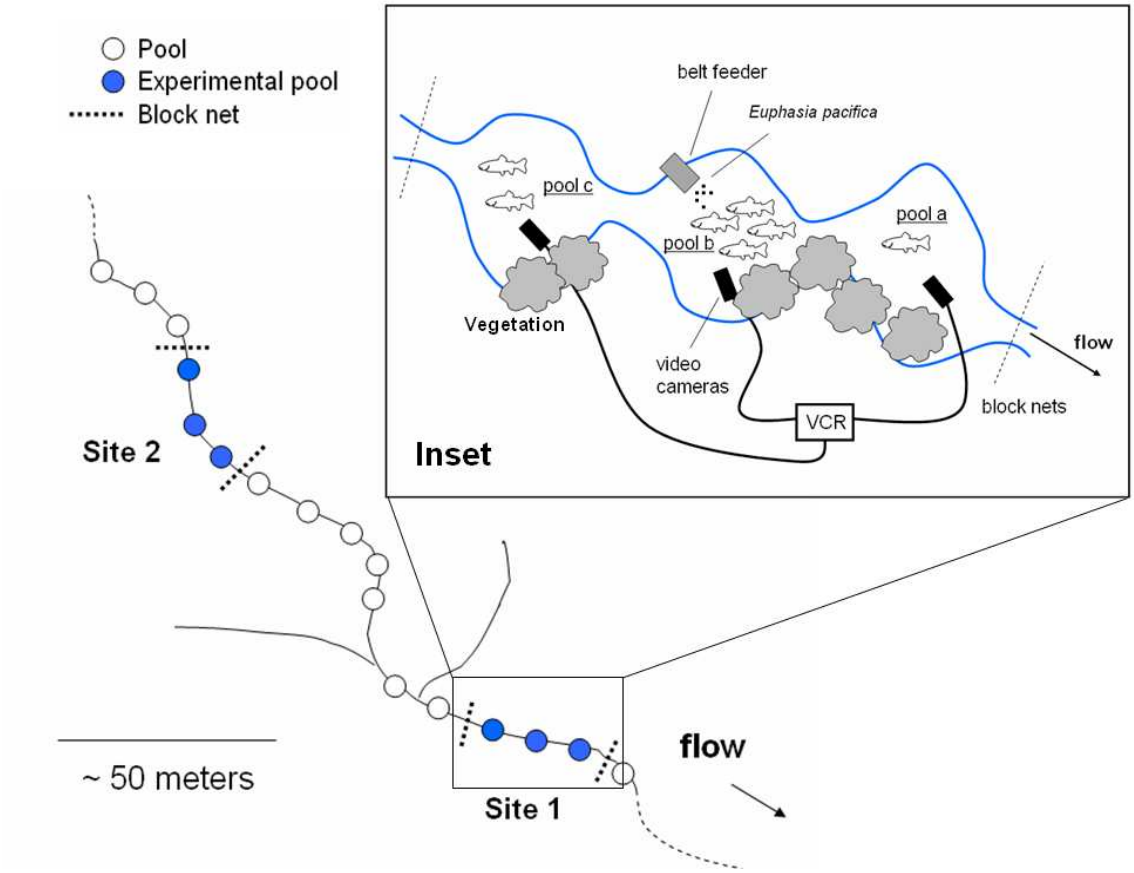

Figure 4.5. Conceptual diagram of isoleg study sites. Each experimental site consisted of three pools (shaded circles) enclosed temporarily within block nets (dashed lines). The inset diagrams position of belt feeder, which delivered krill in the center pools at three percent fish biomass for the entire, three-pool sequence for a period of two to four days. Fish density and biomass was assessed via snorkeling before and after feeding, and fish interactions were videotaped through the course of the experiments.

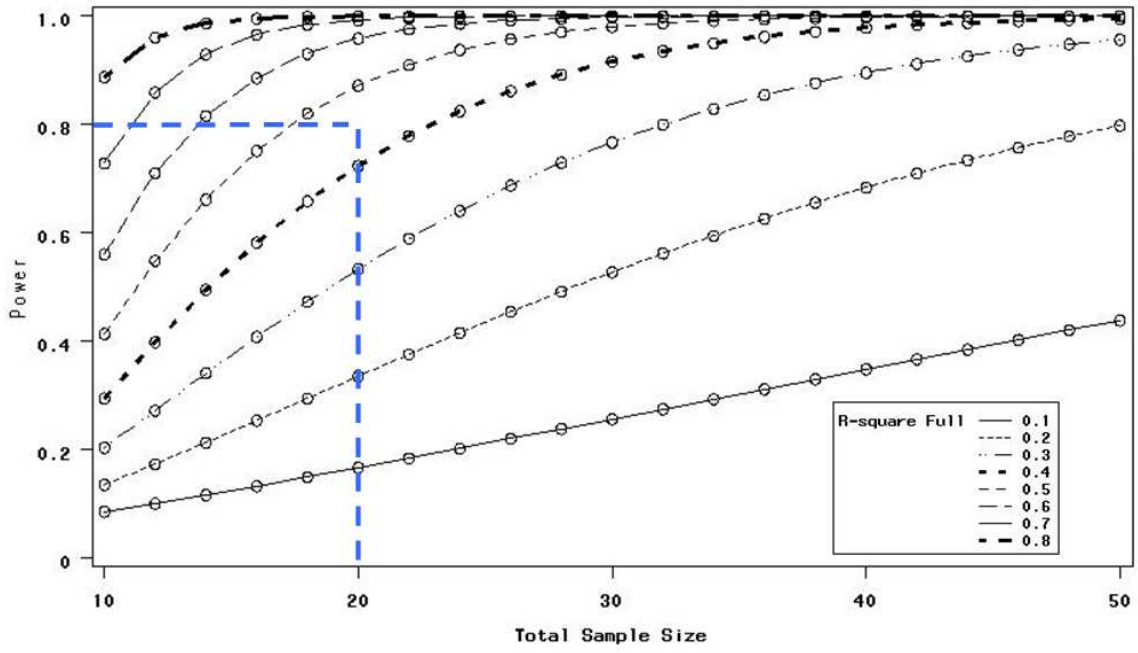

Figure 4.6. Power analysis for multiple regression and three independent variables. Dashed lines represent relationship between desired power level (0.80) and required sample size (n = 20) based on expected R^2 between 0.40 and 0.50 (determined from a pilot project).

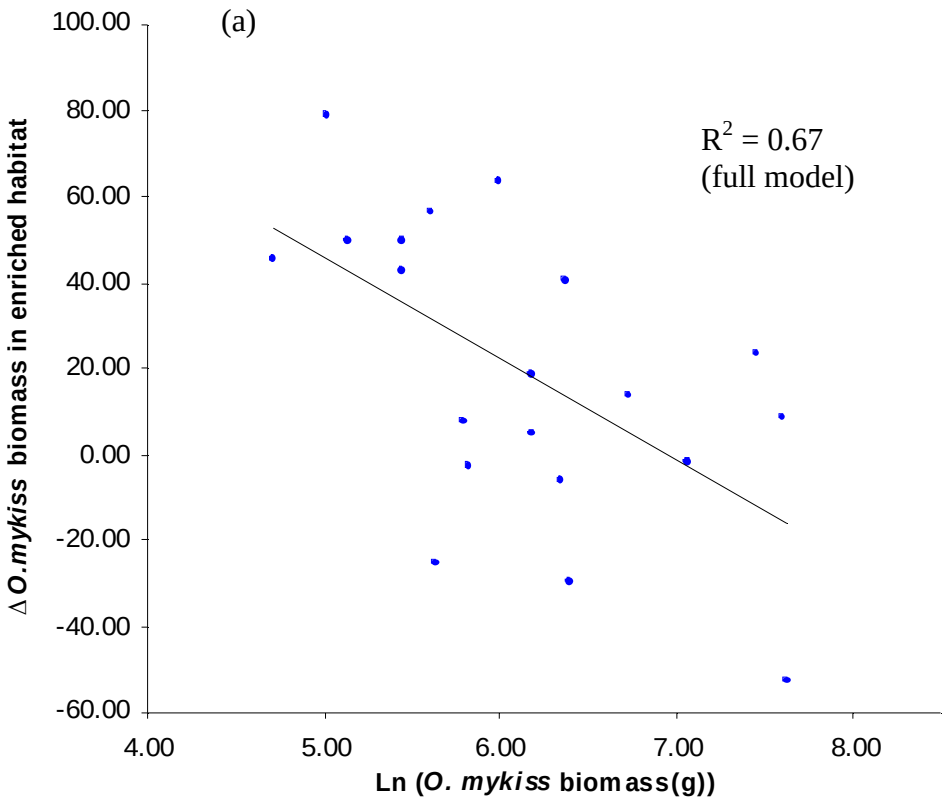

Figure 4.7. (a) Habitat selection by redband trout *O. mykiss* as a function of intraspecific competitor biomass (see Table 4.2a). Selection of the enriched patch by redband trout decreases with increasing conspecifics. (b) Habitat selection by redband trout *O. mykiss* as a function of juvenile Chinook salmon *O. tshawytscha* biomass (see Table 4.2a for model parameters and statistics). Selection of the enriched patch by redband trout increases with increasing Chinook biomass. The full model explained a large proportion of the variance ($R^2 = 0.67$) and was highly significant ($p < 0.0001$).

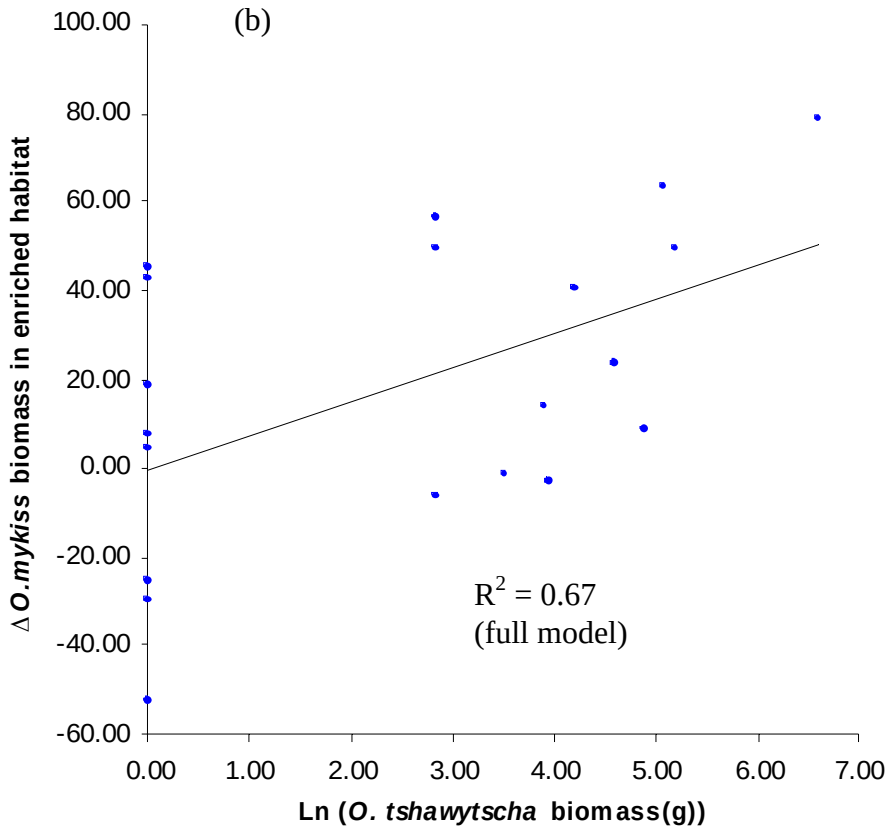

Figure 4.7. Continued.

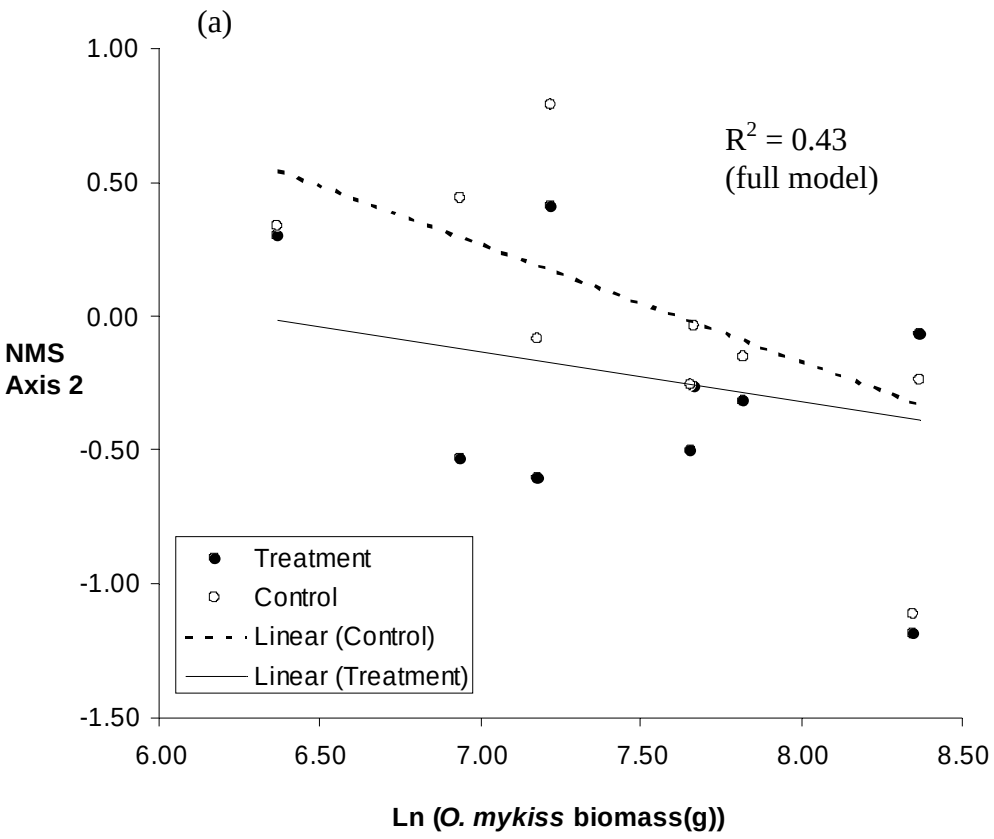

Figure 4.8. Isoclines of redband trout *O. mykiss* behavioral axes (Table 4.1) as a function of fish biomass in experimental sites. Scatterplots are (a) axis 2 (aggressive surface foraging) as a function of conspecific biomass, (b) axis 2 (aggressive surface foraging) as a function of juvenile Chinook *O. tshawytscha* biomass, and (c) axis 3 (territory maintenance) as a function of conspecific biomass. Data points are delineated according to whether the particular video came from a pool with food supplementation (treatment) or an upstream or downstream pool (control). Trend lines are fitted to treatment and control sites for ease of interpretation only, and do not represent model regressions. Both models were significant at the $\alpha = 0.05$ level. The model describing NMS axis 2 explained less than half of the variance ($R^2 = 0.43$), and the model describing NMS axis 3 explained a similar proportion of variance ($R^2 = 0.41$).

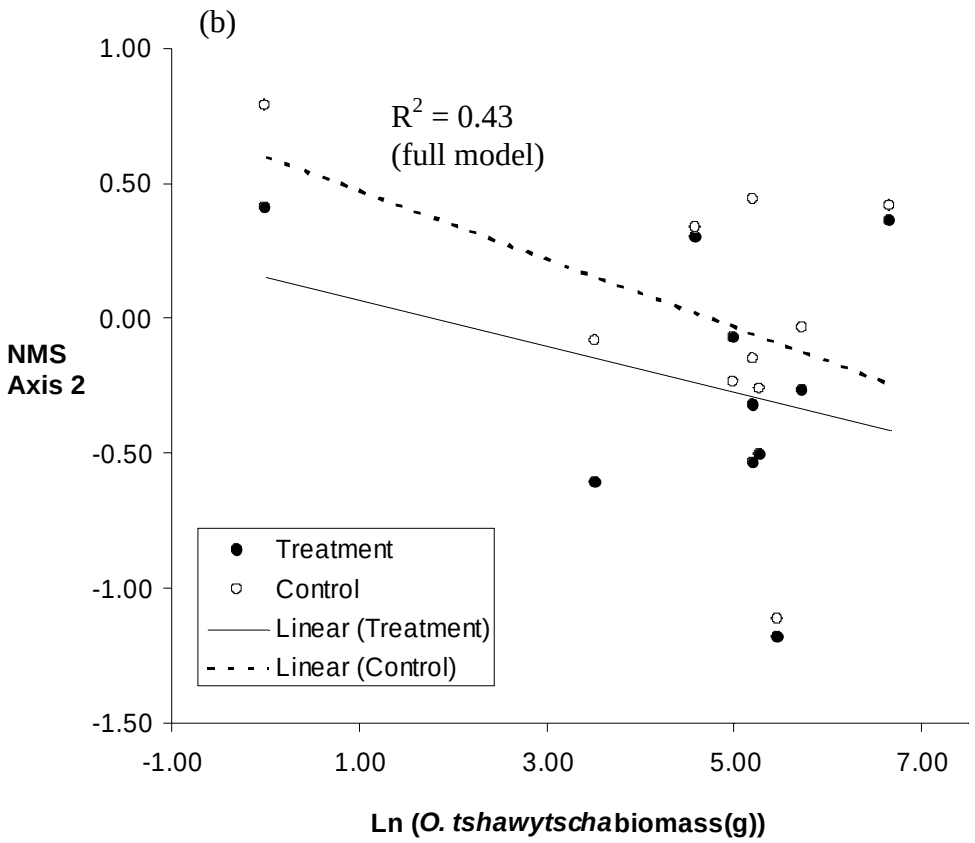

Figure 4.8. Continued.

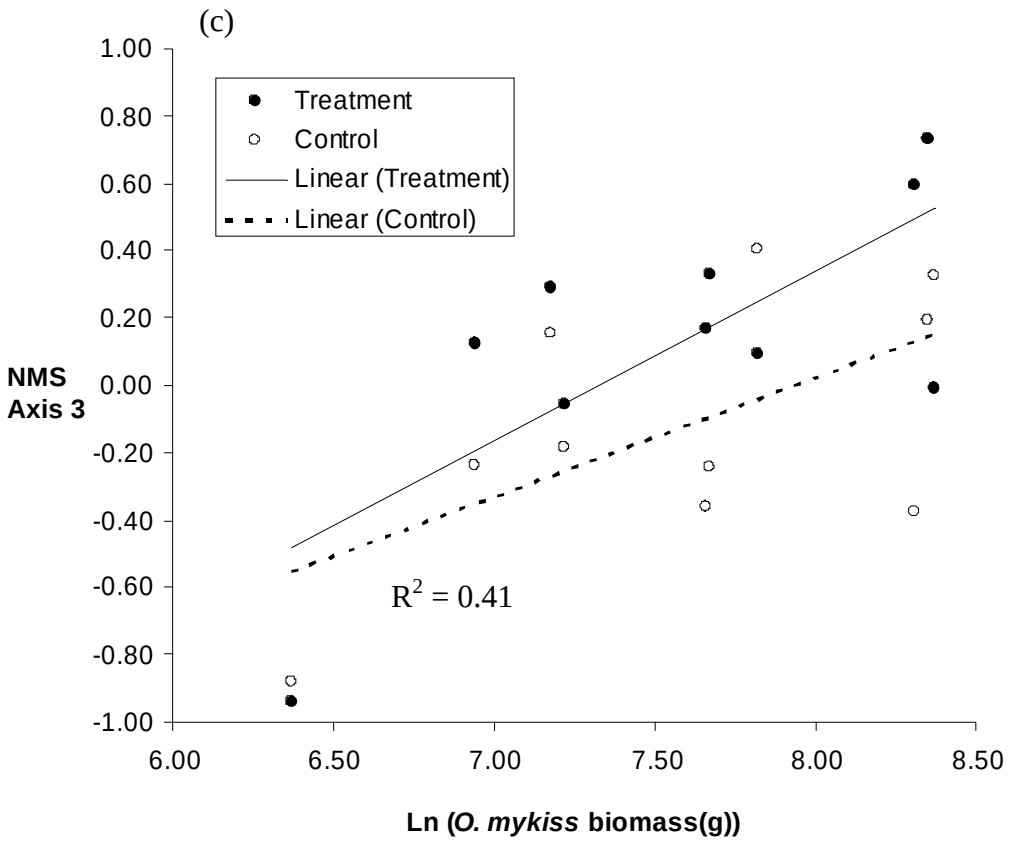

Figure 4.8. Continued.

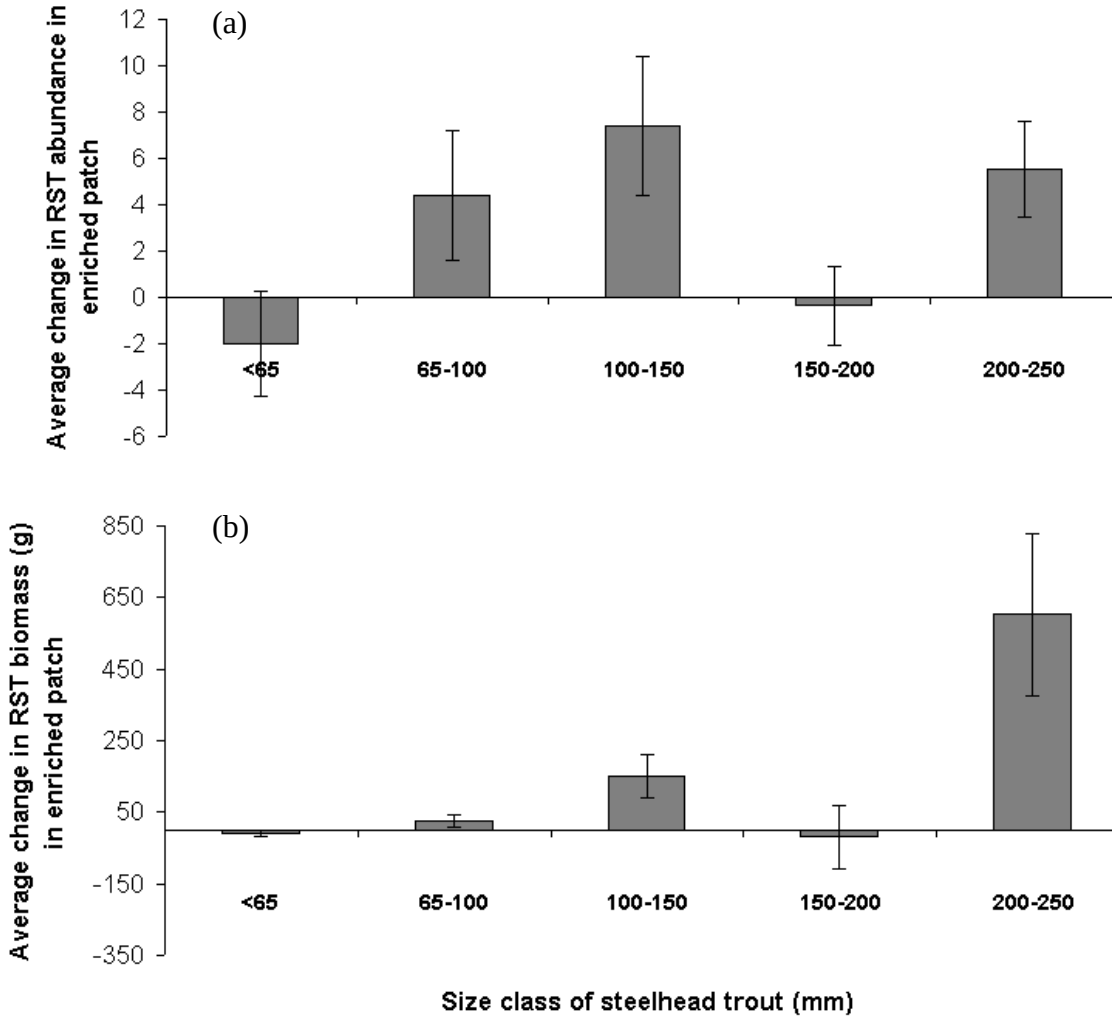

Figure 4.9. Average change in redband trout (RST) (a) abundance and (b) biomass in enriched patches, based on estimates from snorkel surveys adjusted for capture efficiencies of different size classes of fish. Small redband trout (< 65 mm) tended to decrease in numbers and biomass, while larger fish tended to increase in numbers and biomass with the exception of fish in the 150-200 mm size category. The largest size category of fish (200-250 mm) contributed most to the increasing biomass in enriched sites. Error bars are ± one standard error.

Chapter 5

GENERAL CONCLUSIONS

> Stories are a composite of details that hold together to form a picture. Part of what drives us as biologists is a quest for details and specifics, but we should remember to pay attention to how these tell a story
>
> Schroeder 2007, p. ix

My overall goal was to incorporate ideas from the disparate disciplines of landscape ecology and behavioral ecology—taking a whole-assemblage versus single-species approach—into a research program intended to understand patterns of redband trout distribution in the South Fork John Day watershed. My epistemological approach involved starting with a description of patterns in the fish assemblage across the entire watershed (Chapter 2), which led specific hypotheses about the effects of food availability on fish growth and behavior (Chapter 3) and the effects of competitor densities on fish habitat selection (Chapter 4) at the reach and habitat unit scales. Specifically, my objectives were to (1) describe patterns of biological traits of fish and patterns of habitat characteristics throughout the watershed; (2) determine which traits are related to which habitat characteristics at multiple scales; (3) generate and test hypotheses about modes of species coexistence between disparate trait guilds; (4) describe redband trout foraging and aggressive behaviors in context their environment; (5) examine the effect of food addition on redband trout growth, foraging and aggressive behavior, and potentially movement; (6) test the prediction that intra- and interspecific competitor densities will affect salmonid habitat selection of enriched patches; and (7) test the prediction that intra- and interspecific competitor densities will affect redband trout foraging and aggressive behavior. Additionally, the study was conducted in a natural field setting—using remotely-operated underwater video cameras—where I attempted to minimize disturbance by the observers on the organisms under study.

In this concluding section, I will briefly summarize my findings according to each of these objectives, and follow with a discussion about the significance of these results for relevant principles of ecological restoration. In brief, the principles of restoration that the findings from this study support are to (a) recognize stream habitats as dynamic in space and time, (b) work at multiple spatial scales, (c) incorporate knowledge of animal behavior, (d) consider multiple species, and (e) ask the question, 'What are we restoring?'

Summary of findings

1) Patterns of biological traits of fish habitat characteristics (Chapter 2)

Multivariate analyses of biological traits of the fish assemblage and habitat characteristics demonstrated that these features could be described according to current theories in stream ecology stemming from the river continuum concept (Vannote et al. 1980). Traits parsed out into two prevalent guilds: the first representing small, coolwater, broadcast-spawner invertivores tolerant to degraded water quality (COOLWATER); the second representing large, coldwater, simple-nesters sensitive to water quality (COLDWATER). Habitat characteristics parsed out into three types according to Montgomery and Buffington's (1998) description of reach-level channel types: the first representing large, warm water pools with abundant large woody debris and embedded substrates (RESPONSE); the second representing deep pools with undercut banks and mobile substrates (TRANSPORT); and the third representing small, coldwater pools with abundant large woody debris (SOURCE). These trait guilds and habitat characteristics were not necessarily distributed heterogeneously on a downstream-upstream elevation gradient as expected under the river continuum concept, but rather heterogeneously throughout the watershed depending on individual tributaries.

2) Trait-habitat relationships at multiple scales (Chapter 2)

Traits and habitat were associated disparately across three spatial scales, with COOLWATER and COLDWATER traits negatively and positively associated with SOURCE habitats, respectively, at the watershed scale as expected. However, these relationships changed with decreasing spatial scale. At the tributary scale, the trait-habitat relationships in most parts of the watershed were similar to those at the watershed scale except in Black Canyon, a spring-fed stream and designated wilderness area where both trait guilds were negatively associated with SOURCE habitats, probably because of an over-abundance of that habitat type in the tributary. Reach-scale findings revealed even more nuanced patterns of trait-habitat relationships, indicating the importance of conducting studies at multiple scales.

3) Hypotheses of species coexistence between trait guilds (Chapter 2)

Trait-habitat relationships at the reach scale could be classified in terms of prevailing theories of species coexistence (Tokeshi 1999; Sommer and Worm 2003): niche overlap, niche partitioning, or non-associative. Upon testing whether the distribution of habitat characteristics versus the distribution of fish traits were driving the nature of these relationships, I discovered that both were significantly correlated with mode of coexistence, but that traits had a stronger effect than did habitat. This suggested that biotic interactions (e.g., competition, predation, mutualism, etc.) were perhaps an important factor in structuring the distribution of the fish assemblage in this system. This was one possible interpretation about the nature of fish assemblage structure, meant to generate hypotheses to be tested in subsequent field manipulations.

4) Redband trout foraging and aggression in context of their environment (Chapter 3)

Multivariate patterns of redband trout foraging and aggression conformed to existing theories of foraging (stemming from Stephens and Krebs 1986). Three main modes of behavior were noted: 'Low strata foraging' was described by feeding in the water column and benthic zone and moderate interspecific aggressive bouts while avoiding initiation of interspecific aggression. 'Aggressive surface foraging' was described by frequent feeding on the stream surface and high rates of both intraspecific and interspecific aggression. 'Territory maintenance' was described by an absence of any kind of foraging (including rejecting food items), a moderate amount of intraspecific aggression, and low rates of interspecific aggression. Each type of behavior was significantly correlated with environmental conditions in the watershed. Two notable findings were that first, 'aggressive surface foraging'—a behavior associated with a higher expected energetic gain yet potentially more risky in terms of avian predators—occurred in habitats with abundant undercut banks that could be used as refuge, which ironically made the behavior less 'risky.' It was only by putting the behavior in context with the environment it occurred in that revealed the tension created by my naming of the NMS axis. Second, 'territory maintenance'—a behavior associated with little immediate energetic gain—occurred in smaller, embedded habitats lacking interstitial spaces that could be used as refuge, and also in colder habitats where energetic demands were likely to be lower.

5) Effect of food addition on salmonid growth, foraging, and aggression (Chapter 3)

Upon the addition of food at experimental sites in two streams, both redband trout and juvenile Chinook salmon grew at rates nearly an order of magnitude higher than background levels, demonstrating that food is a limiting factor for late-summer salmonid growth in this system. Using the previously-described multivariate framework of redband trout behavior, I found that food addition significantly altered foraging and aggression in a colder stream with lower discharge, but not in a relatively warmer stream with higher discharge. These disparate results were attributed to the relative energetic gain due to

behavioral shifts expected in each type of environment. In Deer Creek where behavior was affected by food addition, both foraging and aggression increased. An experiment was designed to evaluate whether food addition caused migration of salmonids among habitats, but inconclusive results catalyzed a subsequent study on the effects of competitor densities on habitat selection.

6) Effects of competitor densities on salmonid habitat selection (Chapter 4)

Using isoleg theory (Rosenzweig 1979), a graphical model of the effects of competitor densities on habitat selection and behavior based on the ideal free distribution (Fretwell and Lucas 1970; Fretwell 1972), I discovered that intraspecific competition is an important factor for redband trout habitat selection in late summer. Redband trout moved less frequently into food-enriched habitats in the presence of higher densities of conspecifics, and moved into enriched habitat more frequently in the presence of higher densities of juvenile Chinook salmon, perhaps due to habitat effects or heterospecifics attraction. Juvenile Chinook salmon habitat selection could not be determined—they did not move—either because I did not achieve low enough densities of redband trout in the experiments, because the experiments occurred too late in the season, or (though less likely) because Chinook habitat selection is not affected by food abundance or competitor densities.

Regarding interspecific effects, my test of the isoleg model in these two species did not provide conclusive evidence that competitive interactions or any other mechanism leads to the displacement of one species by another at local habitat scales. However, I could not rule out the possibility that redband trout were attracted to sites where Chinook salmon were foraging in the food-supplemented treatment sites, and therefore the influence of one species on another's habitat selection cannot be ruled out—only the interaction is perhaps a positive one (commensalism or mutualism) rather than the expected competitive relationship. While my original intent was to test assumptions about the degree of competition between *O. mykiss* and *O. tshawytscha*, my findings

correspond with a growing body of evidence in many ecological systems that organisms use social information as cues for habitat quality (Danchin et al. 2004). An interesting avenue of future research would be to explicitly test for the mechanism of the positive isoleg slope, to find out whether *O. mykiss* do in fact use social information from other members of the fish assemblage to assess habitat quality.

7) Effects of competitor densities on redband trout foraging and aggression (Chapter 4)

Aggressive surface foraging and territory maintenance behaviors by redband trout were significantly affected by competitor densities much higher than those at which redband trout cease moving into enriched habitat, meaning that redband trout were capable of assessing habitat in terms of its competitive environment. In general, redband trout aggression and foraging rates decreased with increasing competitor densities. I also noted a trend of increasing behavioral diversity among groups of redband trout in the presence of more competitors, and a trend of decreased aggression in sites with enriched habitat. The later trend is in opposition to the findings of a previous experiment where aggression increased with food addition. The disparity between the two findings is attributed to the way in which food was added, with pulsed additions of food leading to higher aggression and even distribution leading to less aggression.

Relevant principles of restoration

a) Recognize stream habitats as dynamic in space and time

Historically, only a small proportion of habitat may have been productive for salmonids (Reeves et al. 1995). In geologic and even ecological timescales, ecologists have recognized that the environment is constantly changing, shifting our perspective from the ‘balance of nature’ to a ‘flux of nature’ metaphor (Callicott 2002). Ebersole and Liss (1997) present a restoration framework that includes protecting the developmental

diversity of stream habitats in order to allow reexpression of the capacity to provide particular functions, such as salmonid production. Recognizing this variability and uncertainty will help inform difficult management decisions that must occur even in the absence of limited data (Wissmar and Bisson 2003a). I found that diverse habitats were distributed heterogeneously throughout the watershed (objective 1), and these habitats were utilized differently by fish with different biological traits (objective 2). Although my study did not explicitly examine temporal dynamics of habitats, environmental conditions of pools in the watershed did conform to geomorphic perspectives of the dynamic nature of reach-level habitats from headwaters to mouth of a river continuum. Not all habitats were ideal for salmonids; some habitats were more ideal for non-game species, which are typically not targets for restoration. These findings support the idea that restoration efforts should incorporate the dynamic nature of habitats. A perspective focusing on increasing only habitats for salmonids would miss the point that environmental conditions for fish in this system are patchy, which seemed to support a relatively diverse fish assemblage as compared to a monoculture of salmonids.

b) Work at multiple spatial scales

One of the most important goals in stream ecology today is identifying factors driving spatial pattern in stream communities (Johnson et al. 2007). Although many recent restoration efforts do incorporate a process-based approach to restoration (e.g., restoring flow regime vs. restoring static habitats as per Poff et al. 1997), many of these efforts occur only in short reaches (Roni et al. 2002). Working at a greater spatial extent of restoration not only incorporates the dynamic nature of riverine habitats (Reeves et al. 1995), but also can reveal nuanced patterns of fish assemblage distribution if data are collected in a nested, hierarchical fashion. In the nearby North and Middle Forks of the John Day, adult spring Chinook salmon were associated with coldwater habitats in summer, but only in context of the larger-scale pattern of the geomorphic distribution of deep pools that were probably selected earlier in the season (Torgersen et al. 1999). Spawning bull trout in a Montana stream network selected valley segments with net

upwelling of hyporheic water, but at local sites selected downwelling zones, presumably for flow of oxygenated water through redds (Baxter and Hauer 200). In the present study, I found that level of resolution of observation affected interpretations regarding which trait guilds were related to environmental conditions (objective 2). Examining patterns at one scale alone would have yielded spurious results, as in the case of the changing association between SOURCE habitats and the COLDWATER trait guild in Black Canyon at the tributary scale. By collecting data in a nested, hierarchical fashion, I was able to generate hypotheses about the nature of species coexistence among geomorphically- and thermally-distinct reaches (objective 3), which helped develop ideas for subsequent studies in the basin (objectives 4-7).

c) Incorporate animal behavior

Not accounting for behavioral responses may lead to restoration efforts that do not make sense in an animal's world (Shumway 1999). Using a model based on the tradeoff between increasing prey encounter and decreased rate of capture of individual prey items, Nislow et al. (1999) discovered that for young Atlantic salmon, adding large woody debris to streams increased available microhabitats and thus energetically-profitable foraging locations. This kind of detailed information about mechanisms of species response builds upon vague notions of why individuals of a given species are found where they are based on broad statistical patterns alone. The present study incorporated a behavioral ecology perspective by examining redband trout behavior in context of prevalent foraging theory (objective 4), with the goal of understanding mechanisms of habitat selection and fish growth (objective 5). One notable finding was that redband trout engaged in behavior that was more likely to yield high energy gain in habitats where refuge was present in the form of undercut banks. These behaviors were described as 'risky' out of context of the habitat they were occurring in, but the potential risk of high surface feeding rates and interaction rates was probably balanced by the shelter afforded by structural refugia. Undercut banks and other refuge characteristics have been

indirectly linked to increased survival rates of salmonids in western U.S. landscapes that are heavily grazed by cattle (Bayley and Li 2008; White and Rahel 2008).

The discipline of behavioral ecology claims ideal free distribution theory (Fretwell and Lucas 1970; Fretwell 1972) as its own. In its most distilled sense, the ideal free distribution incorporates the idea that habitat quality decreases with increasing competitors until per capita resources are equal among what were previously 'rich' and 'poor' habitats. Ideal free distribution theory has previously proven effective in tempering expectations of restoration efforts, as in the case of Giannico and Healey's (1999) caveat that due to the complex behavioral response by juvenile coho salmon to large woody debris addition, a direct linear relationship between fish abundance and restoration efforts may be impossible to achieve. Likewise, I employed a descendant of the ideal free distribution—isoleg theory (Rosenzweig 1979)—in order to understand salmonid habitat selection (objective 6) and redband trout foraging and aggressive behavior (objective 7) as a response to competitor densities. Like the ideal free distribution, isoleg theory incorporates the idea that habitat quality diminishes with competitor densities, but explicitly allows for the potential of the effects of multiple species of competitors with different dominance rankings. The model assumes that 'good' and 'poor' quality habitat exist but that both can be profited from by either species, and tests whether competitor densities affect selection of both habitat types. First and foremost, isoleg theory helped identify a limit to the abundance of redband trout in habitats that were enriched with food, due to intraspecific competition.

This finding bears on restoration efforts that would, for example, expect a linear response between trout production and forest management practices that increase food production in the stream such as managing for a mix of softwoods and hardwoods in riparian areas. Deal (2007) found that red alder *Alnus rubra* production in Pacific coastal forests was linked to greater macroinvertebrate production and supported greater aquatic biodiversity as compared to riparian forests managed exclusively for more commercially-viable softwoods. However, the reality check that ideal free distribution and isoleg theories bring to this expectation is that increasing production of food resources will at

some point yield diminishing returns—regarding attracting organisms that would otherwise capitalize on those resources—due to the effects of competitor densities.

I also extended isoleg theory to beyond its original intent by including behavior as a response to competitor densities. I found that the threshold of conspecific densities at which redband trout begin to cease foraging is greater than that at which they cease selecting enriched patches, indicating that this species would rather select habitats of lower total food availability (but potentially equal per capita food availability) than withstand environments that are so competitive that fish must endure aggression and reduced foraging rates. For restoration ecologists seeking to merely increase trout biomass or production in a system, this finding illuminates a constraint on such aspiring outcomes: for behavioral reasons, fish may migrate out of 'restored' habitats far before negative interactions cause them to detrimentally alter their behavior.

d) Consider multiple species

The 'spillover effect' is the idea that by conducting restoration or conservation efforts for a target species, other species will also benefit (Menninger and Palmer 2006). However, my findings show that different trait guilds are typically associated with different habitats (objective 2), and so by increasing the proportion of one kind of habitat (e.g., 'trout habitat'), a few species may benefit while the others suffer. This might be called then, the 'splash effect,' or the idea that by conducting restoration or conservation efforts for a target species, other species are negatively impacted. Even closely-related species can respond differently to disturbances (Caro 2007). For example, additions of large woody debris in several restoration efforts in western Oregon and Washington streams were linked to increased coho salmon abundance but were associated with decreased redband trout abundance in summer (Roni and Quinn 2001). The idea that restoration can impact non-target organisms in a beneficial or detrimental manner also extends across diverse taxa, as in the case of the disparate macroinvertebrate responses to restoration efforts directed at sport fisheries in Finnish headwater streams (Muotka et al. 2002). This

disparate impact of restoration on macroinvertebrates could then conceivably translate into a trophic cascade, eventually swaying the impact on the target organisms in an unexpected direction. And although multiple species approaches typically require more resources (e.g., time, money, and effort), they more often address the legal requirements of restoration strategies (Beechie et al. 2008), especially if the community or ecosystem is the target of restoration, versus an individual species.

Many stream restoration efforts do not include collecting data, making assessments, or reporting information about non-salmonid members of the fish assemblage, making it nearly impossible to conduct adaptive management using a BACI (before, after, control, impact) design (Baldigo and Warren 2008), especially if there are important biotic interactions occurring between 'target' and 'non-target' species. With changing global climate that may translate into warmer stream temperatures, for example, biotic interactions among fish species could also change, and only with baseline information about mechanisms of those interactions can we begin to predict the ecological significance of large-scale disturbances (Wissmar and Bisson 2003b). Researchers have treated the role of biotic interactions differently at different times in the history of ecology (Odenbaugh 2008), which perhaps stems from the early debates between two plant ecologists—Frederic Clements (1916) who saw communities as a real and integrated features of nature having properties distinct from other levels of organization, and Henry Gleason (1917) who saw communities as mere aggregations of species with similar physiological tolerances. And perhaps the dilemma stems even back to Darwin's (1859) own struggle of determining the relative contribution between biotic and abiotic factors in the process natural selection. By considering both in restoration practices, we stand a better chance of understanding the ecology of all members of the fish assemblage. The kind of information collected in this study on distribution of non-target species (objectives 1-3) may prove useful in the future if society's values shift toward lesser-known fishes, or if we discover these 'minor players' have significant impacts on salmonid populations.

e) Ask the question, 'What are we restoring?'

The paradigm of restoring species, ESUs, or other taxonomic units has been termed 'compositionalism,' as opposed to the paradigm of restoring ecological processes, which has been termed 'functionalism' (Callicott 1999). *Explicit* in the first approach is that conserving or restoring individual species or finer taxonomic resolutions (e.g., the leopard darter, humpback chub, or redband trout) is what we want to protect; while explicit in the second approach is that conserving or restoring functions (e.g., trophic relationships, nutrient dynamics, or energy flux) is the goal. *Implicit* in the first approach is that individual taxa are worth more than just the functional role they play in the ecosystem, while implicit in the second approach is that species are interchangeable with those that fulfill the same role, as in equally-functional but different parts of a machine.

The answer to 'What are we restoring?' depends on the metaphor for restoration that we adopt. Metaphors shape how we perceive, think, and act (Lakoff and Johnson 1980) and are prevalent in restoration ecology (Keulartz 2007) as well as many other ecological disciplines (Chew and Laublichler 2003). A mechanistic or Cartesian view of restoration leads to mechanistic or Cartesian approaches—the breaking down of the whole pattern into irreducible parts, studying the parts, and then attempting to make inferences about the whole. In one sense, my method of deconstructing fish species into biological traits (objectives 1-3) has many similarities to the Cartesian approach. However, I advocate that we can gain much ecological understanding using the trait-based approach, which seeks more general ecological insights about the nature of relationships between organisms and their environment; but that finally we should conserve and restore communities of species, not just functions. This for two reasons, both of them better expressed by the biologist-conservationist Aldo Leopold (1949) than myself. First, individuals and species have intrinsic value in their own right, and thus we have a moral obligation to protect them:

> Time was when biologists somewhat overworked the evidence that [predatory mammals, raptorial birds, and fish-eating birds] preserve the health of game by killing weaklings, or that they control rodents for the farmer, or that they prey only on 'worthless' species. Here again, the evidence had to be economic in order

> to be valid. It is only in recent years that we hear the more honest argument that predators are members of the community, and that no special interest has the right to exterminate them for the sake of a benefit, real or fancied, to itself.

Here Leopold refers to predators, but by only a small effort of the imagination the concept can be extended to all members of the biotic community. Second, the science of ecology is still young on the timescale of human endeavors, and we no doubt have much to learn about the complex and nuanced interactions among even the most well-studied taxa (e.g., salmonids), let alone the lesser-known taxa (e.g., cyprinids, catostomids, and cottids). Granted we still have much to learn, making assumptions about the 'function' of individual taxa and presuming we can replace them with other, seemingly well-fitting pieces of the machine is a dangerous supposition. As Leopold expressed this idea more eloquently, I will give him the podium:

> The outstanding scientific discovery of the twentieth century is not television, or radio, but rather the complexity of the land organism. Only those who know the most about it can appreciate how little we know about it. The last word in ignorance is the man who says of an animal or plant: "What good is it?" If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering.

During the course of this project, I have striven towards a richer understanding of the 'cogs and wheels' driving fish distribution patterns in the South Fork John Day watershed, while at the same time recognizing (and examining) the whole. The research builds on prior work conducted by other students and faculty who seek to explain ecological factors driving redband trout dynamics: the effect of physical habitat characteristics and water temperature; seasonal patterns of their migration, growth, and survival; and the role of elevated stream temperatures on redband trout physiological responses. My approach has been to add the perspectives of community ecology by including potential interactions of the remaining members of the fish assemblage, and to incorporate behavioral ecology by examining foraging and aggression in redband trout. Likewise, restoration practices that incorporate knowledge of a broader range of potential drivers for species distributions will better serve a broader range of restoration goals.

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