The effects of size asymmetries and habitat diversity on interspecific interactions in juvenile salmonids (*Oncorhynchus* sp.)

By

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ABSTRACT

Sympatric coho salmon (Oncorhynchus kisutch) and steelhead trout (O. mykiss) fry tend to occupy pools and riffles, respectively, in coastal streams in northwestern North America. Coho fry emerge earlier, are larger, competitively dominant, and displace steelhead from deep low-velocity pools into shallow high-velocity riffles. The species' morphologies (coho-laterally compressed, steelhead-fusiform) match their habitat associations, suggesting the species are adapted to different hydrologic conditions. Where the three species occur together, cutthroat trout (O. clarki) tend to occupy intermediate depths and velocities. I conducted a series of experiments in artificial stream channels in order to examine the effects of size asymmetries and physical habitat structure on interspecific interactions between coho, steelhead, and cutthroat.

A reciprocal transplant experiment using coho and steelhead revealed that in the absence of interspecific competition both species grow faster in pools than in riffles. Steelhead grew faster than coho in both habitats. There was no evidence of a growth rate trade-off between the species across the two habitat types. The pattern suggests steelhead have a higher intrinsic growth rate than coho, but that the species’ growth rates vary similarly across habitats. Next, I investigated how relative size and species identity affected competitive ability and fighting behavior. In dyadic contests between coho and steelhead, competitive ability depended mostly on the relative size of individuals. Both species dominated when given a size advantage, and neither dominated when the species were size matched, suggesting no difference in innate competitive ability. Fighting behavior was determined mainly by species identity. Coho were more likely to use aggressive chases, whereas steelhead were more likely to use passive displays. The difference in fighting behavior is that predicted to evolve under asymmetric competition if the species’ optimal behaviors depend on different trade-offs between the chance of winning a contest and the cost of escalation. I conducted habitat selection experiments under two competitive scenarios- coho larger (natural asymmetry) and species size matched (asymmetry removed)- in order to determine the relationship between asymmetric competition, density dependent habitat selection, and niche overlap. The size asymmetry increased the per capita effect of coho on steelhead habitat selection by increasing the proportion of steelhead using riffle habitat across a wide range of species’ densities. Asymmetric competition reduced niche overlap between the species at both the habitat and microhabitat scale. The competitive asymmetry affected how individuals arranged themselves within habitat type more than the distribution of individuals among habitat types. In a final experiment, I used cutthroat trout to test the hypothesis that habitat diversity increases species diversity by reducing the negative effects of interspecific competition. In a three species community, cutthroat trout grew faster in the diverse habitat than in homogeneous pool or riffle habitats. Coho and steelhead grew as fast in the diverse habitat as in either homogeneous habitat. The experiment provides partial support for the competition hypothesis, is consistent with observational evidence linking habitat diversity to species diversity in natural salmonid communities, and one of the first to control variation along other niche axes when investigating the relationship between habitat diversity, interspecific competition, and species diversity.

Together, these experiments improve our understanding of the effects of asymmetric competition on behavior and habitat selection among interference competitors. They also illustrate the potential importance of size asymmetries and habitat diversity in structuring juvenile salmonid communities.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT</td>
<td>ii</td>
</tr>
<tr>
<td>TABLE OF CONTENTS</td>
<td>iii</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>v</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>vi</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>viii</td>
</tr>
<tr>
<td>CHAPTER 1: Introduction</td>
<td>1</td>
</tr>
<tr>
<td>CHAPTER 2: The consequences of habitat segregation in a variable environment: testing for a growth rate trade-off in stream rearing salmonids</td>
<td>7</td>
</tr>
<tr>
<td>2.1 ABSTRACT</td>
<td>7</td>
</tr>
<tr>
<td>2.2 INTRODUCTION</td>
<td>7</td>
</tr>
<tr>
<td>2.3 MATERIALS AND METHODS</td>
<td>9</td>
</tr>
<tr>
<td>Study populations</td>
<td>9</td>
</tr>
<tr>
<td>Experimental apparatus and design</td>
<td>10</td>
</tr>
<tr>
<td>Experimental procedure</td>
<td>12</td>
</tr>
<tr>
<td>Analyses</td>
<td>12</td>
</tr>
<tr>
<td>2.4 RESULTS</td>
<td>12</td>
</tr>
<tr>
<td>2.5 DISCUSSION</td>
<td>13</td>
</tr>
<tr>
<td>CHAPTER 3: Evolution of fighting behavior under asymmetric competition: an experimental test with juvenile salmonids</td>
<td>21</td>
</tr>
<tr>
<td>3.1 ABSTRACT</td>
<td>21</td>
</tr>
<tr>
<td>3.2 INTRODUCTION</td>
<td>21</td>
</tr>
<tr>
<td>3.3 MATERIALS AND METHODS</td>
<td>24</td>
</tr>
<tr>
<td>Study area and populations</td>
<td>24</td>
</tr>
<tr>
<td>Fish collection and rearing</td>
<td>24</td>
</tr>
<tr>
<td>Experimental apparatus</td>
<td>25</td>
</tr>
<tr>
<td>Experimental procedure</td>
<td>25</td>
</tr>
<tr>
<td>Statistical analyses</td>
<td>26</td>
</tr>
<tr>
<td>3.4 RESULTS</td>
<td>27</td>
</tr>
<tr>
<td>Competitive ability</td>
<td>27</td>
</tr>
<tr>
<td>Fighting behavior</td>
<td>28</td>
</tr>
<tr>
<td>3.5 DISCUSSION</td>
<td>29</td>
</tr>
</tbody>
</table>
CHAPTER 4: The effects of asymmetric competition on habitat selection and
niche overlap in juvenile salmonids................................. 38

4.1 ABSTRACT................................................................. 38
4.2 INTRODUCTION....................................................... 38
Study system............................................................. 40
4.3 MATERIALS AND METHODS....................................... 41
Isoleg analysis........................................................... 41
Study populations...................................................... 43
Fish rearing............................................................... 43
Experimental apparatus.............................................. 44
Experimental procedure............................................. 45
Analyses................................................................. 45
4.4 RESULTS................................................................. 46
Habitat selection....................................................... 46
Niche overlap........................................................... 48
4.5 DISCUSSION............................................................. 49
Habitat selection....................................................... 49
Niche overlap........................................................... 51
Conclusion.............................................................. 53

CHAPTER 5: Habitat diversity and species diversity: testing the competition
hypothesis with juvenile salmonids................................. 63

5.1 ABSTRACT................................................................. 63
5.2 INTRODUCTION....................................................... 63
5.3 MATERIALS AND METHODS....................................... 66
The system............................................................... 66
Fish collection and rearing.......................................... 67
Experimental design................................................ 67
Analysis................................................................. 69
5.4 RESULTS................................................................. 69
5.5 DISCUSSION............................................................. 70

CHAPTER 6: Concluding remarks........................................ 77

Biogeographic implications......................................... 79
Management implications.......................................... 80

LITERATURE CITED........................................................ 83
## LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1.</td>
<td>Physical conditions and initial fish sizes for the reciprocal transplant experiment conducted in 1998.</td>
</tr>
<tr>
<td>3.1.</td>
<td>Experimental conditions for dyadic behavior trials</td>
</tr>
<tr>
<td>3.2.</td>
<td>Results of split-plot ANOVAs for competitive ability and fighting behavior during dyadic trials</td>
</tr>
<tr>
<td>4.1.</td>
<td>Isoleg regression interaction coefficients for Figure 4.1</td>
</tr>
<tr>
<td>4.2.</td>
<td>Results of regression analyses for coho and steelhead habitat selection when coho have their natural size advantage</td>
</tr>
<tr>
<td>4.3.</td>
<td>Results of regression analyses for coho and steelhead habitat selection when the natural size advantage of coho is removed</td>
</tr>
<tr>
<td>4.4.</td>
<td>Results of ANCOVAs testing for an effect of asymmetric competition on niche overlap measured at the habitat type and microhabitat scales</td>
</tr>
<tr>
<td>5.1.</td>
<td>Description of the experiment testing the effect of habitat diversity on interspecific competition in coho, steelhead, and cutthroat fry</td>
</tr>
</tbody>
</table>
### LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>The mean growth rates of coho and steelhead in artificial pools and riffles calculated from the final weights of all the fish recovered</td>
<td>18</td>
</tr>
<tr>
<td>2.2</td>
<td>The mean coefficient of variation of weight for coho and steelhead reared in artificial pools and riffles</td>
<td>19</td>
</tr>
<tr>
<td>2.3</td>
<td>The mean growth rates of coho and steelhead in artificial pools and riffles calculated from the final weights of the five largest individuals recovered from each treatment</td>
<td>20</td>
</tr>
<tr>
<td>3.1</td>
<td>The mean proportion of time spent in the dominant, upstream position and mean proportion of drift items captured for coho and steelhead in pools and riffles under three size treatments: coho larger than steelhead, size matched, and coho smaller than steelhead</td>
<td>35</td>
</tr>
<tr>
<td>3.2</td>
<td>The mean number of fighting behaviors initiated by coho and steelhead in the six habitat × size combinations</td>
<td>36</td>
</tr>
<tr>
<td>3.3</td>
<td>The proportion of fighting behaviors that were chases, nips, and displays for coho and steelhead in the six habitat × size combinations</td>
<td>37</td>
</tr>
<tr>
<td>4.1</td>
<td>Isoleg phase spaces showing how two species distribute themselves between a mutually preferred and secondary habitat under symmetric and asymmetric competition</td>
<td>58</td>
</tr>
<tr>
<td>4.2</td>
<td>The mean standard lengths (mm) of 20 fish from each of the three experimental groups at four times during the experiment (June 16 to July 18)</td>
<td>59</td>
</tr>
<tr>
<td>4.3</td>
<td>Schematic of the two oval flow tanks used for the habitat selection trials. Each tank had two artificial stream channels</td>
<td>60</td>
</tr>
<tr>
<td>4.4</td>
<td>The isoleg maps showing the proportion of coho and steelhead in the riffle habitat as a function of the species' densities under the two competitive scenarios</td>
<td>61</td>
</tr>
<tr>
<td>4.5</td>
<td>The density dependent reduction in niche overlap resulting from coho having their natural size advantage over steelhead</td>
<td>62</td>
</tr>
</tbody>
</table>
LIST OF FIGURES (cont.)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.1</td>
<td>The mean growth rates of coho, steelhead, and cutthroat fry in two and three species communities in pool, riffle, and diverse habitats</td>
<td>75</td>
</tr>
<tr>
<td>5.2</td>
<td>The ratio of mean coho growth rate to mean steelhead growth rate in the presence and absence of cutthroat trout in pool, riffle, and diverse habitats</td>
<td>76</td>
</tr>
</tbody>
</table>
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CHAPTER 1

Introduction

Interspecific competition can influence community organization and the coevolution of interacting species. These two related and seemingly modest claims share a surprisingly controversial history. Following the observations and writings of early naturalists, the mathematical formalization of competition theory by Lotka and Volterra found empirical support in a series of laboratory microcosm experiments demonstrating that interspecific competition can operate, and that it can result in competitive exclusion (Gause 1934; Crombie 1945). Ecologists proceeded to describe natural communities by drawing (to differing degrees) upon the ideas that competition can (1) influence community organization, and (2) promote adaptive divergence among competing species. Notable examples are Lack’s book on Darwin’s finches (1947), E.O. Wilson’s papers on taxon cycles in ants (1959, 1961), and MacArthur and Wilson’s treatise on island biogeography (1967).

The 1960s and 70s saw the rapid accumulation of observational evidence supporting the ideas that interspecific competition could promote adaptive divergence and regulate community composition. Classic studies comparing communities of tropical birds, desert rodents, and island lizards, revealed a consistent pattern: species’ morphologies differ in a predictable way, and morphological differences are related to the partitioning of resources and/or habitat. The circumstantial evidence was reassuring, and the rise of experimental ecology helped clearly demonstrate that interspecific competition did in fact operate in natural communities, not just in test tubes (Schoener 1983a; Connell 1983). At the same time, a growing body of verbal and mathematical theory provided a number of predictions for how various environmental/biological conditions might regulate competitive interactions and their effect on adaptive divergence, niche shifts, and competitive exclusion. Of relevance to this thesis are the following. Temporally variable environments should impede adaptive divergence because species are less able to specialize on predictable, alternative resources/habitats. Adaptive divergence depends on niche shifts, and competitive interactions that reduce niche overlap should promote adaptive divergence by subjecting species to selective regimes more different than when niche overlap is high. Habitat/resource
diversity should increase species richness by allowing species to reduce niche overlap, thus reducing the negative effects of interspecific competition and the chance of competitive exclusion.

Despite growing empirical and theoretical support, the claim that competition was an important ecological and evolutionary force remained controversial. As acceptance grew for the idea that interspecific competition could affect community organization and evolutionary divergence, Simberloff and his colleagues led an ecological insurgence (Conner and Simberloff 1979; Simberloff and Boecklen 1981; Simberloff 1983). They suggested that chance alone, or evolutionary processes that occurred prior to present competitive relationships, could account for organizational patterns observed in modern communities. Papers were written, tenures were granted, the debate waned, and a classically ecological consensus emerged: it depends. Interspecific competition can operate in natural communities and, depending on environmental and biological conditions, has the potential to regulate community organization and/or promote adaptive divergence (Roughgarden 1983; Rosenzweig 1987).

Because of the controversy over the existence/importance of interspecific competition per se, the majority of empirical work on interspecific competition has simply documented its presence and effects, or compared such between different communities, or the same community across a range of environmental and biological conditions. Thus, observed changes in competitive interactions have usually been associated with changes in species identity or evolutionary history. There has been less work that manipulates the environmental and biological context of interspecific interactions, thus changing the competitive relationship between single sympatric species pairs. Such an approach is appealing because it allows us to manipulate competitive interactions independently of changes in ecological and evolutionary history. This breaks a subtle, but insidious circularity that is implicit in one of evolutionary ecology's central claims, that competition is an important ecological and evolutionary force. If competitive interactions affect evolutionary dynamics, then evolutionary history should affect present competitive interactions (the famous "ghost of competition past" is the most obvious example) (Connell 1980). Strictly speaking, we should like to control species identity and evolutionary history when asking how changing various physical and biological conditions affects competitive interactions.
Because their sizes and habitats are easily manipulated, juvenile salmonids provide an opportunity to investigate the effects of such manipulations on competitive interactions, and I use this approach in all but the first experiment described in this thesis.

This thesis describes a series of experiments that use juvenile coho salmon (Oncorhynchus kisutch), and steelhead (O. mykiss) and cutthroat trout (O. clarki) to test various hypotheses concerning the context and consequences of interspecific competition. Chapters 2-5 are written as individual papers, each with an abstract and all relevant background information, allowing the reader to pick and choose topics of interest. Cutthroat trout were used only in the experiment described in Chapter 5. Here I provide a brief description of the study system followed by a summary of the four main chapters. In Chapter 6 I discuss some of the biogeographical and management implications of the results.

Interspecific competition in juvenile salmonids has been studied for decades, largely because of the cultural and economic importance of the species. Perhaps for the same reason, most of the research has not been placed within the same theoretical context as that on other systems used for studying competition. As a result, other fish, bird, rodent, lizard, and amphibian communities have become “model systems” for studying a range of topics related to interspecific competition: community organization, adaptive radiation, resource partitioning, optimal foraging, habitat selection, interference behavior, ontogenetic niche shifts. A number of features make juvenile salmonids ideal for testing hypotheses concerning the context and consequences of interspecific competition. In particular, they are well suited for studying the relationships between asymmetric competition, contest behavior, habitat selection, and niche overlap. First, of course, is the vast amount of information available on various aspects of their natural history; much of the necessary leg work has already been done. Second, the species have wide geographical ranges across which life history traits relevant to juvenile interactions vary. Third, it is easy to manipulate habitat, juvenile sizes, and species’ densities in the laboratory, and the consequences of such manipulations on behavior, habitat selection, and measures of fitness (e.g. foraging success and growth rate) are easily quantified.

Coho salmon and steelhead trout occur in sympatry in coastal streams in northwestern North America. Both anadromous species spend at least 18 months in fresh water before migrating to the ocean to reach maturity. The fish communities in northwest
streams are dominated by salmonids and have low species richness. In many streams juvenile coho and/or steelhead are numerically dominant and are often the only species present. Three biogeographic patterns are relevant to the experiments in this thesis. First, coho adults spawn earlier than steelhead adults and coho fry emerge earlier than steelhead fry. As a result coho fry are larger than steelhead fry during the first summer in fresh water. The difference in spawning time and fry size is greater in the northern portion of their sympatric range and decreases to the south where spawning and emergence times converge due to a shorter rainy season. Second, in natural streams coho fry tend to occupy deep, low-velocity pool habitat, and steelhead tend to occupy shallow, high-velocity riffle habitat. This pattern also holds between streams; coho are numerically dominant in low gradient streams, whereas steelhead tend to be numerically dominant in high gradient streams. However, both species use a wide range of depths and velocities during fresh water rearing. Where all three species occur in sympatry, cutthroat fry occupy intermediate depths and velocities. Third, juvenile salmonids engage in interference competition for energetically favorable positions in the water column, and competitive ability is determined by relative size. Given their natural size advantage, coho are competitively dominant over steelhead (and cutthroat) and displace them from pools into riffles. In all experiments I used coho and steelhead fry from the Chilliwack River in southwestern British Columbia, Canada. In these populations from the middle of their sympatric range, coho fry emerge earlier and are larger than steelhead fry during their first summer in fresh water.

In Chapter 2, I describe a reciprocal transplant experiment using artificial pools and riffles that tests the hypothesis that habitat segregation between coho and steelhead fry has resulted in the species evolving a trade-off in juvenile growth rates across the two habitat types. Growth rate trade-offs associated with differences in trophic morphology are well documented in lake rearing fishes. The body shapes of coho (more laterally compressed) and steelhead (more fusiform) suggest they are adapted to different hydrological conditions. I reared groups of individuals of each species in allopatry in pools and riffles. I found no evidence for a growth rate trade-off across habitat types (a non-significant species by habitat interaction). Both species grew faster in pools than in riffles. Steelhead had a higher growth rate than coho in both habitats. This pattern suggests steelhead have a higher intrinsic growth rate, but that the species' growth rates vary similarly across the two habitat types. The result
is consistent with theoretical and empirical studies suggesting temporally dynamic environments limit the opportunity for adaptive divergence through specialization on alternative habitats. However, because fish were not reared in isolation, the experiment is inconclusive and cannot rule out the possibility that intraspecific competition affected juvenile growth rates.

In Chapter 3, I test the prediction developed from contest game theory that large-dominant and small-subordinate species engaging in asymmetric interference competition should evolve aggressive and passive fighting behaviors, respectively. I manipulated the size asymmetry between coho and steelhead in order to determine whether differences in fighting behavior persist independently of competitive ability. I observed fighting behavior during dyadic contests in two habitats, mutually preferred pools and energetically demanding riffles, under each of three size treatments: natural size asymmetry, asymmetry removed, and reversed size asymmetry. The results suggest that coho have no innate competitive advantage over steelhead, but that the species have evolved different fighting behaviors. Competitive ability depended primarily on size; large individuals of both species dominated smaller heterospecifics, and neither species dominated when individuals were size matched. Fighting behavior depended primarily on species identity; coho used a higher proportion of aggressive chases, whereas steelhead used a higher proportion of passive displays. The experiment cannot rule out other factors (e.g. interspecific competition per se, differences in the strength of intraspecific competition, habitat associations) that may be responsible for the observed differences in fighting behavior, but to my knowledge represents the first empirical support for the prediction that asymmetric competition can promote behavioral divergence. The results also compliment previous work suggesting asymmetric competition can promote morphological divergence, and provide a richer context for other aspects of the coho-steelhead system.

In Chapter 4, I describe a habitat selection experiment designed to explore the equivocal relationship between asymmetric competition, density dependent habitat selection, and niche overlap. Specifically, the experiment addresses the prediction that asymmetric competition can reduce niche overlap by increasing the per capita effect of the dominant on habitat selection by the subordinate. I conducted 120 habitat selection trials over a wide range of species' densities under each of two competitive scenarios; coho larger than
steelhead, and species size matched. When coho had their natural size advantage competition was highly asymmetric and habitat selection by both species depended almost exclusively on coho density. Removing the size advantage of coho nearly eliminated the competitive asymmetry. Habitat selection by steelhead was influenced equally by intra- and interspecific competition when the species were size matched. Habitat selection by coho depended on both species’ densities but more on intraspecific density.

Under each competitive scenario I calculated niche overlap for 100 density combinations at two spatial scales: the habitat scale (pools and riffles), and the microhabitat scale (mean overlap averaged over three niche axes: distance, depth, water velocity). Asymmetric competition reduced niche overlap at both spatial scales, significantly so at the microhabitat scale. At the microhabitat scale, the reduction in niche overlap under asymmetric competition was greatest at low densities and disappeared at high densities. Because I manipulated the size asymmetry in a single species pair, this experiment controls for the effects of evolutionary history on competitive interactions and provides a novel exploration of the relationship between asymmetric competition, density dependent habitat selection, and niche overlap.

In Chapter 5, I included cutthroat trout to test two predictions of the hypothesis that the positive relationship between habitat diversity and species diversity arises from a reduction in the negative effects of interspecific competition. By allowing species to partition habitats and avoid competition, habitat diversity should 1) facilitate the addition of an ecological intermediate species into an existing community, and 2) reduce the negative competitive effects of that species on existing members of the community. I introduced two (coho and steelhead) and three species (coho and steelhead plus cutthroat) communities into each of three artificial stream habitats: homogeneous pool, homogeneous riffle, and a diverse habitat. The results provided partial support for the predictions. Cutthroat had their highest growth rate in the diverse stream habitat. Though habitat diversity did not eliminate the negative competitive effects of cutthroat on coho and steelhead growth rates, in the three species community coho and steelhead grew as fast in the diverse habitat as in either homogeneous habitat. The results are consistent with data on species number and evenness from natural communities, where variation along other niche axes confounds the relationship between habitat diversity, interspecific competition, and species diversity.
CHAPTER 2

The consequences of habitat segregation in a variable environment: testing for a growth rate trade-off in stream rearing salmonids

2.1 ABSTRACT

In the coastal streams of northwestern North America, juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) partition habitat according to water depth and velocity. Early emerging coho fry are larger, competitively dominant, and occupy low velocity pool habitats; steelhead fry emerge later, are smaller, and occupy high velocity riffle habitats. The species have body shapes consistent with their habitat associations; coho are more laterally compressed, steelhead more fusiform. Using artificial stream channels, I conducted a reciprocal transplant experiment to test the prediction that habitat segregation has resulted in a growth rate trade-off in coho and steelhead across the two habitat types. I found no evidence for a growth rate trade-off. Both species grew faster in pools than in riffles. Steelhead grew faster than coho in both habitats. The pattern suggests evolutionary divergence in intrinsic growth rates, but no differential specialization to the two habitat types. The lack of a significant species by habitat interaction is in contrast to similar studies of fish communities from freshwater lakes, suggesting the opportunity for adaptive divergence may be greater in predictable lotic environments than in temporally dynamic lentic environments.

2.2 INTRODUCTION

Interspecific interference competition can influence habitat selection (Morse 1974; Colwell and Fuentes 1975; Schoener 1983a). Because fitness depends on the interaction between the phenotype and environment (Levins 1968; Wade and Kalisz 1990), habitat segregation can promote adaptive divergence by subjecting species to different selection pressures (Rosenzweig 1987; Schluter 2000). Typically, studies in community ecology begin by quantifying patterns of habitat segregation, then use measures of niche overlap or patterns of co-abundance to infer the relationship between interspecific competition and habitat selection (e.g. Werner et al. 1977; Case 1983; Brown 1989; Norton 1991; Rodriguez 1995). Removal/addition experiments quantify the strength of interactions by measuring
niche shifts or changes in fitness in the focal species (Werner and Hall 1977; Pimm et al. 1985; Hairston et al. 1987; Thompson and Fox 1993; Kocik and Taylor 1994). These approaches describe the relationship between interspecific competition and habitat segregation, but fail to identify the evolutionary consequences of habitat segregation. That is, they describe what species do, not what they can do (Rosenzweig 1981; 1987).

Testing the hypothesis that habitat segregation results in adaptive divergence requires reciprocal transplant experiments that measure components of fitness for each species in their own and the other species’ habitat. The approach has been applied to a number of systems (Howard and Harrison 1984; Losos and Sinervo 1989; Repasky and Schluter 1996), including fishes from freshwater lakes (Schultz and Northcote 1972; Werner 1977; Ehlinger and Wilson 1988; Schluter 1993, 1995; Robinson et al. 1996). I am not aware of any reciprocal transplant experiments using stream rearing fishes. Streams and lakes represent fundamentally different environments within which fish communities develop and their component species evolve (Chapman 1966; Echelle and Kornfield 1984). Lake environments may promote evolutionary divergence by allowing species to specialize on predictable habitats and/or resources, whereas temporally dynamic streams may prevent divergence by forcing species to utilize a broad range of habitats (Levins 1962, 1963, 1968; Van Valen 1965; Roughgarden 1972; Slatkin and Lande 1976; Wilson and Yoshimura 1994). I used artificial stream channels and a reciprocal transplant approach to determine whether habitat segregation between stream rearing juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) has resulted in the species exhibiting a growth rate trade-off across habitat types.

Coho and steelhead occur sympatrically in coastal streams from Alaska to central California; the range of coho extends farther north to the Bering Sea, while the historic distribution of steelhead extends south into Baja, Mexico (Meehan and Bjornn 1991). Both species are anadromous. Coho are strictly semelparous, whereas steelhead are optionally iteroparous. Adult coho return to freshwater to spawn from July to January, with spawning occurring later at lower latitudes (Sandercock 1991; Weitkamp et al. 1995). In coastal streams, adult steelhead spawn between January and April throughout most of their range (Withler 1966; Busby et al. 1996). After emerging as fry in the spring, coho spend 16 to 30 months in freshwater before “smolting” and migrating to the ocean (Drucker 1972;
Steelhead fry emerge later than coho and spend two to five years in freshwater before smolting. Because juveniles of other salmon species spend only days to months in coastal streams (Groot and Margolis 1991), coho and steelhead are often the dominant, and in some cases the only, fish species present in northwest streams (Chapman 1965; Burns 1972; Bugert et al. 1991; Reeves et al. 1993). Interspecific competition may be a stronger coevolutionary force in low diversity communities because species interactions are more consistent (Connell 1980).

In the coho-steelhead system, observational and experimental studies provide evidence that: coho and steelhead fry partition habitat according to depth and velocity, with earlier emerging coho occupying deep, low velocity pool habitats and later emerging steelhead occupying shallow, high velocity riffle habitats (Hartman 1965; Bisson et al. 1988; Bugert et al. 1991); coho are competitive dominants, and steelhead display niche expansion to pool habitats in allopatry (Hartman 1965; Bugert and Bjornn 1991); habitat segregation is dynamic, with each species utilizing overlapping depth/velocity combinations seasonally and between juvenile age-classes (Hartman 1965; Bustard and Narver 1975; Bisson et al. 1988; Bugert et al. 1991); though both species have generalist body forms (Webb 1984), juvenile morphologies are consistent with the species’ habitat associations, with steelhead being more fusiform and coho more laterally compressed (Bisson et al. 1988).

2.3 MATERIALS AND METHODS

Study populations

I studied the same sympatric populations of coho and steelhead described by Hartman (1965) from the Chilliwack River in southwestern British Columbia, Canada (49.1° N, 121.6° W). The Chilliwack River drains a slightly glaciated mountainous basin of 1250 km² and enters the Fraser River approximately 100 km from the Pacific Ocean. Peak flows occur in the fall and winter during the rainy season and in the spring during snow melt. Water temperatures range from 2 to 15° C. Coho fry begin emerging in March and April; steelhead emerge from May through July. The basin contains four other species of Pacific salmon (*Oncorhynchus* sp.) and coastal cutthroat trout (*O. clarki*); Dolly Varden (*Salvelinus malma*) and non-salmonids are relatively rare. A federal salmon hatchery is located at river kilometer (RK) 32, where hatchery stocks of chum (*O. keta*), chinook (*O. tshawytscha*), and coho
salmon are maintained, and wild steelhead are propagated for conservation and recreation purposes.

Experimental apparatus and design

The reciprocal transplant experiment was conducted in 12 identical artificial stream channels (4 m length x 0.9 m width). The experimental design consisted of two pool and two riffle habitats randomly assigned to four channels within each of three blocks. The blocks were arranged longitudinally (upstream, middle, downstream) to control for temperature increases as the water flowed from a common head tank into the four channels of block one, into the channels of block two, and finally into block three. Water entering the head tank was held near 11° C throughout the experiment and filtered to prevent macroinvertebrates from entering the channels. The channels were covered with burlap to simulate canopy shade and prevent avian depredation. I created pools and riffles by varying the amount of gravel in the channels (6 cm diameter, from a local quarry). The physical habitat of each channel was described by calculating the mean depth and water velocity of twelve points (20, 45, 70 cm width along each of four transects at 0.5, 1.5, 2.5, 3.5 m). Water velocity was measured with an electronic flow meter at one half the depth at each point. For the riffle treatments I also measured the surface velocity by calculating the mean time (n = 5) it took a small piece of foam rubber to drift the length of the channel. The physical characteristics of the riffle and pool treatments are similar to those in small streams containing coho and steelhead (Bisson et al. 1988; Bugert et al. 1991) (Table 2.1).

Experimental procedure

On April 28, 1998, I pole seined ≈ 450 newly emerged coho fry from small tributaries and side channels between RK 50 and 60, where Hartman (1965) observed the highest densities of coho and steelhead fry, and wild adults of both species are known to spawn. Fish were transported to the lab, where they were divided into two groups and held at 12° C in indoor troughs (3.7 length x 0.35 width x 0.20 m depth). After one day I began introducing commercial hatchery feed into the troughs. On May 3, 30 coho fry were placed into each of the 12 experimental units. Fish were assigned to each treatment sequentially to avoid a collection bias between blocks. Fish were anesthetized with tricane methanesulfate and their standard length (to 1 mm) and weight (to 0.01 g) recorded. Beginning on May 4, 2.5 g of standard hatchery feed (Moore-Clark® #1 Crumble) was introduced into each experimental
unit over eight hours (≈ 0900-1700 daily) using belt feeders. This size and amount of food approximated natural invertebrate drift sizes and the highest natural drift rates in nearby streams (Keeley and McPhail 1998), and was used to minimize the chance of density dependent growth limitation during the experiment. Though natural drift rates increase with water velocity (Hill and Grossman 1993), I chose to use the same drift rate in riffles and pools for two reasons. First, drift rates within pools vary depending on microhabitat (Nielsen 1992), and at the heads of pools, where dominant fish forage, should be similar to drift rates in riffles. Second, varying the amount of food across the two treatments would confound the design, making it impossible to isolate the effect of hydrologic conditions on growth rate.

Water temperature was recorded (to 0.5° C) every three days at the outflow of each of the 12 channels. Coho fry were removed from the treatments after 47 days (June 18) using baited minnow traps, dip netting, and electrofishing, euthanized, and their lengths and weights recorded.

Because of conservation concerns, I was not permitted to collect steelhead fry from the natural streams. Instead, I collected wild steelhead fry from the Chilliwack hatchery. Hatchery personnel captured wild adults with line and hook during their spawning migration to the upper river. On June 10, I collected approximately 400 newly emerged steelhead fry from the Chilliwack hatchery. The fish were a random sample from 20 families (one female and one male). The fish were handled identically to the coho and placed in the experimental treatments on June 19. All experimental conditions and procedures were as for the coho. Steelhead were removed from the treatments on August 4, after 46 days.

Repeated measures ANOVA of the temperature data (n = 15 for each of the 24 treatments) revealed significant block ($F_{2,19} = 13.49, P < 0.001$) and species effects ($F_{1,19} = 12.04, P < 0.01$), but no habitat effect ($F_{1,19} = 0.25, P = 0.63$). The temperature differences were small: the block means (SD), calculated from the 8 treatment means were: 11.5 (0.08), 11.7 (0.1), and 11.8 (0.07) for blocks one, two, and three, respectively. The mean temperatures of the four treatment/species combinations are shown in Table 2.1. An ANOVA on the initial lengths and weights revealed no initial treatment differences (length: $F_{1,714} = 0.01, P = 0.92$, weight: $F_{1,714} = 0.71, P = 0.40$), but that coho were slightly heavier than steelhead at the beginning of the experiment (length: $F_{1,714} = 2.34, P = 0.13$, weight: $F_{1,714} = 34.29, P < 0.0001$) (Table 2.1).
Analyses

In this experiment the stream channel is the independent experimental unit. For each channel I calculated two response variables. I calculated the mean growth rate for each of 24 independent observations as: (mean weight of fish recovered at the end of the experiment – mean weight of all fish at the beginning of the experiment) / (number of days). I calculated the Coefficient of Variation (CV) of final weight using the correction factor \((1 + \frac{1}{4} n)\) to account for different numbers of fish recovered (Sokal and Rohlf 1995). These data met the assumptions of ANOVA and were analyzed using Type III Sums of Squares with block (random), habitat, species as main effects. A growth rate trade-off would result in a significant habitat by species interaction effect in the ANOVA.

2.4 RESULTS

I was able to recover more fish from the pool (mean = 22.3, SD = 6.9) than riffle (10.8, 4.1) habitats \((F_{1,18} = 25.34, P < 0.0001)\). This difference resulted from both mortality (there appeared to be less fish in riffles at the end of the experiment) and fish burying themselves in the gravel when I tried to remove them from the riffle habitats. The percent of fish recovered did not depend on species \((F_{1,18} = 1.10, P = 0.31)\) or the interaction between habitat and species \((F_{1,18} = 1.26, P = 0.28)\). For all four habitat-species combinations the number of fish recovered was positively related to mean growth rate, significantly so for steelhead in pool habitats \((t = 3.1, P < 0.05)\), opposite the relationship expected if density dependent growth limitation was important. For this reason I did not use the number of fish recovered as a covariate in analyses of growth rates.

When all recovered fish were used to calculate mean growth rate, both species grew significantly faster in pools than in riffles \((F_{1,18} = 44.39, P < 0.0001)\), and steelhead grew significantly faster than coho \((F_{1,18} = 63.45, P < 0.0001)\) (Figure 2.1). The habitat \times species term was nonsignificant \((F_{1,18} = 2.04, P = 0.17)\).

The final weights of coho were significantly more variable than steelhead \((F_{1,17} = 26.14, P < 0.0001)\) (Figure 2.2), but the CV of final weight did not depend on habitat \((F_{1,17} = 1.47, P = 0.24)\) or the number of fish recovered (ANCOVA: \(F_{1,17} = 0.04, P = 0.84)\). Coho weights were also more variable at the beginning of the experiment, but not to the degree observed at termination of the experiment (coho mean CV = 23, SD = 3.0, \(n = 12\); steelhead...
mean CV = 19, SD = 2.6, n = 12; $F_{1,18} = 11.13, P < 0.01$). The difference between the species in the CV of final weight suggests that growth suppression resulting from intraspecific competition was more pronounced in coho (Keeley 2001 and references therein).

In an attempt to correct for the influence of competitive growth suppression, I recalculated the mean growth rate for each treatment as: \((\text{mean weight of the five heaviest fish recovered at the end of the experiment} - \text{mean weight of all fish at the beginning of the experiment}) / (\text{number of days})\). This correction did not change the qualitative pattern observed using all fish, but probably provides a better estimate of the species’ growth rates in the absence of intraspecific competition (Ejike and Schreck 1980) (Figure 2.3). Both species grew faster in pools than in riffles ($F_{1,18} = 37.93, P < 0.0001$), steelhead grew faster than coho overall ($F_{1,18} = 7.9, P < 0.01$), and the habitat by species interaction remained non-significant ($F_{1,18} = 0.18, P = 0.68$). Coho grew almost twice as fast in pools as in riffles, while steelhead grew 57% percent faster in pools than in riffles. In pools steelhead grew 18% faster than coho. In riffles steelhead grew 47% faster than coho.

In summary, both species grew faster in pools, steelhead had higher growth rates than coho, and the species did not show evidence of a growth rate trade-off across the two habitat types.

2.5 DISCUSSION

This experiment tested the hypothesis that habitat segregation between stream rearing coho and steelhead fry has resulted in the species evolving a growth rate trade-off across the two habitat types. I found no evidence that habitat segregation has resulted in differential adaptation to the different hydrologic conditions associated with the two habitat types. The significant species effect in both estimates of growth rate suggests that steelhead have a higher intrinsic growth rate than coho.

I suggest two related explanations for why habitat segregation has not resulted in the evolution of a growth rate trade-off across habitat types. First, adaptive divergence by fry may be constrained by habitat use during other life history stages. Both species display ontogenetic niche shifts and utilize a broad range of depth/velocity combinations during their freshwater residence period (Bustard and Narver 1975; Bisson et al. 1988). Also, the species
spend half their lives in the ocean, meaning they experience similar hydrological conditions during much of their life histories. Second, the potential for evolutionary divergence via specialization to different habitats may be limited by the temporally dynamic nature of stream environments. Energetically favorable positions in the water column can change seasonally to daily with flow and temperature, and hourly due to changes in the rate and composition of invertebrate drift (Chapman 1966). If individuals of each species must utilize a similarly broad range of hydrologic conditions in order to maximize pre-smolt components of fitness (growth and survival), natural selection should limit the opportunity for specialization on different habitat types (Levins 1963, 1968; Slatkin and Lande 1976).

The growth rates documented in this study are consistent with those observed under natural conditions. Overwinter growth rates of coho fry are higher in pond and off-channel pool habitats than in main channel (high velocity) habitats (Quinn and Peterson 1996). When isolated in shallow and deep water habitats, steelhead fry in a northern California stream grew faster in the deep water habitat by ≈ 60%, an amount similar to present study (Harvey and Nakamoto 1997). Kruzic et al. (2001) isolated hatchery reared coho fry in natural pools and riffles and found no growth rate trade-off across habitat types. This result is difficult to interpret because final densities were significantly lower in the riffle habitats, which may have increased growth rates. Growth rates measured in natural environments are difficult to interpret because factors other than hydrologic conditions can influence behavior and growth. Pools and riffles may have different drift rates (Hill and Grossman 1993), temperature profiles (Bilby 1984), levels of depredation (Grand and Dill 1997), and densities of inter- and/or intraspecific competitors. I attempted to control these factors, so observed growth rates can more confidently be attributed to evolved interspecific differences or similarities. Reciprocal transplant experiments incorporating other ecological factors will compliment the present results.

The significant species effects suggest steelhead have a higher intrinsic growth rate than coho (Figures 2.1, 2.3). This result is consistent with an interspecific response to countergradient selection (Levins 1979; Berven et al. 1979), whereby the species with the shorter growing season exhibits a faster growth rate than the species with the longer growing season. Evidence for countergradient variation has been documented for a number of fish species where populations from northern latitudes, which experience shorter growing
seasons, have higher intrinsic growth rates (Conover 1990). In this system, steelhead have a shorter growing season than coho because fry emerge later in the season. Under laboratory conditions, Wurtsbaugh and Davis (1977) and Everson (1973) measured growth rates of steelhead and coho fry, respectively. The mean food conversion efficiencies (total growth / food intake x 100) at ≈12 °C were 24 % for steelhead and 20 % for coho. This is likely a minimum difference since elevated temperatures reduced conversion efficiencies in both species, and daily temperatures in the steelhead experiment were varied between 7 and 16 °C, whereas in the coho experiment temperature was held constant at 12.5 °C. Circumstantial evidence for countergradient variation in growth rate comes from the observation that the size difference between coho and steelhead fry decreases through the summer growing season (Hartman 1965; Burns 1972). Finally, even though the species’ effect remained significant when only the largest fish were considered, this experiment cannot rule out the possibility that coho growth rates were reduced relative to steelhead by competitive growth suppression. Controlling for the effects of competitive growth suppression would require a similar experiment where individual fish were reared in isolation.

Studies of fish communities from lakes help place the present results in a broader context. Schluter (1993, 1995) used reciprocal transplant experiments to study a pair of stickleback species (Gasterosteus spp.) that forage in the limnetic and benthic zones of lakes. He documented a strong trade-off between habitats in both foraging efficiency and growth rate. Similar trade-offs in foraging efficiency have been documented for lake populations of limnetic cutthroat trout and benthic Dolly Varden (Schultz and Northcote 1972), and within a polymorphic bluegill (Lepomis macrochirus) population (Ehlinger and Wilson 1988). There is also observational evidence for a growth rate trade-off in a polymorphic population of pumpkinseed sunfish (Lepomis gibbosus) from a northeastern (USA) lake (Robinson et al. 1996). In each case, the fitness trade-offs of these species/ecotypes suggest adaptive divergence via specialization on alternative trophic resources.

In contrast, coho and steelhead exhibited no trade-off in growth rate between habitats, indicating a common optimum habitat in the absence of interspecific competition and a lack of adaptive divergence to hydrologic conditions. The present results may represent a more general pattern in the potential for evolutionary divergence within fish communities from hydrologically dynamic streams versus hydrologically stable lakes (Echelle and Kornfield
Interestingly, the growth rates of coho and steelhead in pools and riffles in this experiment are similar to those of morphologically and ecologically intermediate (Bisson et al. 1988) cutthroat trout \((O. clarki)\) fry reared in natural pools and riffles (Rosenfeld and Boss 2001). Studying fish assemblages from mid-western streams (USA), Poff and Allan (1995) found the frequency of specialist species decreased with increasing hydrological variability. Schluter (1996) described examples of incipient speciation driven by divergent trophic specialization in seven different taxa inhabiting postglacial lakes. Though many of the taxa (or closely related taxa) in his review also have stream rearing populations, similar adaptive radiations in postglacial stream communities have yet to be identified (Troffe (2000) presents evidence for a trophic polymorphism in mountain whitefish \((Prosopium williamsoni)\) rearing in large rivers).

In conclusion, I found no evidence that coho and steelhead fry have evolved a growth rate trade-off across pool and riffle habitats. The experiment cannot rule out that such a trade-off might exist in the absence of intraspecific competition, or in the presence of interspecific competition (see Chapter 5). Furthermore, the species morphologies are consistent with adaptation to alternative habitats. Given these caveats, I suggest the absence of a growth rate trade-off may be due to ontogenetic niche shifts by each species and the dynamic nature of stream environments, both of which could prevent specialization on alternative habitat types.
TABLE 2.1. Physical conditions and initial fish sizes for the reciprocal transplant experiment conducted in 1998. All values are means (SD). Depth and velocity means were calculated from the mean values of each experimental channel (six replicates for each of the four treatment combinations). Surface velocity was measured 5 times in each riffle. Temperature means are from the means of 15 measurements taken in each treatment during the experiment. The length and weight means are for all fish placed in each of the four treatment combinations (n = 180).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Pools</th>
<th>Riffles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth (cm)</td>
<td>16.1 (1.5)</td>
<td>4.3 (0.3)</td>
</tr>
<tr>
<td>Velocity (cm/s)</td>
<td>3.8 (0.2)</td>
<td>11.4 (0.8)</td>
</tr>
<tr>
<td>Surface velocity (cm/s)</td>
<td>N.A.</td>
<td>22.3 (0.9)</td>
</tr>
<tr>
<td>Temperature (°C)</td>
<td>coho steelhead</td>
<td>coho steelhead</td>
</tr>
<tr>
<td>Initial length (mm)</td>
<td>11.8 (0.1)</td>
<td>11.8 (0.1)</td>
</tr>
<tr>
<td>Initial weight (g)</td>
<td>31.6 (1.8)</td>
<td>31.4 (1.8)</td>
</tr>
<tr>
<td></td>
<td>0.49 (0.11)</td>
<td>0.45 (0.08)</td>
</tr>
</tbody>
</table>
FIGURE 2.1. The mean growth rate (± 1 SE) of coho and steelhead in artificial pools and riffles. The response variable is the mean growth rate based on final weight of all fish recovered from each treatment (n = 6 for each point).
FIGURE 2.2. The mean coefficient of variation (CV) (± 1 SE) of weight for coho and steelhead reared in artificial pools and riffles (n = 6 for each point).
FIGURE 2.3. The mean growth rate (± 1 SE) of coho and steelhead in artificial pools and riffles. The response variable is the mean growth rate based on final weight of the five largest fish recovered from each treatment (n = 6 for each point).
Evolution of fighting behavior under asymmetric competition: an experimental test with juvenile salmonids

3.1 ABSTRACT

Theory suggests that large-dominant and small-subordinate species engaging in asymmetric interference competition should evolve aggressive and passive fighting behaviors, respectively. To test this prediction, I manipulated the size/competitive asymmetry of juveniles from sympatric populations of large-dominant coho salmon (*Oncorhynchus kisutch*) and small-subordinate steelhead trout (*O. mykiss*) and asked whether differences in fighting behavior persisted independently of competitive ability. I observed fighting behavior during dyadic contests in two habitats, mutually preferred pools and energetically demanding riffles, under each of three size treatments: natural size asymmetry, asymmetry removed, and reversed size asymmetry. The results supported the prediction. Competitive ability depended primarily on size; large individuals of both species dominated smaller heterospecifics and neither species dominated when size matched. Fighting behavior depended primarily on species identity; coho used a higher proportion of aggressive chases, whereas steelhead used a higher proportion of passive displays. Large individuals were more likely to chase, small individuals more likely to display, and coho more likely to chase in pools than in riffles. As evidence that asymmetric competition can promote behavioral divergence, these results compliment previous work suggesting asymmetric competition promotes morphological divergence, and provide a richer context for other features of the coho-steelhead system.

3.2 INTRODUCTION

Interspecific competition is often asymmetric, with individuals of one species reducing the fitness of members of another species more than the reciprocal effect (*a*$_{ij}$ > *a*$_{ji}$) (Lawton and Hassell 1981; Connell 1983; Schoener 1983a). Competitive asymmetries can result from exploitation competition if one species utilizes a limiting resource more efficiently than the other species (Tilman 1982; Morin and Johnson 1988; Giller and Doube
1989), or interference competition if individuals of one species dominate heterospecific contests for mutually preferred habitat (Morse 1974; Case and Gilpin 1974; Gill 1974). In animals, competitive asymmetries generally result from size asymmetries, with individuals of the larger species dominating fighting contests against smaller heterospecifics (Morse 1974; Schoener 1983a). Game theoretic models designed to predict fighting behavior during intraspecific contests provide predictions for how fighting behavior might evolve under interspecific asymmetric competition. When confronted with a competitor, an individual should optimize its fighting behavior based on the perceived trade-off between the chance and value of winning the contest, and some combination of the cost of fighting and the chance of losing the contest (Parker 1974; Maynard Smith and Parker 1976). When interspecific contests are asymmetric, this trade-off differs for the two species. If size is a reliable indicator of competitive ability, then the optimal behavior for individuals of the large-dominant species should be escalation with aggressive fighting behaviors, whereas individuals of the small-subordinate species should be less willing to escalate and more likely to use passive fighting behaviors (Persson 1985). If fighting behavior is heritable and influences life-time fitness, then species engaging in asymmetric interference competition should evolve different fighting behaviors.

Testing the prediction that asymmetric competition promotes divergent evolution in fighting behavior is difficult because environmental conditions, interspecific competition per se, and the strength of intraspecific competition may all influence fighting behavior. Still, two approaches can provide informative tests of the prediction. The first involves comparing two pairs of sympatric populations, one where competition is asymmetric and one where competition is symmetric or asymmetric in the opposite direction, and showing that the fighting behaviors of individuals from the four populations differ in the predicted direction. This is equivalent to a doubly sympatric test of character displacement (Brown and Wilson 1956), where fighting behavior is the character and asymmetric competition, not interspecific competition per se, is the factor of interest. The approach is well established, but in the present context limited by the requirement that other factors that can influence behavior (e.g. productivity, intra- and interspecific density, community composition, predators) must be controlled across the four populations (Grant 1972).
The second approach is to study sympatric populations that experience asymmetric competition and manipulate the phenotypic trait (i.e. size) that determines competitive ability. The prediction would be supported if interspecific differences in fighting behavior persist when the size/competitive asymmetry is removed and reversed. Numerous studies have shown that large-dominant species and small-subordinate species use aggressive and passive fighting behaviors (e.g. Nishikawa 1985; Alatalo and Moreno 1987; Bleich and Price 1995; Marvin 1998), but such studies say little about evolved differences in fighting behavior, only that large individuals use different fighting behaviors than small individuals. The questions we must ask are: 1) does a large-dominant species use aggressive fighting behaviors when the size/competitive asymmetry is removed and reversed?, and 2) is the opposite true for the small-subordinate species? In this paper I use this phenotypic manipulation approach with juvenile coho salmon (Oncorhynchus kisutch) and steelhead trout (O. mykiss) to test the prediction that asymmetric competition is associated with evolved differences in fighting behavior.

Juvenile coho and steelhead occur sympatrically in coastal rivers and streams of western North America and provide a typical example of size-based asymmetric interference competition. Anadromous, semelparous coho return to freshwater to spawn from July to January, with spawning occurring later at lower latitudes (Sandercock 1991; Weitkamp et al. 1995), whereas anadromous, iteroparous steelhead spawn between January and April throughout their range (Withler 1966; Busby et al. 1996). Interspecific differences in the time of adult spawning and fry emergence result in early-emerging coho having a latitude dependent size advantage over late-emerging steelhead during the first summer in freshwater. The size advantage of coho fry is large in northern populations and negligible near the southern end of their sympatric range (Hartman 1965; Burns 1972; Bugert et al. 1991). Juvenile salmonids use a variety of fighting behaviors during intra- and interspecific interference competition for energetically favorable foraging positions in the water column (Hartman 1965; Fausch 1984; Taylor and Larkin 1986; Nielsen 1992; Sabo and Pauley 1997). Both coho and steelhead grow faster in deep, low-velocity pools than in shallow, high-velocity riffles (Quinn and Peterson 1996; Harvey and Nakamoto 1997; Chapter 2). In natural streams coho and steelhead fry tend to occupy pools and riffles, respectively (Hartman 1965; Bisson et al. 1988; Bugert et al. 1991). Given their natural size advantage,
coho are competitively dominant and increase the proportion of steelhead occupying riffle habitat, while steelhead have little effect on habitat selection by coho (Bugert and Bjornn 1991).

Because large-dominant coho and small-subordinate steelhead should perceive different trade-offs during interspecific contests, theory predicts coho should evolve more aggressive fighting behavior than steelhead. To test for differences in fighting behavior between juveniles from sympatric populations of coho and steelhead, I observed fighting behavior during dyadic contests in pools and riffles under each of three size treatments: coho larger than steelhead (natural asymmetry), coho equal to steelhead (asymmetry removed), and coho smaller than steelhead (reversed asymmetry).

3.3 MATERIALS AND METHODS

Study area and populations

I studied populations of coho and steelhead from the Chilliwack River in southwestern British Columbia, Canada (49.1° N, 121.6° W), near the center of their sympatric range (Hartman 1965). The Chilliwack River drains a slightly glaciated mountainous basin of 1250 km² and enters the Fraser River approximately 100 km from the Pacific Ocean. Peak flows occur in the fall and winter during the rainy season and in the spring during snow melt. Water temperatures range from 2 to 15°C. Adult coho spawn in the fall and fry begin emerging in March and April; adult steelhead spawn in the winter and fry emerge May through July. A federal salmon hatchery located at river kilometer 32 maintains hatchery populations of chum (O. keta), chinook (O. tshawytscha), and coho salmon, and propagates wild steelhead for conservation and recreation purposes.

Fish collection and rearing

To minimize the chance of environmental differences affecting fighting behavior, I reared individuals of each species in similar conditions before and during the experiment. On April 23, 1999, I seined approximately 200 newly emerged coho fry from small tributaries and side channels between river kilometers 50 and 60, where Hartman (1965) observed the highest densities of coho and steelhead fry and wild adults of both species spawn. Because of conservation concerns, I was not permitted to collect steelhead fry from the same area. On May 25, I collected approximately 200 newly emerged steelhead fry from
the Chilliwack hatchery. The fry were a random sample from 12 families of wild parents (one
two female x one male). In the lab, coho were placed in identical holding troughs (3.7 length x
0.35 width x 0.20 m depth) in groups of 100 and held at 9.5° C and fed maintenance rations
of standard hatchery feed (Moore-Clark® #1 Crumble) until steelhead were collected. From
May 25 until June 10, coho and steelhead were held at similar densities (≈ 100 fish / trough)
at 9.5° and 11° C, respectively, and fed to satiation one and two times daily, respectively. On
June 10, one month before the beginning of the experiment, I separated fry of each species
into “small”, “medium”, and “large” groups based on visual estimates. Fifty of each size
class of each species were placed in separate troughs. I grouped fish by size to minimize the
chance of prior size asymmetries and dominance hierarchies influencing fighting behavior.
From June 10 until the completion of the experiment all fish were held at 11° C and fed
maintenance rations once daily.

Experimental apparatus

Dyadic contests were conducted in a flow-through aquarium with a 25 cm wide x 25
cm deep x 50 cm long clear plexiglass observation chamber screened at both ends. Water
depth was controlled with an adjustable dam 50 cm behind the back screen. Small gravel
(mean diameter = 10.8 mm [n = 25, SD = 1.9]) was spread across the bottom of the
observation chamber. Standard hatchery feed (same as above) was introduced at the water
surface at the front of the observation chamber through a tube draining a bucket sitting atop a
magnetic stirrer. By maintaining a constant inflow, the depth and velocity of the riffle and
pool treatments were essentially invariant across replicates. For this reason I did not quantify
these parameters during the experiment but instead calculated the mean depth and velocity of
nine points (7, 15, and 21 cm width along three transects 5, 25, and 45 cm from the front of
the observation chamber) for five riffles and five pools; between each habitat replicate I
emptied the tank and reset the dam to simulate experimental conditions. For each of the ten
replicates, I took a single estimate of surface velocity by recording the time it took a small
piece of foam rubber to drift the length of the observation chamber (Table 3.1). Water
temperature was maintained at 11° C throughout the experiment.

Experimental procedure

The experimental design consisted of two habitats (pool and riffle) crossed with three
size treatments (coho larger than steelhead, size matched, and coho smaller than steelhead)
for a total of six treatments. The six treatments were replicated in random order on ten non-consecutive days (blocks) between July 10 and July 25. Size matched fish were of equal length. For the size asymmetry treatments fish differed by approximately 6 mm, similar to the size advantage of coho during mid-summer in local populations (Hartman 1965) and that found to influence the outcome of dyadic contests between yearling coho and cutthroat trout (*O. clarkii*) (Sabo and Pauley 1997) (Table 3.1). Approximately 24 hours before each block of trials, two fish from each of the six holding troughs were lightly anesthetized with tricaine methanesulfate and their standard length (to 1 mm) and weight (to 0.01g) recorded. Fish were then held individually in flow-through buckets until trials were run the following afternoon. During the experiment, fish remaining in the holding troughs were fed after the next day’s test fish were removed, so all test fish were starved for two days to insure active foraging during the trials.

Before each trial 0.05 g of the hatchery feed (same as above) was mixed into the gravity feed bucket with the discharge tube pinched shut. The two test fish were placed in the observation chamber and given five minutes to acclimate. After the acclimation period the feeding tube was opened and the trial began with the first foraging attempt by either fish. Following the trial the test fish were marked with an adipose fin clip to insure they were not reused and returned to the appropriate holding trough. Each trial lasted 10 minutes, during which I recorded the following information: the number of seconds each fish spent in the dominant, upstream position closer to the food source; the number of drift items entering the observation tank; the number of drift items captured by each fish; the total number of fighting behaviors initiated by each fish. Fighting behaviors were divided into three classes of decreasing aggressiveness (Chapman 1962; Hartman 1965; Taylor and Larkin 1986; Sabo and Pauley 1997): chases- an individual actively attacked and attempted to displace the heterospecific competitor; nips- an individual bit the heterospecific competitor; displays- an individual stiffened its body and/or dorsal and anal fins in view of the heterospecific competitor.

**Statistical analyses**

Six response variables were analyzed. The proportion of time a fish spent in the dominant, upstream position and the proportion of total drift items captured were used as measures of competitive ability. The total number of fighting behaviors initiated, and the
proportion of those behaviors that were chases, nips, and displays were used to characterize fighting behavior. To determine the effect of habitat, size, and species on the response variables I used split-plot ANOVAs (Type III SS) in PROC GLM in SAS (1990). In a split-plot design, the different treatment effects and their interactions are tested over different error terms depending on whether they are varied as main-plot or sub-plot factors (Snedecor and Cochran 1980). In this experiment, habitat (pool or riffle) and fish size (smaller, matched, or larger) are main-plot factors, while species (coho or steelhead) is the sub-plot factor. Block (random), habitat and size and their two way interaction were tested over the main-plot error term. Species and all two and three way interactions involving species were tested over the sub-plot error term (Table 3.2). To meet the assumptions of ANOVA, the total number of fighting behaviors initiated was log_{10}(x+1) transformed and all proportional data were arcsine transformed. For graphical clarity, I present the untransformed data. Of the 120 fish observed, 17 did not initiate any fighting behaviors; these fish are not included in the three ANOVAs on behavior type.

3.4 RESULTS

*Competitive ability*

Size was the most important factor influencing position ($F_{2,45} = 31.3$, $P < 0.0001$) (Figure 3.1; Table 3.2). Large and small fish occupied the dominant, upstream position 77 and 23% of the time, respectively. Species identity did not effect position ($F_{1,54} = 1.6$, $P = 0.22$), though coho spent slightly more time than steelhead in the dominant, upstream position (54 and 46%, respectively). There was a significant species × size interaction effect ($F_{2,54} = 3.7$, $P < 0.05$). While both species were dominant when given a size advantage, the degree of dominance was greater for coho experiencing their natural size advantage than for steelhead when the natural size asymmetry was reversed (Figure 3.1). Neither habitat or its interaction effects influenced position.

The results for foraging success were similar to those for position except that both species captured more drift items in pools than riffles ($F_{1,45} = 9.5$, $P < 0.005$) (Figure 3.1; Table 3.2). Size was again the most important factor, with large fish capturing the highest proportion of drift items ($F_{2,45} = 29.6$, $P < 0.0001$). There were moderately significant species and species × size interaction effects. Overall, coho captured slightly more drift...
items than steelhead (45 and 38 %, respectively) \( (F_{1,54} = 4.27, P < 0.05) \), and had higher foraging success under the natural size asymmetry than did steelhead when the size asymmetry was reversed (species × size: \( F_{2,54} = 2.3, P = 0.11 \)). In summary, competitive ability during dyadic contests depended mainly on the relative size of the two species. When fish were size matched, coho had no competitive advantage, and were even slightly subordinate, relative to steelhead. Their slight overall competitive advantage resulted from being more dominant under the natural size asymmetry than were steelhead when the size asymmetry was reversed.

**Fighting behavior**

Of the 17 fish that initiated no fighting behaviors, 9 were small steelhead, all of which spent no (6 fish) or little (24, 45, and 267 seconds) time in the dominant, upstream position. Two small coho (0 and 202 s in the upstream position) initiated no behaviors. Three large coho (51, 600, 600 s in the upstream position) and one size matched coho (0 s) initiated no behaviors. Two large steelhead initiated no behaviors and spent no time in the dominant, upstream position. Thus, there was a tendency for small fish and steelhead (Chi-Squared tests, \( 0.05 < P < 0.15 \)) not to initiate any fighting behaviors.

The total number of fighting behaviors initiated depended mostly on the direction of the size asymmetry, with size matched (mean # of behaviors = 9.1, SE ± 0.88), and large fish (8.0 ± 1.19), initiating more behaviors than small fish (4.4 ± 0.89) \( (F_{2,45} = 11.0, P < 0.0001) \) (Figure 3.2; Table 3.2). However, the number of behaviors each species initiated differed with size and habitat. Coho initiated more fighting behaviors than steelhead when matched with larger heterospecifics (species × size: \( F_{2,54} = 7.9, P < 0.001 \)). There was a moderately significant tendency for both the species to initiate more fighting behaviors when in the “other species’ habitat” (species × habitat: \( F_{1,54} = 3.2, P = 0.08 \); coho initiated more behaviors in riffles than in pools, whereas steelhead initiated more behaviors in pools than in riffles. When the combined behaviors of a dyad is analyzed using single factor ANOVA, size matched (mean # of behaviors = 18.4 ± 1.54) and asymmetry reversed (16.1 ± 1.75) pairs initiated more total behaviors than natural asymmetry pairs (8.7 ± 2.25) \( (F_{2,48} = 12.59, P < 0.0001; \) posterior multiple comparisons, Tukey’s HSD, \( \alpha = 0.05 \)).

There were clear differences in the fighting behaviors of the two species (Figure 3.3; Table 3.2). Coho were more likely than steelhead (27 and 11 %, respectively) to use
aggressive chases ($F_{1,38} = 11.5, P = 0.002$). Though both species were more likely to chase when given a size advantage ($F_{2,44} = 3.25, P < 0.05$), the trend was extreme for steelhead. In 20 contests under the natural size asymmetry, small steelhead did not initiate a single chase against larger coho. In contrast, when the natural size asymmetry was reversed 18% of small coho behaviors were chases against larger steelhead. There was a tendency for coho to initiate more chases in pools than in riffles ($F_{1,38} = 3.42, P = 0.08$). Steelhead were more likely than coho to use passive displays (62 vs. 52%) ($F_{1,38} = 6.9, P = 0.01$). Just as large fish were more likely to chase, small fish were more likely to display ($F_{2,44} = 6.98, P < 0.005$). There was also a significant interaction between species and habitat ($F_{1,38} = 7.85, P < 0.01$); coho displayed more frequently in riffles than in pools (62 vs. 41%), whereas steelhead displayed more frequently in pools than in riffles (71 vs. 52%). The proportion of fighting behaviors that were nips did not vary across any of the experimental factors.

3.5 DISCUSSION

I used a phenotypic manipulation approach to test the prediction that large-dominant and small-submissive species experiencing different trade-offs during interspecific contests will evolve aggressive and passive fighting behaviors, respectively. Coho, which under natural conditions are larger and competitively dominant, used a higher proportion of aggressive chase behaviors. Steelhead, alternatively, used a higher proportion of passive display behaviors. While competitive ability during dyadic contests depended mostly on relative size, fighting behavior was determined mainly by species identity. That coho and steelhead used aggressive and passive behaviors, and that these behaviors persisted independently of competitive ability, supports the prediction that asymmetric competition can promote evolutionary divergence in fighting behavior.

The phenotypic manipulations were largely successful at removing and reversing the natural competitive asymmetry. Competitive ability was influenced mainly by size; each species was dominant when given a 6 mm size advantage, and neither species dominated when size matched (Figure 3.1). Coho tended to be more dominant relative to steelhead under the natural and reversed size asymmetry treatments. This result suggests coho may be slightly superior interference competitors, but it may also be related to the relative weights of the species. Coho have a more laterally compressed body shape and are heavier than
steelhead of the same length (Bisson et al. 1988) (Table 3.1). If relative weight, in addition to length, influenced competitive ability, then the phenotypic manipulations would have failed to remove completely and reverse sufficiently the natural competitive asymmetry. This explanation is consistent with the relative advantage of coho in size asymmetry treatments. However, in the size matched treatments, where lengths were equal but coho had a weight advantage, there was no evidence that coho had a competitive advantage (Figure 3.1). Still, the importance of relative weight may have differed across the size treatments and cannot be ruled out as the cause of the small species effect I observed.

The species initiated the same number of fighting behaviors overall, but different numbers across the three size treatments (Figure 3.2). Small coho initiated more fighting behaviors than small steelhead, suggesting that small-subordinate coho are more willing than small-subordinate steelhead to escalate against a competitive dominant. This result is consistent with the predicted difference in fighting behavior and helps explain the size-dependent difference in competitive ability. There was a marginally significant trend for the species to initiate more behaviors in the other species’ habitat than in their own. In particular, coho used more displays in riffles and steelhead used more displays in pools (Figure 3.3). The habitat dependent increase in passive fighting behavior observed in both species suggests their perception of competitive ability varies with habitat, though I found no evidence that habitat affected the species’ relative competitive abilities (Figure 3.1). Size matched fish and large fish initiated more behaviors than small fish, and when a dyad’s cumulative number of behaviors is considered, size matched and reversed asymmetry pairs initiated more total behaviors than natural asymmetry pairs. The first result is consistent with the widely supported prediction (Parker 1974; Maynard Smith and Parker 1976) that size-matched competitors are more likely than asymmetric competitors to escalate during fighting contests.

The key result of the experiment is that coho and steelhead use fighting behaviors that differ in the direction predicted by the size/competitive asymmetry they experience under natural conditions (Figure 3.3). Coho used a higher proportion a aggressive chases and steelhead used a higher proportion of passive displays. Though interspecific differences in fighting behavior under asymmetric competition have been documented in numerous taxa (Nishikawa 1985; Alatalo and Moreno 1987; Bleich and Price 1995; Marvin 1998), until now
it was not known whether such differences persist independently of the morphological trait that determines competitive ability. Empirical studies of asymmetric competition have focused on its role in structuring communities via segregation along various niche axes (e.g. Morse 1974; Thompson and Fox 1993 and therein; Robinson and Terborgh 1995; Bleich and Price 1995), not on its potential to promote evolutionary divergence in fighting behavior. Similarly, theoretical (Rummel and Roughgarden 1985; Taper and Case 1985, 1992; Brown and Vincent 1987; Law et al. 1997) and empirical studies (Roughgarden and Pacala 1989; Case and Bolger 1991) of coevolution under asymmetric competition have focused on changes in the morphological trait (usually size) responsible for the competitive asymmetry, not divergence in fighting behavior. In as far as they apply to ethological traits, these models suggest asymmetric competition should facilitate evolutionary divergence in fighting behavior, particularly as the relative degree of inter- to intraspecific size asymmetries increases (Law et al. 1997). The results of Law et al. (1997) provide the testable prediction that the degree of evolutionary divergence in fighting behavior between coho and steelhead should mirror the latitudinal cline in juvenile size asymmetry. Behavioral differences should be greater at higher latitudes where size asymmetries are larger, and diminish at lower latitudes where emergence times and fry sizes converge (Cody 1969, 1973).

A number of theoretical and empirical studies provide a broader context for the differences in fighting behavior documented here. Case and Gilpin (1974) incorporated interference and exploitation competition into a Lotka-Volterra model and made three predictions supported by the coho-steelhead system (see also Morse 1974). Competitors that dominate heterospecific encounters should have similar fundamental and realized niches, while the subordinate species should experience niche shifts to the less favorable habitat in sympatry (Bugert and Bjornn 1991). In sympatry, individuals of the subordinate species should utilize habitats where costly interference behaviors are less profitable for the dominant species. The tendency for coho to initiate fewer energetically costly chases and more energetically conservative displays (Pucket and Dill 1985) in the high velocity riffle habitat is consistent with this prediction (Figure 3.3). Finally, Case and Gilpin predicted that there should be a trade-off between interference and exploitation abilities, with the inferior interference competitor being more efficient at utilizing consumable resources. This prediction is supported by experiments showing that steelhead have higher energy conversion
efficiencies and growth rates than coho (Fraser 1969; Everson 1973; Wurtsbaugh and Davis 1977; Chapter 2- Note that the two explanations for different intrinsic growth rates are confounded; growing season lengths are related to the size asymmetry).

The results of the phenotypic manipulation experiment are consistent with the prediction that asymmetric competition promotes evolutionary divergence in fighting behavior, but interspecific competition per se and the intensity of intraspecific competition are also likely to influence the evolution of fighting behavior. Because coho and steelhead partition habitat, individuals should engage in more intra- than interspecific interactions (Hartman 1965; Gill 1974; Morse 1976). Individuals often respond more aggressively to conspecific or ecologically similar congeneric intruders (Myrberg and Thresher 1974; Ebersole 1977; but see Minock 1972; Ambrose and Meehan 1977, for contrary results), particularly when there is strong spatial segregation between species (Robinson and Terborgh 1995; Nishikwa 1985; Hairston et al. 1987). Two experiments using juvenile salmonids are relevant in this context. Sabo and Pauley (1997) found evidence for character displacement in competitive ability by observing dyadic encounters between juvenile coho and cutthroat trout from two populations, one sympatric with coho, the other isolated in allopatry above a waterfall. They found that allopatric cutthroat were better interspecific competitors than sympatric cutthroat, but that there was no difference in the types of fighting behavior used by individuals from the two populations. Rosenau and McPhail (1987) found that coho fry from a high density population were dominant to, and initiated more fighting behaviors than, coho from a low density population. Again, however, there were no differences in the types of fighting behaviors used by individuals from the two populations. Thus, while the presence of heterospecific competitors and the intensity of intraspecific competition influence competitive ability, they do not appear to influence fighting behavior in juvenile salmonids. Future research should combine phenotypic manipulations with variation in all three ecological factors- the degree of competitive asymmetry, the presence of a heterospecific competitor, and the intensity of intraspecific competition- in order to clarify the relative importance of each in the evolution of fighting behavior.
TABLE 3.1. Physical conditions and fish sizes for the six experimental treatments. All values are means (SD). For the physical conditions the means are calculated from the mean depth and velocity of five pools and riffles. The fish lengths and weights, and drift rates are the means for the 10 replicates of each treatment.

<table>
<thead>
<tr>
<th></th>
<th>Pools</th>
<th>Riffles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth (cm)</td>
<td>15 (0)</td>
<td>4.5 (0)</td>
</tr>
<tr>
<td>Velocity (cm/s)</td>
<td>7.6 (0.3)</td>
<td>19.2 (0.7)</td>
</tr>
<tr>
<td>Surface velocity (cm/s)</td>
<td>6.3 (0.8)</td>
<td>16.7 (1.2)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Coho</th>
<th>Steelhead</th>
<th>Difference</th>
<th>Coho</th>
<th>Steelhead</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coho &gt; Steelhead</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length (mm)</td>
<td>43.5 (0.8)</td>
<td>37.7 (1.1)</td>
<td>5.8 (0.6)</td>
<td>43.2 (0.9)</td>
<td>37.3 (0.8)</td>
<td>5.9 (0.6)</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>1.35 (0.09)</td>
<td>0.81 (0.07)</td>
<td>0.54 (0.09)</td>
<td>1.30 (0.11)</td>
<td>0.79 (0.07)</td>
<td>0.51 (0.13)</td>
</tr>
<tr>
<td>Drift rate (# / min.)</td>
<td>2.52 (0.33)</td>
<td></td>
<td></td>
<td>2.45 (0.27)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Coho = Steelhead</th>
<th></th>
<th></th>
<th>Coho = Steelhead</th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Length (mm)</td>
<td>40.1 (1.8)</td>
<td>40.1 (1.8)</td>
<td>0 (0)</td>
<td>40.4 (2.1)</td>
<td>40.4 (2.1)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>1.04 (0.16)</td>
<td>0.98 (0.19)</td>
<td>0.08 (0.07)</td>
<td>1.08 (0.16)</td>
<td>1.03 (0.14)</td>
<td>0.05 (0.05)</td>
</tr>
<tr>
<td>Drift rate (# / min.)</td>
<td>2.47 (0.37)</td>
<td></td>
<td></td>
<td>2.36 (0.31)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Coho &lt; Steelhead</th>
<th></th>
<th></th>
<th>Coho &lt; Steelhead</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Length (mm)</td>
<td>38.1 (0.9)</td>
<td>43.8 (1.1)</td>
<td>5.7 (0.5)</td>
<td>37.6 (0.7)</td>
<td>43.4 (0.8)</td>
<td>5.8 (0.6)</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>0.86 (0.16)</td>
<td>1.28 (0.13)</td>
<td>0.42 (0.16)</td>
<td>0.85 (0.06)</td>
<td>1.29 (0.11)</td>
<td>0.44 (0.09)</td>
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<tr>
<td>Drift rate (# / min.)</td>
<td>2.39 (0.21)</td>
<td></td>
<td></td>
<td>2.54 (0.47)</td>
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</table>
TABLE 3.2. F-statistics for the split-plot ANOVAs on the six response variables. Block, habitat, and size were tested over the main-plot error. Species and all of its interactions were tested over the sub-plot error term. Of the 120 fish observed 17 did not initiate any fighting behaviors. These fish are not included in the analyses of behavior type. For these three ANOVAs the error degrees of freedom are 44 and 38 for the main-plot and sub-plot, respectively.

<table>
<thead>
<tr>
<th>Factor</th>
<th>d.f.</th>
<th>F d.f.</th>
<th>Time dominant</th>
<th>Foraging success</th>
<th>Total behaviors</th>
<th>Proportion of chases</th>
<th>Proportion of nips</th>
<th>Proportion of displays</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
<td>9</td>
<td>9, 45</td>
<td>0.12</td>
<td>0.29</td>
<td>0.52</td>
<td>1.11</td>
<td>1.00</td>
<td>0.98</td>
</tr>
<tr>
<td>Habitat</td>
<td>1</td>
<td>1, 45</td>
<td>0.01</td>
<td>9.53**</td>
<td>0.05</td>
<td>3.12†</td>
<td>2.70</td>
<td>0.07</td>
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<tr>
<td>Size</td>
<td>2</td>
<td>2, 45</td>
<td>31.3***</td>
<td>29.6***</td>
<td>11.0***</td>
<td>3.25*</td>
<td>0.67</td>
<td>6.98**</td>
</tr>
<tr>
<td>Habitat x Size</td>
<td>2</td>
<td>2, 45</td>
<td>1.98</td>
<td>0.09</td>
<td>0.46</td>
<td>0.42</td>
<td>0.37</td>
<td>0.33</td>
</tr>
<tr>
<td>Main-plot Error&lt;sup&gt;a&lt;/sup&gt;</td>
<td>45, 44</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>1, 54</td>
<td>1.55</td>
<td>4.27*</td>
<td>1.53</td>
<td>11.46**</td>
<td>0.01</td>
<td>6.94*</td>
</tr>
<tr>
<td>Species x Habitat</td>
<td>1</td>
<td>1, 54</td>
<td>0.24</td>
<td>0.10</td>
<td>3.19†</td>
<td>3.42†</td>
<td>1.07</td>
<td>7.85**</td>
</tr>
<tr>
<td>Species x Size</td>
<td>2</td>
<td>2, 54</td>
<td>3.67*</td>
<td>2.31</td>
<td>7.99***</td>
<td>0.09</td>
<td>0.74</td>
<td>0.62</td>
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<tr>
<td>Species x Hab. x Size</td>
<td>2</td>
<td>2, 54</td>
<td>0.12</td>
<td>0.26</td>
<td>1.30</td>
<td>0.16</td>
<td>0.69</td>
<td>0.37</td>
</tr>
</tbody>
</table>

<sup>a</sup> Main-plot Error = Block x Habitat + Block x Size + Block x Habitat x Size = 45 df

<sup>b</sup> Sub-plot Error = Block x Species + Block x Species x Habitat + Block x Species x Size + Block x Species x Habitat x Size = 54 df

† P < 0.10, *P < 0.05, **P < 0.01, ***P < 0.001
FIGURE 3.1. The mean proportion of time spent in the dominant, upstream position and mean proportion of drift items captured for coho and steelhead in pools and riffles under three size treatments: coho larger than steelhead (C>S, natural size asymmetry), size matched (C=S, asymmetry removed), and coho smaller than steelhead (C<S, reversed size asymmetry). Error bars = 1 SE. See Table 3.2 for ANOVA results.
FIGURE 3.2. The mean number of fighting behaviors initiated by coho and steelhead in the six treatments. Treatment codes are as in Figure 3.1. Error bars = 1 SE. See Table 3.2 for ANOVA results.
FIGURE 3.3. The proportion of fighting behaviors that were chases, nips, and displays for coho and steelhead in the six treatments. Treatment codes are as in Figure 3.1. Error bars = 1 SE. See Table 3.2 for ANOVA results.

coho | steelhead
OS c=s c<s
POOL
RIFFLE

CHASES
NIPS
DISPLAYS

C>S C=S C<S C>S C=S C<S
POOL RIFFLE

37
CHAPTER 4

The effects of asymmetric competition on habitat selection and niche overlap in juvenile salmonids

4.1. ABSTRACT
I conducted an experiment in artificial stream channels using juvenile coho salmon (Oncorhynchus kisutch) and steelhead trout (O. mykiss) to explore the poorly understood relationship between asymmetric competition, habitat selection, and niche overlap. Under natural conditions coho fry are larger, occupy deep, low-velocity pools, and displace steelhead into shallow, high-velocity riffles. I conducted habitat selection trials over a wide range of species’ densities under each of two competitive scenarios; coho larger than steelhead, and species size matched. When coho had their natural size advantage competition was highly asymmetric and habitat selection by both species depended almost exclusively on coho density. Removing the size advantage of coho reduced the per capita effect of coho on steelhead habitat selection, which depended equally on intra- and interspecific competition. When the species were size matched, habitat selection by coho depended more on intra- than interspecific competition. Asymmetric competition reduced niche overlap non-significantly at the habitat scale (pool, riffle) and significantly at the microhabitat scale averaged over three niche axes (distance from the front of the channel, water depth, and water velocity). The effect of asymmetric competition on niche overlap at the microhabitat scale was density dependent- it reduced niche overlap at low densities and had little effect high densities. Because I manipulated competitive ability without changing the species identity, this experiment controls the effects of evolutionary history on competitive interactions and provides a novel exploration of the relationship between asymmetric competition, density dependent habitat selection, and niche overlap.

4.2. INTRODUCTION
Competition can affect patterns of habitat use and the coevolution of interacting species (Rosenzweig 1987; Schluter 2001). When competitive effects are measured as
changes in habitat use rather than vital rates, asymmetric competition is characterized by a dominant species displacing a subordinate species from a mutually preferred habitat (Morse 1974; Pacala and Roughgarden 1982; Connell 1983; Schoener 1983a; Robinson and Terborgh 1995; Thompson and Fox 1993). Theory suggests habitat shifts associated with asymmetric competition may facilitate evolutionary divergence by subjecting species to selection pressures more different than when competition is symmetric (Rummel and Roughgarden 1985; Taper and Case 1992; Law et al. 1997). Yet, for a number of reasons, the relationship between asymmetric competition, habitat use, and niche overlap remains poorly understood. First, present community organization is influenced by past evolutionary processes (Lawlor 1980; Connell 1980; Rosenzweig 1987, 1991); if competitive asymmetries are observed to vary among different species pairs, evolutionary legacies necessarily confound the change in ecological interactions. Second, low niche overlap may indicate weak competition if species have evolved distinct habitat preferences, or strong competition if asymmetric competition forces individuals of a subordinate species from a mutually preferred habitat (Connell 1980; Rosenzweig 1987). Finally, the relationship between interspecific competition, habitat selection, and niche overlap can vary with species’ densities (Pimm and Rosenzweig 1981; Morris 1999).

One way to address these issues is to manipulate the competitive asymmetry between a single species pair then quantify the effects of that manipulation on habitat selection and niche overlap over a range of species’ densities. In this paper I describe such an experiment. I conducted habitat selection trials over a wide range of species’ densities using juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) under two competitive scenarios: when coho were larger than steelhead, the natural size (competitive) asymmetry, and when the size advantage of coho was removed. I use isoleg analysis (see *Isoleg analysis* below) to quantify the strength of intra- and interspecific competition and their joint effect on habitat selection by each species under each competitive scenario. I then calculate niche overlap at two spatial scales under each competitive scenario. The experiment and analyses extend traditional approaches for studying interspecific competition and help illustrate how the relationship between
asymmetric competition, habitat selection, and niche overlap is both scale and density dependent.

**Study system**

Coho and steelhead occur sympatrically in coastal streams of northwestern North America. Anadromous, semelparous coho return to freshwater to spawn from July to January, with spawning occurring later at lower latitudes (Sandercock 1991; Weitkamp et al. 1995). Anadromous, iteroparous steelhead spawn between January and April throughout their range (Withler 1966; Busby et al. 1996). Differences in the timing of adult spawning and fry emergence result in early emerging coho having a latitude dependent size advantage over steelhead during their first summer in freshwater. In the northern portion of their sympatric range coho fry emerge earlier and are larger than steelhead. At the southern edge of their sympatric range emergence times converge and fry are of similar size during their first summer in freshwater (Hartman 1965; Burns 1972; Bugert et al. 1991).

Juvenile salmonids engage in intra- and interspecific interference competition for energetically favorable positions in the water column (Hartman 1965; Fausch 1984; Taylor and Larkin 1986; Nielsen 1992). Competitive ability depends on size, with larger individuals outcompeting (Sabo and Pauley 1997; Chapter 3) and displacing (Chapman 1962) smaller individuals from favorable habitat. Both coho and steelhead grow faster in deep, low-velocity pools than in shallow, high-velocity riffles (Quinn and Peterson 1996; Harvey and Nakamoto 1997; Chapter 2). In natural streams coho and steelhead fry tend to occupy pools and riffles, respectively (Hartman 1965; Bisson et al. 1988; Bugert et al. 1991). When given their natural size advantage coho are competitively dominant and increase the proportion of steelhead occupying riffle habitat, whereas steelhead have little effect on habitat selection by coho (Bugert and Bjornn 1991).

Thus, the coho-steelhead system has two attractive features for an experimental investigation of the effect of asymmetric competition on habitat selection and niche overlap. First, the species are mobile at the spatial scale relevant to selecting two discrete habitat types, high-quality pools and low-quality riffles. Second, competitive ability depends on the relative size of individuals, which varies naturally throughout their sympatric range and is easily manipulated in the laboratory.
4.3. MATERIALS AND METHODS

Isoleg analysis

Isoleg analysis is an elegant approach for quantifying and visualizing the effects of intra- and interspecific competition on habitat selection (Rosenzweig 1981; Morris 1999). The analysis is based on the principle that habitat selection is an optimal foraging process and that an individual’s fitness maximizing behavior depends on the density of conspecific and heterospecific competitors; it is a multispecies accounting of the same density-dependent processes that result in an ideal free/despotic distribution for single species (Fretwell and Lucas 1970). Isoleg analysis can describe a variety of community structures: distinct habitat preferences or the “ghost of competition past” (Rosenzweig 1981, 1987, 1991; Morris 1999); shared habitat preference (Pimm et al. 1985, Rosenzweig 1986; Abramsky et al. 1990; Sandlin 2000); same preferred but different secondary habitats (Rosenzweig and Abramsky 1986; Abramsky et al. 1990). For the coho-steelhead system the shared preference model is appropriate because both species have higher growth rates in pools than in riffles.

The analysis produces isolegs, lines of equal choice, in a two dimensional phase space where the axes are the numbers of individuals of the two species (Figure 4.1). The isolegs divide the phase space into regions of different patterns of habitat use. When species display partial habitat preferences, the isolegs represent gradual changes in the proportional distribution of individuals of each species among the two habitat types (Rosenzweig 1986). The slopes, intercepts, and curvatures of the isolegs are determined by the relative strengths of intra- and interspecific interactions and how individuals of each species perceive the relative value of the two habitat types.

The location and shape of partial preference isolegs are determined using multiple regression. If the dependent variable ($P_i$) is the proportion of individuals of species $i$ occupying the secondary habitat, the isolegs are described by the coefficients of the regression equation:

$$P_i = \beta_i + \beta_{ii} (N_i) + \beta_{ij} (N_j) + \beta_{ij} (N_i \times N_j) + \epsilon \quad (4.1),$$
where the $N_i$ and $N_j$ are the numbers of individuals species $i$ and $j$ in the system. The intercept, $\beta_i$, measures the preference of the species $i$ for the primary habitat in the absence of competition. The interaction coefficients, $\beta_{ii}$ and $\beta_{ij}$, measure the per capita effect of intra- and interspecific competition on habitat selection by species $i$. They are predicted to be positive. The term $\beta_{ij}$ measures the effect of joint density. Because the per capita value of the secondary habitat should decrease faster with density than the value of the preferred habitat, it is predicted to be negative (Pimm et al. 1985). The isolegs can be mapped onto the phase space following regression analysis by fixing values of $P_i$ and finding the combinations of $N_i$ and $N_j$ that satisfy the equation. An identical equation is used to find the isolegs of species $j$.

Figure 4.1 shows how changing a competitive asymmetry changes the isolegs (see Table 4.1 for the interaction coefficients that produce the isolegs). If competition is perfectly symmetric ($\beta_{ii} = \beta_{ij} = \beta_{ji} = \beta_{jj}$), species identity does not matter, and the species have identical isolegs. If the joint density coefficients ($\beta_{ij}$ and $\beta_{ji}$) are zero, the isolegs are linear and proportional use of the secondary habitat increases with total density (Figure 4.1A). If the value of the secondary habitat decreases faster with joint density than the value of the primary habitat, the joint density coefficients become negative, the isolegs curve, and individuals select the primary habitat over a wider range of (co)densities (Figure 4.1B). If the joint density coefficients are sufficiently negative then the species may actually move back into the preferred habitat when total density is high (Figure 4.1C). This can happen if either the carrying capacity (i.e. per capita value) of the secondary habitat decreases faster with density, or if interference competition is sufficiently stronger in the secondary habitat than in the primary habitat.

If competition is asymmetric ($\beta_{ij} > \beta_{ji}$) the locations, slopes, and shapes of the isolegs change. By convention the dominant species' density is on the x-axis. When the joint density interaction coefficients are zero, the slopes of the subordinate species' isolegs become steeply negative, indicating habitat selection by the subordinate species depends more on the density of the dominant species than on its own density. The isolegs of the dominant species will be nearly vertical, indicating its habitat use depends only on its own density (Figure 4.1D). If the degree of asymmetry and the magnitudes of the joint density coefficients increase, the slopes of the subordinate isolegs rotate from
negative to positive as the density of the dominant increases, indicating that the value of
the secondary habitat to the subordinate species decreases with higher joint densities
(Figure 4.1E). The slopes of the dominant species’ isolegs become steeply positive for
the same reason; as the number of subordinates increases, the relative value of the
secondary habitat decreases. If the dominant species has a stronger preference for the
preferred habitat ($\beta_j < \beta_i$) and a larger intraspecific interaction coefficient ($\beta_{ji} > \beta_{ii}$), its
isoleg values increase and contract along the $x$-axis (Figure 4.1F). If the difference in per
capita value between the habitats is greater, the magnitudes of the joint density terms
increase further, and the rotation and curvature of both species’ isolegs become more
pronounced (Figure 4.1F).

In this paper I use isoleg analysis to explore the relationship between asymmetric
competition and density dependent habitat selection in juvenile coho and steelhead.

Study populations

I studied sympatric populations of coho and steelhead from the Chilliwack River
in southwestern British Columbia, Canada (49.1° N, 121.6° W), near the center of their
sympatric range (Hartman 1965). The Chilliwack River drains a slightly glaciated
mountainous basin of 1250 km$^2$ and joins the Fraser River approximately 100 km from
where it enters the Pacific Ocean at Vancouver, B.C. Water temperatures range from 2 to
15° C. Adult coho spawn in the fall and fry begin emerging in March and April; adult
steelhead spawn in the winter and fry emerge May through July. During their first
summer in freshwater coho fry are 5 – 10 mm longer than steelhead fry (Hartman 1965).
A federal salmon hatchery located at river kilometer 32 propagates wild steelhead for
conservation and recreation purposes.

Fish rearing

On April 19, 2000, I seined $\approx$250 newly emerged coho fry from small tributaries
and side channels between river kilometers 50 and 60, where Hartman (1965) observed
the highest densities of coho and steelhead fry and wild adults of both species spawn.
Because of conservation concerns, I was not permitted to collect steelhead fry from the
same area. On May 16, I collected 250 newly emerged steelhead fry from the Chilliwack
hatchery. The fry were a random sample from 10 families of wild parents (one female $\times$
one male). After collection, fish were transported to the University of British Columbia
(Vancouver) and held in de-chlorinated municipal water before and during the experiment. Water temperature increased gradually from 5° to 10° C between April 19 and June 15 and remained at 10° C for the remainder of the summer. On April 21, I separated the coho into two groups of 125 “small” and “large” fish based on visual estimates. Each group was placed in an identical 700 liter holding tank. From April 21 to May 15 the small and large groups were fed to satiation with standard hatchery feed (Moore-Clark® #1 Crumble) once and twice daily, respectively. From May 16 until the experiment ended on July 18, each group of coho was fed maintenance rations once daily. On May 16 steelhead were placed in two groups of 125 in identical 700 liter holding tanks and fed to satiation twice daily (same feed as above) until June 10, after which they were fed maintenance rations once daily. Four times during the experiment (June 16 to July 18) I measured the standard length of 20 large coho, small coho, and steelhead. Though fish grew during the experiment, small coho and steelhead lengths were never different ($F_{1,152} = 0.06; P = 0.80$), and large coho were consistently 10-12 mm longer than steelhead ($F_{1,152} = 1167.9; P < 0.0001$) (Figure 4.2).

**Experimental apparatus**

The habitat selection trials were conducted in two oval flow tanks, each with two identical artificial stream channels (200 length x 50 width x 20 cm depth) (Figure 4.3). Water was introduced with two hoses, with water level maintained by a single drain pipe. A circular flow was created by placing two submersible pumps at each end of each tank. In each channel I used small gravel to create a single pool-riffle sequence. On the inside window of each channel I drew distance-depth coordinate axes with 1 cm intervals. I used an electronic flow meter to measure the water velocity at the same 132 locations in each channel. At 10 cm distance intervals from 0-70 cm, I took 12 velocity measurements: four depths (0, 5, 10, 20 cm), at each of three sections, near (outside), middle, and far (inside). In the pool-riffle transition sections (80-100 cm) the depth and number of measurements decreased gradually. In the riffle habitats (100-200 cm) I took three velocity measurements at 10 cm distance intervals. Velocity fields were nearly identical for the four channels. The pools were turbulent with low velocity (0-1 cm/second); in the transition sections water velocities increased from 1 to 6 cm/s; the riffle sections had uniform velocities of 14 cm/s. Food (same as above) was introduced
into the channels with feeders (plastic disks glued onto light timers) suspended above the water at the head of each pool (0 cm distance) and riffle (100 cm distance) (Figure 4.3). Each feeder introduced drift at a rate of 0.08 g / hour, near the average for local streams (Keeley and McPhail 1998). During the trials I observed fish from behind a blind of black cloth vertical viewing slits cut at 10 cm intervals.

**Experimental procedure**

Trials were conducted between June 16 and July 18. For each competitive scenario (asymmetric-coho larger than steelhead, symmetric-sizes equal) I conducted habitat selection trials at 115 different density combinations. The number of each species was varied independently from 0 to 20 by 2 to create 121 observations for each competitive treatment. Preliminary observations indicated that this range of densities produced the full range of behaviors for each species, from strong preference for pools to a nearly equal distribution between pools and riffles. The 10 trials with no coho (2 – 20 steelhead) were conducted only once and the data were used for both competitive treatments, giving a total of 120 (121 minus the “observation” where both species were absent) density combinations for each pair of isoleg analyses.

For each treatment, the 115 density combinations were randomly ordered in a list. Each morning two density combinations of each treatment were selected sequentially from the list. The trials were assigned randomly to one of the four channels. Fish were removed from the holding tanks, counted into each of the four channels, the observation blinds were put into position, and the feeders were turned on. The trials lasted three hours, a time determined from preliminary observations as sufficient to stabilize the distribution of individuals between the two habitat types. After three hours I slid furtively from the back to front of the channels behind the observation blind and recorded the following information for every fish: species, whether it was in the pool or riffle, its distance from the front of the channel, and its depth in the water column. At the end of a trial fish were removed from the channels and returned to the holding tanks. This four trial procedure was repeated two or three times daily until all 230 trials were complete.

**Analyses**

The coefficients of (Equation 4.1) were calculated using linear regression in PROC REG in SAS (SAS Institute 1990). The proportion of individuals in the riffle
habitat was used as the response variable in all four regression models. After removing the observations where a species was absent, each isoleg model was based on 110 observations. The regression equations were solved for appropriate isoleg values to create a phase space for each species under each competitive scenario (isoleg phase spaces were graphed using Mathematica®, Wolfram 1996).

For every observation having two non-zero values ($n = 100$ for each competitive scenario) I calculated niche overlap using Pianka’s (1973) symmetrical $\alpha$, where:

$$\alpha_{sc} = \sum_a p_{sa} p_{ca} \sqrt{\frac{\sum_a p_{sa}^2 \sum_a p_{ca}^2}{\sum_a p_{sa}} \sum_a p_{ca}}$$

and $p_{sa}$ and $p_{ca}$ are the proportion of steelhead and coho in habitat type $a$. Every fish in every trial was identified with an interval along each of the three microhabitat niche axes. For distance fish were scored into 10 cm intervals the length of the channel. There were four intervals for depth (0-5, 5-10, 10-15, and 15-20 cm) and three for velocity (0-5, 5-10, 10-15 cm/s). For every observation I calculated $\alpha$ at the habitat scale ($\alpha_{hab}$, pool-riffle), and the microhabitat scale ($\alpha_{micro}$), where $\alpha_{micro} = 1/3 [\alpha_{sc} \text{ (distance)} + \alpha_{sc} \text{ (depth)} + \alpha_{sc} \text{ (velocity)}]$, which is appropriate because the three niche axes were not independent (May 1975). To determine if the size based competitive asymmetry affected niche overlap I used ANCOVA (PROC GLM in SAS; Type III Sums of Squares) with treatment as a main effect, coho number, steelhead number, and their product as covariates, and all main effect interaction terms. For each competitive scenario, I regressed $\alpha_{hab}$ and $\alpha_{micro}$ onto coho number, steelhead number, and their product. For both measures of niche overlap I graphed the difference between the functions (asymmetric – symmetric) to illustrate the density dependent effect of asymmetric competition on niche overlap measured at each spatial scale.

4.4 RESULTS

Habitat selection

Changing the relative size of the species changed the form of interspecific competition and patterns of density dependent habitat selection (Figure 4.4). When coho
had their natural size advantage, interspecific competition was strongly asymmetric. The per capita effect of coho on steelhead habitat selection was thirty times higher than that of steelhead on coho (which was actually negative), and five times as great as the effect of steelhead on its own habitat selection (Table 4.2). As a result, the steelhead isolegs are nearly vertical. The steelhead isolegs rotated and curved from a negative to positive slope across the density space because the two species interacted differently as their densities increased. When coho were rare they decreased the relative value of pools for additional steelhead. As their density increased, coho moved into riffles and decreased the relative value of riffles for additional steelhead. The significant intercept value (0.25) suggests that steelhead are not pure habitat selectors and use riffles even in the absence of competition. Coho habitat selection depended almost entirely on intraspecific competition, as indicated by their nearly vertical, non rotating, isolegs. The slightly negative joint density interaction coefficient resulted in positively sloping isolegs; at any given coho density, the addition of steelhead decreased the value of riffles more than the value of pools. Coho appear to have a stronger preference than steelhead for pools at low densities (an intercept term not significantly different from zero).

Removing the natural size asymmetry resulted in nearly symmetric interspecific competition. The per capita effect of coho on steelhead habitat selection was similar to that of steelhead on coho habitat selection (Table 4.3). For steelhead, similar intra- and interspecific interaction coefficients and the high relative magnitude of the negative joint density interaction term resulted in severely warped isolegs. The relative value of the riffle habitat was lower when the species had similar densities than when densities were dissimilar (similar to Figure 4.1C). The per capita effect of steelhead on their own habitat selection was almost twice as large (though the difference was not significant) as when interspecific competition was asymmetric, suggesting that asymmetric interspecific competition reduced the strength of intraspecific competition. Again, the significant intercept value (0.25) suggests steelhead are not pure habitat selectors. Though the interspecific interaction coefficients were similar, the per capita effect of coho on their own habitat selection was three times the per capita effect of steelhead, resulting in nearly vertical isolegs. However, the coho isolegs rotated and curved as coho density increased, indicating steelhead did affect coho habitat selection. At low coho densities, additional
steelhead decreased the relative value of pools, whereas at high coho densities, adding steelhead decreased the relative value of riffles. Coho habitat selection can be described as that of a strongly interacting dominant. Interestingly, the per capita effect of coho on their own habitat selection did not decrease when their size was reduced; changing the size of coho did not appear to change the strength of intraspecific competition.

**Niche overlap**

Asymmetric competition reduced niche overlap at both spatial scales (Figure 4.5). At the habitat type scale asymmetric competition reduced niche overlap at all densities, but the effect was not statistically significant (Table 4.4). The greatest reduction in niche overlap occurred at high coho and low steelhead densities. The reason for this is seen in Figure 4.4. Asymmetric competition reduced the proportion of coho, and increased the proportion of steelhead, in the riffle habitat when coho were common and steelhead were rare.

When niche overlap is measured as the average along three microhabitat niche axes (distance, depth, velocity), asymmetric competition significantly reduced niche overlap (Figure 4.5; Table 4.4). The effect was strongest at low densities and disappeared as density increased because niche overlap increased faster with density under asymmetric competition (significant interaction effects in Table 4.4). The reduction in niche overlap occurred because the species arranged themselves differently along the distance and depth niche axes under the two competitive scenarios. The effect of asymmetric competition on niche overlap along the velocity axis was non-significant and similar to that for habitat type ($F_{1,192} = 0.78, P = 0.38$). This was because the water velocities in pools and riffles were invariant within habitat type, but uniformly different between habitat types.

Asymmetric competition tended to increase niche overlap along the distance niche axis (asymmetric mean = 0.41 (SD = 0.20); symmetric mean = 0.35 (0.19); $F_{1,192} = 1.19, P = 0.28$). This occurred primarily because the competitive asymmetry changed how the two species arranged themselves in the pool habitats. Taking the mean distance of fish in pool habitats across all density combinations, coho and steelhead were nearly twice as close together under asymmetric competition (mean of mean coho distance = 54.1, (SD =12.7); steelhead = 61.8 (12.7)) as when the species were size matched (coho = 49.3
When the species were size matched coho held positions significantly closer to the front of pools over all density combinations ($F_{1,197} = 7.54, P < 0.01$)

Niche overlap along the depth niche axis was significantly lower under asymmetric competition (asymmetric mean = 0.68 (SD = 0.24); symmetric mean = 0.74 (0.18); $F_{1,192} = 18.05, P < 0.0001$). This occurred because large coho displaced more steelhead into riffle habitats, where fish could only occupy a single depth interval (0-5 cm), but also because the species again arranged themselves differently in pools under the two competitive scenarios. As above, taking the mean depth of fish in pool habitats across all density combinations, coho and steelhead were more segregated when competition was asymmetric (coho = 12.1 (4.8); steelhead = 14.6 (7.1)) than when the species were size matched (coho = 11.6 (1.8); steelhead = 12.1 (2.8)). Steelhead were significantly deeper in pools under asymmetric competition than when the species were size matched ($F_{1,192} = 10.53, P < 0.005$).

4.5 DISCUSSION

Habitat selection

Changing the relative size of coho and steelhead changed the per capita effects of intra- and interspecific competition, and as a result patterns of habitat selection and the location and shape of both species' isolegs. When coho had their natural size advantage, competition was strongly asymmetric. The interspecific interaction coefficients differed by nearly two orders of magnitude, and habitat selection by both species depended almost exclusively on coho density. The steelhead isolegs rotated from steeply negative to steeply positive as coho density increased, whereas those of coho were nearly vertical throughout the phase space.

When the natural size advantage of coho was removed interspecific competition was symmetric. For steelhead, competition was "truly" symmetric in the sense that the ratio of the inter- to intraspecific interaction coefficients was near unity; the species identity of competitors had little effect on steelhead habitat selection. The high magnitude of the joint density interaction coefficient relative to the two interspecific interaction coefficients resulted in severely warped isolegs indicative of strong density
dependent interactions at high joint densities. Only when one species was rare and the other common did the relative value of the riffle habitat increase for steelhead. Had the joint density interaction coefficient been slightly less negative, the steelhead isolegs would have rotated through the vertical (the per capita effect of coho was slightly higher) but warped to near horizontal at low coho and high steelhead densities. For size matched coho, the interspecific and joint density interaction terms were similar to those for steelhead; the species affected one another’s habitat selection similarly. However, the species had different isolegs because coho had a three-fold higher intraspecific interaction coefficient than steelhead. The nearly vertical and rotating isolegs suggest that when coho and steelhead are size matched, coho behave as a strongly interacting dominant.

Two interesting things happened when the size asymmetry between coho and steelhead was removed. First, the intraspecific interaction coefficient for steelhead doubled. Reducing the competitive dominance of coho increased the strength of intraspecific competition in steelhead. This makes sense if the presence of large coho inhibited territorial behavior in steelhead, which would reduce the strength of intraspecific density dependent competition. Second, the intraspecific interaction coefficient for coho did not decrease. This is surprising because territory size increases allometrically with fish size in stream rearing salmonids (Keeley and McPhail 1998), meaning the carrying capacity of pools should be higher for small coho. There are two possible explanations. First, because large coho displace more steelhead into the riffle habitat, there was more space available in the pool habitat. Alternatively, large coho may have a stronger preference for pools than small coho and, as intraspecific density increases, reduce territory size in pools rather than move into riffles (Dill et al. 1981; Schoener 1983b).

Steelhead habitat selection was less predictable than coho habitat selection. Both regression models for coho habitat selection were significant and explained 20 to 30% of the variation in the data. The model for steelhead habitat selection was significant only under asymmetric competition, and explained only 10% of the variation in the data. This occurred for two reasons. First, there was more total variation in steelhead habitat selection. Second, steelhead habitat selection was not significantly affected by steelhead
density under either competitive scenario. The significantly positive intercepts of the steelhead regressions and the apparent absence of intraspecific density-dependent selectivity suggest steelhead is the habitat generalist of the two species system. This is consistent with the general pattern of competitive subordinates having wider fundamental (and realized) niches, and being less selective than competitive dominants (Morse 1974).

Niche overlap

Asymmetric competition reduced niche overlap in a way that underscores two long-standing caveats for studying the relationship between interspecific competition and niche overlap (Colwell and Futuyma 1971; Lawlor 1980). First, the effect of asymmetric competition on niche overlap is density dependent. This result would not have been apparent if the effects of asymmetric competition on habitat selection and niche overlap were studied using a traditional additive or replacement experimental design (Scheiner and Gurevitch 1993). Second, the effect of asymmetric competition on niche overlap depends on the scale, or “grain”, at which niche overlap is measured (Levins and McArthur 1966; Vandermeer 1972). This result is particularly relevant to the coevolutionary consequences of competition (Rosenzweig 1986, 1991; Chesson and Rosenzweig 1991). If the target (e.g. behavior vs. morphology) of natural selection changes with spatial scale or along different niche axes, then asymmetric competition may promote evolutionary divergence in some traits but not others. It is important to appreciate that asymmetric competition does not necessarily reduce niche overlap among habitat selecting species. If asymmetric interspecific competition is associated with stronger intraspecific competition in the dominant species, the effect on niche overlap of increased use by the subordinate of the secondary habitat may be cancelled out by a similar response in the dominant.

At both spatial scales, the reduction in niche overlap under asymmetric competition depended on the species’ densities. At the habitat scale, the reduction in niche overlap was slight, yet more pronounced when coho were common and steelhead were rare. At the microhabitat scale, asymmetric competition reduced niche overlap at low but not high densities. This was because at low densities segregation at the microhabitat scale was greater under asymmetric competition, and as densities increased there was less space available for the species to segregate themselves along the different
microhabitat niche axes (significant interaction terms in Table 4.4B). Interestingly, under both competitive scenarios at both spatial scales niche overlap was relatively low, not high, when species' densities were low (data not shown). This is opposite the expectation for a shared preference community; niche overlap should be high when densities are low and both species select the preferred habitat, and decrease as densities increase and the subordinate moves into the secondary habitat (Colwell and Futuyma 1971; Vandermeer 1972; Rosenzweig 1981). Niche overlap increased with density because the species displayed different partial preferences for the pool habitat at low densities but more similar preferences as their densities increased, particularly when they were size matched (Figure 4.4).

Under asymmetric competition the species had significantly lower niche overlap at the microhabitat scale, particularly along the depth niche axis. When competition was symmetric, coho and steelhead occupied the front and back of pools, respectively, but were at similar depths, and both species appeared to forage actively. When competition was asymmetric more steelhead were forced into the riffle habitat and those that remained in the pools were displaced toward the bottom of the water column. The effect of asymmetric competition on steelhead position and behavior was more dramatic than indicated by the change in niche overlap. Many of the steelhead that remained in the pool habitat did not forage and simply held positions above the gravel or near the water surface on the periphery of the stream channel. Thus, asymmetric competition affected the distribution and behavior of steelhead within habitat types more than their distribution between hydrologically distinct habitat types. This result is consistent with the results of Chapters 2 and 3, which suggest that the two species have diverged more behaviorally than in their abilities to grow in different habitats, and the notion that behavioral divergence is the necessary precursor to divergence in other phenotypic traits (West-Eberhard 1989)

I know of two other studies that have controlled species identity when studying the relationship between asymmetric competition and niche overlap (Pacala and Roughgarden (1982) used two different two species Anolis lizard communities to show that asymmetric competition reduced niche overlap). First, Thompson and Fox (1993, and references therein) have shown that an age- and size-class dependent competitive
asymmetry between Australian rodents influences patterns of habitat selection. Second, Hairston and his colleagues have studied sympatric populations of salamanders in the southeastern United States (reviewed in Hairston et al. 1987). On one mountain range the species overlap broadly along an altitude gradient, whereas on another the two species have distinct altitudinal distributions. A series of experiments suggest that: competition is more asymmetric in the populations with low altitudinal overlap; microhabitat and diet overlap do not differ between locations; individuals from the low overlap populations are superior interference competitors. Thus, similar to coho-steelhead system, asymmetric competition reduces niche overlap. However, the scale or “grain” at which asymmetric competition reduces niche overlap is opposite that observed in this study. Hairston has suggested the evolution of interference behavior as an alternative to resource and/or microhabitat partitioning in the face of competition (termed “alpha-selection” by Gill 1974).

Conclusion

I manipulated a natural size asymmetry between coho salmon and steelhead trout to examine the equivocal relationship between asymmetric competition, density dependent habitat selection, and niche overlap. The results confirmed two poorly tested predictions of competition theory: asymmetric competition increases the niche shift of the subordinate species, and as a result decreases niche overlap between species. The approach of combining isoleg analysis with measures of niche overlap over a broad range of co-densities illustrates how the relationship between asymmetric competition, habitat selection, and niche overlap depends on density, spatial scale, and niche dimensionality.
TABLE 4.1. Regression coefficients for the isolegs in Figure 4.1. Coefficients are defined in the *Isoleg analysis* section of the text. Figures 4.1A-C are for symmetric competition, 4.1D-4.1F for asymmetric competition. Both axes range from 0 to 20.

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<th>Figure</th>
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<th>$\beta_{ij}$</th>
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TABLE 4.2. Results of regression analyses for coho and steelhead habitat selection when coho have their natural size advantage over steelhead.

A) Dependent variable: proportion of steelhead in riffle habitat.

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<td>0.10</td>
</tr>
<tr>
<td>Error</td>
<td>106</td>
<td>2.99</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Total</td>
<td>109</td>
<td>3.33</td>
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<tr>
<th>Parameter</th>
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<th>P</th>
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<tbody>
<tr>
<td>Intercept</td>
<td>0.251</td>
<td>0.0647</td>
<td>$\beta = 0$</td>
<td>3.88</td>
<td>0.0002</td>
</tr>
<tr>
<td>Coho density ($x$)</td>
<td>0.0118</td>
<td>0.00547</td>
<td>$\beta \leq 0$</td>
<td>2.17</td>
<td>0.016</td>
</tr>
<tr>
<td>Steelhead density ($y$)</td>
<td>0.0027</td>
<td>0.00521</td>
<td>$\beta \leq 0$</td>
<td>0.52</td>
<td>0.30</td>
</tr>
<tr>
<td>$x \times y$ interaction</td>
<td>-0.000296</td>
<td>0.000441</td>
<td>$\beta \geq 0$</td>
<td>-0.67</td>
<td>0.25</td>
</tr>
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</table>

B) Dependent variable: proportion of coho in riffle habitat.

<table>
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<tr>
<th>Source</th>
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<th>F</th>
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<td>Model</td>
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<td>0.54</td>
<td>13.9</td>
<td>0.0001</td>
<td>0.28</td>
</tr>
<tr>
<td>Error</td>
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<td>1.38</td>
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<td></td>
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<th>Standard error</th>
<th>$H_0$</th>
<th>t value</th>
<th>P</th>
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</thead>
<tbody>
<tr>
<td>Intercept</td>
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<td>0.0439</td>
<td>$\beta = 0$</td>
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<td>0.18</td>
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<tr>
<td>Coho density ($x$)</td>
<td>0.0118</td>
<td>0.00354</td>
<td>$\beta \leq 0$</td>
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<td>0.0006</td>
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<tr>
<td>Steelhead density ($y$)</td>
<td>-0.000374</td>
<td>0.00371</td>
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<td>-0.10</td>
<td>0.46</td>
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<td>$x \times y$ interaction</td>
<td>-0.0000415</td>
<td>0.000299</td>
<td>$\beta \geq 0$</td>
<td>0.139</td>
<td>0.45</td>
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</table>
TABLE 4.3. Results of regression analyses for coho and steelhead habitat selection when coho and steelhead are the same size.

A) Dependent variable: proportion of steelhead in riffle habitat.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>S.S.</th>
<th>F</th>
<th>P</th>
<th>$R^2$</th>
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<tbody>
<tr>
<td>Model</td>
<td>3</td>
<td>0.064</td>
<td>0.86</td>
<td>0.46</td>
<td>0.02</td>
</tr>
<tr>
<td>Error</td>
<td>106</td>
<td>2.626</td>
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<tr>
<td>Total</td>
<td>109</td>
<td>2.69</td>
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<td></td>
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</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Parameter</th>
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<th>Standard error</th>
<th>$H_0$</th>
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<th>$P$</th>
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<tbody>
<tr>
<td>Intercept</td>
<td>0.251</td>
<td>0.0606</td>
<td>$\beta = 0$</td>
<td>4.14</td>
<td>0.0001</td>
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<tr>
<td>Coho density ($x$)</td>
<td>0.00623</td>
<td>0.00513</td>
<td>$\beta \leq 0$</td>
<td>1.22</td>
<td>0.11</td>
</tr>
<tr>
<td>Steelhead density ($y$)</td>
<td>0.00457</td>
<td>0.00489</td>
<td>$\beta \leq 0$</td>
<td>0.94</td>
<td>0.17</td>
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<tr>
<td>$x \times y$ interaction</td>
<td>-0.00611</td>
<td>0.00413</td>
<td>$\beta \geq 0$</td>
<td>-1.48</td>
<td>0.07</td>
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</table>

B) Dependent variable: proportion of coho in riffle habitat.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>S.S.</th>
<th>F</th>
<th>$P$</th>
<th>$R^2$</th>
</tr>
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<tbody>
<tr>
<td>Model</td>
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<td>0.40</td>
<td>8.8</td>
<td>0.0001</td>
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</tr>
<tr>
<td>Error</td>
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<td>1.61</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Total</td>
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<td>2.01</td>
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<td></td>
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</table>

<table>
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<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Standard error</th>
<th>$H_0$</th>
<th>t value</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.0469</td>
<td>0.0474</td>
<td>$\beta = 0$</td>
<td>0.99</td>
<td>0.32</td>
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<tr>
<td>Coho density ($x$)</td>
<td>0.0144</td>
<td>0.00382</td>
<td>$\beta \leq 0$</td>
<td>3.77</td>
<td>0.0002</td>
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<td>Steelhead density ($y$)</td>
<td>0.00505</td>
<td>0.004</td>
<td>$\beta \leq 0$</td>
<td>1.26</td>
<td>0.11</td>
</tr>
<tr>
<td>$x \times y$ interaction</td>
<td>-0.000426</td>
<td>0.000323</td>
<td>$\beta \geq 0$</td>
<td>-1.32</td>
<td>0.10</td>
</tr>
</tbody>
</table>
TABLE 4.4. Results of the ANCOVAs on niche overlap measured at the habitat type and microhabitat niche axes scales. For both models the two treatments are coho larger than steelhead (asymmetric competition) and coho and steelhead size matched (symmetric competition).

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A) α habitat scale</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>1</td>
<td>0.0013</td>
<td>0.12</td>
<td>0.73</td>
</tr>
<tr>
<td>Steelhead number</td>
<td>1</td>
<td>0.0092</td>
<td>0.81</td>
<td>0.36</td>
</tr>
<tr>
<td>Coho number</td>
<td>1</td>
<td>0.0014</td>
<td>0.12</td>
<td>0.72</td>
</tr>
<tr>
<td>Steelhead × Coho</td>
<td>1</td>
<td>0.0029</td>
<td>0.26</td>
<td>0.61</td>
</tr>
<tr>
<td>Treatment × SH</td>
<td>1</td>
<td>0.0046</td>
<td>0.04</td>
<td>0.84</td>
</tr>
<tr>
<td>Treatment × Coho</td>
<td>1</td>
<td>0.0093</td>
<td>0.81</td>
<td>0.36</td>
</tr>
<tr>
<td>Treat. × SH × Coho</td>
<td>1</td>
<td>0.0013</td>
<td>0.12</td>
<td>0.73</td>
</tr>
<tr>
<td>Error</td>
<td>192</td>
<td>0.011</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>B) α microhabitat scale</strong></td>
<td></td>
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</tr>
<tr>
<td>Treatment</td>
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<td>0.13</td>
<td>13.1</td>
<td>0.0004</td>
</tr>
<tr>
<td>Steelhead number</td>
<td>1</td>
<td>0.016</td>
<td>1.68</td>
<td>0.19</td>
</tr>
<tr>
<td>Coho number</td>
<td>1</td>
<td>0.071</td>
<td>7.36</td>
<td>0.007</td>
</tr>
<tr>
<td>Steelhead × Coho</td>
<td>1</td>
<td>0.029</td>
<td>3.05</td>
<td>0.08</td>
</tr>
<tr>
<td>Treatment × SH</td>
<td>1</td>
<td>0.068</td>
<td>7.1</td>
<td>0.008</td>
</tr>
<tr>
<td>Treatment × Coho</td>
<td>1</td>
<td>0.085</td>
<td>8.84</td>
<td>0.003</td>
</tr>
<tr>
<td>Treat. × SH × Coho</td>
<td>1</td>
<td>0.039</td>
<td>4.13</td>
<td>0.04</td>
</tr>
<tr>
<td>Error</td>
<td>192</td>
<td>0.0097</td>
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</tr>
</tbody>
</table>
FIGURE 4.1. The proportion of individuals (isolegs) in the secondary habitat as a function of the number of individuals of each species in the system. If competition is symmetric the species have the same isolegs. If there is no density dependence in the secondary habitat, the isolegs are linear with slope = -1 (A). If the relative per capita value of the secondary habitat decreases faster with density, individuals occupy the preferred habitat over a wider range of co-densities and the isolegs bend (B). If the carrying capacity of the secondary habitat is sufficiently low, individuals may move back into the primary habitat at high co-densities (C). When competition is asymmetric the dominant (bold lines) and subordinate species (thin lines) have different isolegs. If the co-density interaction coefficients are zero, the subordinate has nearly vertical isolegs because its habitat selection depends primarily on the number of individuals of the dominant species, whose isolegs are vertical (D). If there is density dependence in the secondary habitat, the co-density interaction coefficients become negative and the subordinate isolegs curve and rotate through vertical, while the dominant isoleg slopes positively (E). If the dominant species is more selective for the primary habitat and experiences stronger intraspecific competition, its isolegs contract along the x-axis (F). If the co-density interaction coefficients are more negative, the curvature of both sets of isolegs increases (F). See Table 4.1 for the interaction coefficients, and the text (Isoleg analysis) for details.
FIGURE 4.2. The mean standard lengths (mm) of 20 fish from each of the three experimental groups at four times during the experiment (June 16 to July 18). Error bars are ± 1 SE.
FIGURE 4.3. Schematic of the two oval flow tanks used for the habitat selection trials. Each tank had two artificial stream channels.
FIGURE 4.4. The isolegs showing the proportion of coho and steelhead in the riffle habitat as a function of the species' densities under the two competitive scenarios. See Tables 4.1, 4.2 for the interaction coefficients that produce the figures.
FIGURE 4.5. The density dependent reduction in niche overlap resulting from coho having a size advantage over steelhead. Niche overlap was calculated at two spatial scales: $\alpha$ habitat scale- proportion of individuals of each species in pools and riffles, $\alpha$ microhabitat- the mean of three $\alpha$s along distance, depth, and velocity niche axes. See Table 4.4 for ANCOVA results.
CHAPTER 5

Habitat Diversity and Species Diversity: Testing the Competition
Hypothesis with Juvenile Salmonids

5.1 ABSTRACT

I experimentally tested two predictions of the hypothesis that the positive relationship between habitat diversity and species diversity arises from a reduction in the negative effects of interspecific competition. By allowing species to partition habitat and avoid competition, habitat diversity should 1) facilitate the addition of an ecological intermediate into an existing community, and 2) reduce the negative effects of that species on existing members of the community. I tested these predictions with juveniles of three sympatric salmonid species: coho salmon (*Oncorhynchus kisutch*), steelhead trout (*O. mykiss*), and cutthroat trout (*O. clarki*), which in natural streams occupy deep low-velocity pools, shallow high-velocity riffles, and intermediate habitats, respectively. I introduced two (coho and steelhead) and three species communities into each of three artificial stream habitats: pools, riffles, and diverse. The results supported the predictions. Cutthroat grew fastest in the diverse stream habitat. Though habitat diversity did not eliminate the negative effects competition, in the three species community coho and steelhead grew as fast in the diverse habitat as in either homogeneous habitat. The results help explain patterns in species number and evenness observed in natural communities, where variation along other niche axes confounds the relationship between habitat diversity, interspecific competition, and species diversity.

5.2 INTRODUCTION

Few ideas in ecology enjoy the historical legacy, intuitive appeal, and empirical support as does that of a causal relationship between habitat diversity and species diversity (Elton 1933; MacArthur and MacArthur 1961; Pianka 1966; MacArthur 1972; Ricklefs and Schluter 1993; Rosenzweig 1995). The pattern has evolutionary and ecological explanations, both of which invoke the niche concept, interspecific competition, and the partitioning of habitat (defined here as “the physical arrangement of
objects in space” following McCoy and Bell (1991)) and/or consumable resources by ecologically similar species (MacArthur and Wilson 1967; Rosenzweig 1995). Habitat diversity may promote speciation if traits related to differential habitat utilization strengthen reproductive isolation between phenotypically divergent forms (Mayr 1963; Rosenzweig 1978; Futuyma 1986; Schluter 1996). Habitat diversity may increase species diversity by allowing ecologically similar species to utilize different habitats, thus reducing the negative effects of interspecific competition and the chance of competitive exclusion (MacArthur and Levins 1964, 1967; Levins 1968; Schoener 1974; Abrams 1983).

Empirical support for the “competition hypothesis”, that habitat diversity increases species diversity by reducing the negative effects of interspecific competition, is unsatisfying for two related reasons. First, habitat diversity is often directly or indirectly related to productivity, which can independently influence species interactions and species diversity. Second, changes in habitat diversity are usually related to variation along other environmental niche axes (e.g., consumable resources, predators, parasites, climate, disturbance regimes) that can influence competitive interactions, species’ vital rates, and species diversity.

Though the form of the relationship can vary (Tilman 1982; Abrams 1995; Rosenzweig 1995) productivity influences species diversity (Connell and Orias 1964; MacArthur 1972; Brown 1973; Davidson 1977; Tilman 1982; Abramsky and Rosenzweig 1984; Huston 1985; Abrams 1988; Rosenzweig and Abramsky 1993; Srivastava and Lawton 1998). The relationship between habitat diversity and species diversity is often confounded by a correlation between habitat diversity and productivity. In many animal communities species diversity is positively related to the structural diversity of plant communities, which results from, and in some cases creates, spatial variation in productivity (MacArthur 1964; Pianka 1967; Whiteside and Harmsworth 1967; Rosenzweig and Winakur 1969; Orians 1969; Murdoch et al. 1972; Gorman and Karr 1978; Tonn and Magnuson 1982; Lawton 1983; Siemann et al. 1998). Even if not directly related to productivity, the physical structure that creates habitat diversity may regulate the availability and/or diversity of consumable resources (Kohn 1968; Harner
The distinction between habitat diversity and other types of environmental variation is clarified by considering Hutchinson's (1957) definition of the niche "hypervolume" and the conceptually analogous partitioning of interspecific competition along different environmental axes (Birch 1957; Park 1962; May 1975). A species' "fundamental" niche is a volume within a multidimensional space whose axes are different abiotic and biotic conditions: habitat, consumable resources, predators, time, climate, disturbance regime, essentially anything external to the species (Hutchinson 1957). Species may compete for habitat and resources, resources but not habitat, or habitat but not resources. The latter cases correspond to the two traditional, nonexclusive forms of interspecific competition, exploitation and interference, respectively (Birch 1957; Park 1962; Case and Gilpin 1974), and are those invoked in the competition hypothesis. Explicitly testing the hypothesis that habitat diversity can increase species diversity by reducing the strength of interspecific competition requires that variation along other environmental axes be controlled. I know of no field studies that have isolated the effect of habitat diversity on species diversity, and laboratory experiments widely cited as supporting the competition hypothesis (Crombie 1945; Huffaker 1958; Huffaker et al. 1963; Reed 1978) actually involve species interactions other than traditional forms of competition.

With the confounding effects of productivity and niche dimensionality in mind, I use a simple community of three salmonid species (Oncorhynchus spp.) to experimentally test two predictions of the competition hypotheses. By allowing ecologically similar species to partition habitat and avoid interspecific competition, habitat diversity should: 1) facilitate the addition of an ecologically intermediate species into an existing community, and 2) reduce the negative competitive effects of the additional species on the existing members of the community.
5.3 MATERIALS AND METHODS

The system

Juvenile coho salmon (*O. kisutch*), steelhead trout (*O. mykiss*), and cutthroat trout (*O. clarkii*) occur together in coastal streams of northwestern North America and provide an attractive system to test the predictions of the competition hypothesis. All three species are anadromous (both trout species also exhibit non-anadromous life histories); coho are semelparous and migrate to the ocean as smolts after 18 or 30 months in freshwater; both trout species are optionally iteroparous and smolt after 2 to 5 years in freshwater (Hartman 1965; Trotter 1989; Sandercock 1991). As yearlings all three species forage on insect drift and engage in intra- and interspecific interference competition to acquire and defend energetically favorable positions in the water column (Chapman 1962; Hartman 1965; Fausch 1984; Nielsen 1992; Sabo and Pauley 1997). Favorable foraging positions can result in higher juvenile growth and survival rates, making juvenile growth rate a measure of fitness relevant to populations' vital rates and community composition (Bilton et al. 1982; Quinn and Peterson 1996; Harvey and Nakamoto 1997). Few streams support populations of all three species; small, low-gradient streams often contain only coho and/or cutthroat, while larger, high-gradient streams are dominated by steelhead, with few coho or cutthroat (Hartman and Gill 1968; Reeves et al. 1993). In communities with all three species cutthroat trout are often rare (Bisson et al. 1988; Reeves et al. 1993) and yearlings of the three species partition habitat in a predictable way. Coho occupy energetically favorable pools (deep, low velocity), steelhead occupy energetically demanding riffles (shallow, high velocity), and cutthroat utilize intermediate depths and velocities (Bisson et al. 1988). As in many species assemblages, there is observational evidence that habitat diversity is positively related to species number and evenness in this three species assemblage (Reeves et al. 1993), but the hypothesis that habitat diversity reduces the strength of interspecific competition remains untested.

In this experiment I control productivity and variation along other environmental niche axes to test the two predictions of the competition hypothesis: that habitat diversity will 1) increase the growth rate of ecologically intermediate cutthroat in a three species
community, and 2) reduce the negative effect of cutthroat on coho and steelhead compared to homogeneous pool and riffle habitats.

Fish collection and rearing

In the spring of 1999 I collected wild yearlings of all three species soon after emergence from the egg stage. Because of conservation concerns, only coho were taken from natural streams. On March 19 I collected \( \approx 300 \) newly emerged cutthroat from the Fraser Valley provincial trout hatchery located 70 km inland from the mouth of the Fraser River in British Columbia, Canada (49° N, 122° W). The fish were a random sample from the offspring of 10 families (one female, one male) of wild cutthroat trout. On April 23, I pole seined \( \approx 400 \) newly emerged coho from small tributaries of the Chilliwack River, which enters the Fraser River 100 km from the Pacific Ocean. On May 25, I collected \( \approx 400 \) newly emerged steelhead from the Chilliwack River hatchery. The fish were a random sample from the offspring of 12 families (one female, one male) of wild steelhead trout. All fish were held in allopatry in groups of \( \approx 100 \) in identical rearing troughs (3.7 m length x 0.35 m width x 0.20 m depth) from the time of collection until the experiment began on June 18. Cutthroat and coho were held at 9.5° C and fed maintenance rations of standard hatchery feed (Moore-Clark® #1 Crumble) from collection until May 25. From May 25 until June 10 all fish were held at 11° C and fed to satiation one to three times daily. From June 11 to June 17 all fish were held at 11° C and fed to satiation once daily. The rearing program was designed to eliminate interspecific size asymmetries that result in size dependent competitive asymmetries (Sabo and Pauly 1997; Chapters 3 and 4; Table 5.1). I chose to control for this variation because emergence times vary within and between species throughout their sympatric range and I wanted to isolate the effect of habitat diversity on interspecific interactions.

Experimental design

The experimental design consisted of three habitat treatments (pool, riffle, and diverse) crossed with two communities (coho and steelhead, all three species) with the 6 treatments replicated once in each of three blocks (\( n = 18 \)). The experimental units were small stream channels made of plywood lined with plastic (wetted surface area: 4 m length x 0.9 m width). Each channel was screened with plastic mesh at both ends to prevent fish from escaping. The blocks were arranged so that filtered water flowed from a
common head tank into the 6 channels of block one, from each of those channels into block two, then into block three. This design controlled for temperature increases as water flowed through the blocks. I manipulated the amount and location of gravel (6 cm diameter from a local quarry) in the channels to create two of each habitat type in randomly chosen channels within each of the three blocks. Pools were uniformly deep with low water velocities. Riffles were uniformly shallow with high water velocities. Diverse habitats had a wider range of depth/velocity combinations and were created by splitting the channel into four quadrants with pool and riffle areas on alternate sides in the front and back of the channel with a small riffle transition zone in the center (a "figure 8" shape). The diverse habitat treatment simultaneously increased habitat "heterogeneity" by adding new (intermediate) depth/velocity combinations and altered habitat "structure" by changing the amount of area in pool and riffle (McCoy and Bell 1991; Downes et al. 1998) (Table 5.1). Within each block the two replicates of each of the three habitat types were randomly assigned to one of two communities. The two species community consisted of 9 coho and 9 steelhead (numerical dominants); the three species community contained an additional 5 cutthroat (rare ecological intermediate).

The entire experimental setup was covered with burlap to simulate canopy shade and prevent avian predation (I observed none). I recorded the temperature (to 0.5° C) at the outflow of each channel every three days during the experiment. A repeated measures ANOVA revealed that water temperature did not change from block one to block two, but that block three was warmer than the other two (block, \( P < 0.0001 \)) on some days (block x time, \( P < 0.0001 \)). However, the mean temperatures of the three blocks (calculated as the mean of the six channel means over the 13 sample dates) were similar (blocks 1,2 = 11.4 ° C, block 3 = 11.5 ° C).

The experiment lasted 40 days, from June 18 to July 27. At the beginning of the experiment fish of each species were selected for the 18 channels sequentially to avoid any capturability or size bias. Fish were lightly anesthetized with tricaine methanesulfate and their standard length (mm) and weight (g) were recorded (Table 5.1). From June 19 to July 26, belt feeders were used to introduce 0.45 g of food (same as above) to each of the 18 channels throughout the day (≈0900-1500 hours). On July 27 fish were removed from the channels using minnow traps, dip netting, and electroshocking, and their
standard lengths and weights recorded. I was able to recover all of the fish from only
two of the experimental channels. Of the remaining 16 channels, I observed all of the
fish in 10 channels, all but one fish in 4 channels, and all but two fish in the remaining
two. In no case were less than 4 cutthroat, or less than 7 coho or steelhead recovered. I
used the fish recovered from each channel to calculate the mean absolute growth rate
(g/day) for each species as \((\text{mean weight out} - \text{mean weight in})/40\). Preliminary analyses
revealed that within communities (two or three species) the mean growth rate of each
species did not depend on the number (con-, heterospecific, total) of fish seen or
recovered (numbers used as covariates in ANCOVA, all \(P > 0.2\)). Thus, I assume that
the number of fish placed in the channels represented the number during the experiment
and the calculated growth rates accurately estimate the actual mean growth rate of each
species.

**Analysis**

I tested the two predictions of the competition hypotheses using analysis of
variance (Type III sums of squares) with block (random), habitat, and community
composition as main effects and the mean growth rates of the three species as dependent
variables. To determine whether habitat diversity facilitated the addition of an ecological
intermediate, I tested for a significant habitat effect on the mean growth rate of cutthroat
tROUT in the three species community \((n = 9)\). To test if habitat diversity reduced the
negative effect of cutthroat on the existing members of the community, I tested for a
significant habitat \(\times\) community interaction effect on the mean growth rates of coho and
steelhead using ANOVA \((n = 18)\) and MANOVA \((n = 36)\).

**5.4 RESULTS**

The results of the experiment are shown in Figure 5.1. Habitat diversity
facilitated the invasion of the community by a rare ecological intermediate. Cutthroat
tROUT grew 54% and 68% faster in the diverse habitat than in pool and riffle habitats,
respectively \((F_{2,4} = 6.93, P = 0.05)\). Coho salmon grew significantly faster in pool and
diverse habitats than in riffle habitat \((F_{2,10} = 9.55, P < 0.005)\), but their growth rates were
not significantly reduced by the presence of cutthroat trout \((F_{1,10} = 2.30, P = 0.16)\) in any
of the three habitat types \((F_{2,10} = 0.69, P = 0.52)\). Steelhead growth rates were uniformly
low and not significantly affected by habitat ($F_{2,10} = 0.93, P = 0.43$), the presence of cutthroat ($F_{1,10} = 2.79, P = 0.13$), or their interaction ($F_{2,10} = 1.82, P = 0.21$). When the growth rates of coho and steelhead are considered together using MANOVA, habitat influenced the effect of cutthroat trout on the two species (habitat x community: Wilks' Lambda = 0.33, $F_{4,18} = 3.3, P = 0.03$). In pools the addition of cutthroat depressed the growth rates of both coho and steelhead (by 11 and 10 %, respectively). In riffles the addition of cutthroat reduced the growth rate of only coho (by 11 %), while in the diverse habitat the addition of cutthroat reduced the growth rate of only steelhead (by 26 %). This habitat by community interaction effect is seen more clearly in the effect of cutthroat on the ratio of coho to steelhead growth rates across the three habitat types (Figure 5.2). With $\log_{10}(\text{ratio})$ as the dependent variable, ANOVA revealed significant habitat ($F_{2,10} = 25.59, P < 0.001$) and habitat x community interaction effects ($F_{2,10} = 7.85, P < 0.01$). In summary, the results offer partial support for the two predictions of the competition hypothesis. In the diverse habitat cutthroat trout achieved their highest growth rate. Though habitat diversity did not eliminate the negative effects of competition, in the three species community the growth rates of coho and steelhead in the diverse habitat were as high as in either homogeneous habitat (Figure 5.1).

5.5 DISCUSSION

This experiment provides one of first explicit tests of the hypothesis that the positive relationship between habitat diversity and species diversity results from a reduction in the strength of interspecific competition. To test the two predictions of the competition hypothesis, I used a simple community of three species with known habitat associations, eliminated depredation, and controlled variation along two environmental axes, productivity and resource diversity, that usually confound the relationship between habitat diversity, interspecific competition, and species diversity.

Cutthroat trout, the rare ecological intermediate, grew faster in diverse habitat than in homogeneous pool or riffle habitat. Because cutthroat were not reared in allopatry, we cannot reject the hypothesis that cutthroat grow fastest in diverse habitat regardless of interspecific interactions, but evidence supports the interpretation that habitat partitioning in the diverse habitat allowed cutthroat to avoid the negative
competitive effects of coho. First, cutthroat prefer energetically favorable pool habitat in allopatry, but not in the presence of coho (Glova 1986). Second, coho are aggressive interference competitors and not displaced from their preferred pool habitat by either cutthroat (Glova 1986) or steelhead (Hartman 1965). Third, juvenile growth rates for all three species are higher in energetically favorable pool habitat (Quinn and Peterson 1996; Harvey and Nakamoto 1997; Rosenfeld and Boss 2001). If habitat mediated interspecific competition were not important, then cutthroat should have grown as fast in the pool habitat as in the diverse habitat. That cutthroat grew slower and both coho and steelhead were negatively affected by their presence in the pool habitat suggests that interspecific competition was stronger in this homogeneous habitat. That coho growth was not reduced by the presence of cutthroat in the diverse habitat suggests habitat partitioning reduced the negative effects of interspecific competition between these two species.

The effect of cutthroat on the growth rates of coho and steelhead depended on habitat type. Cutthroat reduced the growth rates of both species in pools, that of coho in riffles, and that of steelhead in the diverse habitat. While habitat diversity did not eliminate the negative effects of cutthroat on coho and steelhead, in the full community all three species grew as fast or faster in the diverse habitat as in the homogeneous habitats. In the energetically demanding riffle habitat, it appears that cutthroat gained consumable resources at the expense of coho but not steelhead, which achieved their highest growth rate relative to the other species. In the diverse habitat, where cutthroat had their highest growth rate, steelhead growth rates were reduced while coho were unaffected. Though I was unable to observe habitat utilization patterns during the experiment, this result suggests that cutthroat were able to successfully intercept drift items from the physically intermediate habitats between pools and riffles, which are energetically favorable relative to the riffle areas. In the two species community steelhead did not experience an increased growth rate in the diverse habitat, suggesting they were unable, unwilling, or did not profit from utilizing those same intermediate habitats.

How habitat mediated interspecific competition affects juvenile growth rates likely depends on variation along other niche axes that were controlled in this
experiment. Depredation can influence competitive interactions and species diversity in general (Paine 1966). The perception of predation risk can influence juvenile foraging behavior and habitat selection (Grand and Dill 1997; Reinhardt 1999), and may vary among the three species (Abrahams and Healey 1993). Productivity (Hill and Grossman 1993) and resource diversity (Nielsen 1992) can vary with habitat and may independently or interactively affect competitive interactions (Slaney and Northcote 1974) and growth rates (Nielsen 1992). Factorial experiments using this and other communities will help clarify how the relationship between habitat diversity, interspecific competition, and species diversity is mediated by productivity and variation along other niche axes.

Though higher juvenile growth rates should increase survival rates in all three species, their different life histories may influence the importance of early juvenile growth to survival and, eventually, lifetime fitness (Stearns 1992). Because coho must smolt and migrate to the ocean earlier than steelhead or cutthroat, there may be a premium on early juvenile growth for this species. Alternatively, the two trout species are able to delay smoltification and may be more willing to forgo early juvenile growth in favor of avoiding depredation and/or the energetic costs of interference competition. Finally, temporal variation along various environmental axes may influence species diversity by differentially effecting components of fitness during and beyond the yearling stage (Huston 1979; Chesson 1990).

I designed this experiment to test the competition hypothesis and the connection between these results and species number and species evenness, the two variables that contribute the traditional indices of species diversity (e.g. the Shannon-Wiener index, \( H' \)), is necessarily tenuous. The composition of natural communities depends not only on habitat dependent competition during the yearling stage, but on estuarine habitat (Hartman and Gill 1968) and interspecific differences in marine survival rate, female fecundity, and adult spawning and juvenile emergence success. Still, the congruence between the present results and data from natural salmonid communities is encouraging. Steelhead had their highest relative growth rate in the riffle habitat and are numerically dominant in high gradient/velocity streams. Coho had their highest growth rate advantage in pools and are numerically dominant in low gradient/velocity streams. In the diverse habitat all three species achieved growth rates equal to or greater than in
homogeneous habitats, and natural streams with diverse habitat tend to contain all three species (Hartman and Gill 1968; Bisson et al. 1988; Reeves et al. 1993).
TABLE 5.1. Habitat conditions and initial fish sizes of the six treatments. Each number represents the mean of the mean values of the three treatment replicates. The mean values and coefficients of variation (C.V.) for water depth and velocity are based on the same 12 evenly distributed points for each channel. Full factor ANOVAs on body length and size revealed only species effects. Steelhead (mean = 35.7 mm) were longer than coho (35.0, P = 0.02) but neither was longer than cutthroat (35.5, P > 0.1). Coho (mean = 0.64 g) were heavier than steelhead (0.59, P = 0.06) but not cutthroat (0.61, P > 0.2).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Two species community</th>
<th>Three species community</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pool habitat</td>
<td>Riffle habitat</td>
</tr>
<tr>
<td>Mean depth (cm),</td>
<td>16.6</td>
<td>4.9</td>
</tr>
<tr>
<td>Mean C.V. of depth</td>
<td>12</td>
<td>18</td>
</tr>
<tr>
<td>Mean velocity (cm/s),</td>
<td>5.7</td>
<td>12.9</td>
</tr>
<tr>
<td>Mean C.V. of velocity</td>
<td>22</td>
<td>14</td>
</tr>
<tr>
<td>Mean coho length (mm),</td>
<td>34.7</td>
<td>35.0</td>
</tr>
<tr>
<td>Mean S.D. of coho length</td>
<td>1.1</td>
<td>1.4</td>
</tr>
<tr>
<td>Mean coho weight (g),</td>
<td>0.62</td>
<td>0.63</td>
</tr>
<tr>
<td>Mean S.D. of coho weight</td>
<td>0.09</td>
<td>0.12</td>
</tr>
<tr>
<td>Mean steelhead length,</td>
<td>35.6</td>
<td>36.1</td>
</tr>
<tr>
<td>Mean S.D. of sh length</td>
<td>1.6</td>
<td>2.1</td>
</tr>
<tr>
<td>Mean steelhead weight,</td>
<td>0.59</td>
<td>0.61</td>
</tr>
<tr>
<td>Mean S.D. of sh weight</td>
<td>0.11</td>
<td>0.10</td>
</tr>
<tr>
<td>Mean cutthroat length,</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Mean S.D. of ct length</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Mean cutthroat weight,</td>
<td>NA</td>
<td>NA</td>
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<td>Mean S.D. of ct weight</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>
FIGURE 5.1. The mean growth rates of the three species in the two and three species communities in each of the three habitats. Coho are the circles, steelhead the squares, and cutthroat the triangles. Each point represents the mean (± SE) of three estimates of the mean growth rate of the species. Open symbols are for the two species community (coho and steelhead), closed symbols for the three species community (coho, steelhead, and cutthroat).
FIGURE 5.2. The ratio of mean coho growth rate to mean steelhead growth rate ($\log_{10}$) in the three habitat types in the absence (open symbols) and presence (closed symbols) of cutthroat trout. Error bars are ± 1 SE.
CHAPTER 6

Concluding remarks

The experiments described in this thesis used juvenile salmonids to address questions of general ecological and evolutionary interest. In particular I think they have addressed a number of poorly studied issues concerning the context and consequences of asymmetric competition. The four experiments also improve our understanding of the potential role of interspecific competition among juveniles in structuring salmonid communities. The results of my experiments suggest the following: habitat segregation between coho and steelhead is not associated with a growth rate trade-off between habitat types in allopatry; coho have no intrinsic competitive advantage over steelhead during dyadic contests, but the species appear to have evolved behaviors that differ in the manner predicted by the natural size/competitive asymmetry; when habitat selection is incorporated into competitive interactions, coho are competitive dominants, the degree of dominance is much greater when they have a size advantage, and increasing the competitive asymmetry reduces niche overlap between the species; habitat diversity appears to reduce the negative effects of interspecific competition among salmonid fry, and of the three species steelhead growth rates are the least variable across different habitat types.

Before discussing the implications of these results a number of caveats deserve mention. First, all of the experiments were conducted in artificial stream channels; this was cost effective and allowed me test specific hypotheses, but limits the relevance of my results to natural communities. Second, all of the experiments were conducted at a single water temperature (10-11°C). One could argue without rebuttal that all of the results depend on various species × temperature effects. Third, there are hatchery coho in the Chilliwack basin. I have no idea how many stray hatchery coho spawned in the streams where I collected my study fish. This is particularly relevant to the fighting behavior experiment as artificial selection in hatchery conditions has been shown repeatedly to influence juvenile behavior. I discussed this issue with personnel at the Chilliwack Hatchery and chose areas they thought were relatively "wild". Fourth, I manipulated
phenotypes by subjecting fry to different temperature and feeding regimes. Though densities and rearing conditions were controlled as much as possible, it would have been preferable to manipulate fry sizes by collecting gametes and controlling emergence timing by manipulating temperatures during the egg stage. Finally, I used a single sympatric species pair to investigate questions motivated in part by biogeographical patterns. The benefit of this approach is that it allowed me to manipulated ecological interactions while controlling for evolutionary history; I could test the effects of the experimental factors against a single evolutionary backdrop. Just as it dangerous to make inferences about ecological interactions without controlling for evolutionary history (a conundrum that requires combining manipulative and comparative approaches), it is conjectural to make biogeographical inferences by manipulating ecological interactions in a single sympatric species pair. If the consequences of my phenotypic and habitat manipulations depend on evolutionary history, then similar experiments on sympatric populations with different evolutionary histories should yield different results. In particular, we might expect the co-evolutionary processes that influence the juvenile ecologies of coho and steelhead to vary depending on the abundances and degree of size asymmetry of the species.

Let me begin the discussion by stating that I do not think competitive interactions between juveniles are the major force determining the distribution and relative abundance of salmonids in northwestern North America. I suspect the radiation of *Oncorhynchus* from iteroparous ancestral trout to semelparous pink salmon (*O. gorbuscha*) lacking life history variation was driven by temporal and spatial reproductive isolation among adults. It is no coincidence that we identify races, stocks, and populations by the timing and location of adult reproduction, the same phenotypic/niche axes that are partitioned by species and remain highly labile within species (Schluter 1996b). I think interspecific variation in juvenile ecology (behavior, habitat selectivity, freshwater residence time) and adult life history (itero- semelparous, the presence/absence/degree of life history variation) are the evolutionary consequences of differences in the timing and the location of adult spawning. This view is consistent with patterns in species diversity observed at a number of geographic scales, and predictions of life history theory concerning the relative value of iteroparous and semelparous strategies in variable (freshwater) and
stable (marine) environments (Murphy 1968; Stearns 1992; Orzack and Tuljapurkar 1989). That being said, it is appropriate to consider my results in the context of (1) biogeographic patterns in species abundance and the timing of life history events, and (2) anthropogenic changes in freshwater habitat, species abundance, and juvenile size asymmetries.

**Biogeographic implications**

My results help explain two biogeographic patterns in the coho-steelhead system. First, though both species decline numerically to the south, the relative abundance of coho declines with decreasing latitude (Sandercock 1991; Bradford et al. 1997). Second, at a given latitude the relative abundance of the two species depends on stream habitat, with coho common in low gradient streams with high proportions of pool habitat (Reeves et al. 1993; Young 1999), and steelhead relatively common in high gradient streams with more riffle habitat (Burns 1972; Reeves et al. 1993).

The second observation has been attributed to low overwinter survival of coho in high-velocity riffle habitats (e.g. Tschaplinski and Hartman 1983; Nickelson et al. 1992a, 1992b). (A recent experiment by Kruzic et al. (2001) found that summer survival of coho fry was lower in riffles than pools.) The results of the reciprocal transplant experiment suggest that summer rearing habitat can influence the relative difference in the growth rates of coho and steelhead. While there was no growth rate trade-off across habitats, steelhead grew relatively faster than coho in riffles than in pools. The dyadic contest and habitat selection experiments suggest that size asymmetries influence competitive ability and habitat selection, which should in turn influence subsequent growth rates. Finally, the habitat diversity experiment showed that steelhead growth rates are nearly invariant across habitats and communities, and that in competition with coho they enjoy their highest relative growth rate in riffle habitats. To the degree that overwinter survival is size dependent, summer growth rates provide an additional and complimentary explanation for the scarcity of coho in streams with limited pool habitat.

The latitudinal cline in relative abundance is related to a similar cline in the relative timing of life history events. Because the rainy season is shorter at lower latitudes, the spawning and emergence times, and fry sizes of coho and steelhead converge near the southern edge of their sympatric range (Withler 1966; Sandercock...
1991; Weitkamp et al. 1995; Busby et al. 1996). Two examples illustrate this pattern. In a southeastern Alaska stream dominated by coho, coho fry began emerging in May (mean = 39 mm), steelhead in July, and by August coho were 44-48 mm while steelhead had a mean length of 36 mm (Bjornn et al. 1991). In a central California stream dominated by steelhead, adult spawning and fry emergence times overlapped and in June the mean lengths of coho and steelhead fry were 51 and 47 mm, and by October 54 and 57 mm, respectively (Burns 1972). To the degree that juvenile size differences influence competitive ability, habitat use, and growth rates, the timing of life history events may affect juvenile interactions, components of fitness, and thus regional patterns of co-abundance. Finally, my results suggest that changing the relative size of the species should change competitive interactions and patterns of habitat use; to the degree that coho and steelhead fry behaviors and habitat preferences co-evolve, co-evolutionary dynamics may vary geographically depending on the relative timing of life history events.

I suspect that intrinsic life history differences (and thermal tolerances) impose primary control over the species’ distributions. In the southern portion of the species’ sympatric range, thermal and precipitation extremes and more variable ocean conditions should increase the chance of recruitment failure for both species. Environmental variation generally favors iteroparity (Murphy 1968; Orzack and Tuljapurker 1989), a life history strategy available to steelhead but not coho. Consistent with the predictions of life history theory, the frequency and degree of iteroparity in steelhead increase at lower latitudes (Withler 1965; Busby et al. 1996). As yet, there has been no exploration of the relationship between environmental variation, species’ abundances, and the degree of intraspecific life history variation. The data are available and such work will help clarify the role of life history variation (particularly that of semelparity as a “key innovation” (Nitecki 1990)) in the adaptive radiation of the genus.

Management implications

My results suggest management activities that change stream habitat, and/or the relative abundance/size of juvenile salmonids have the potential to alter interspecific interactions and juvenile growth rates. Timber harvest and related activities reduce habitat complexity and the amount of pool habitat in northwest streams (Salo and Cundy
Changes in water temperatures associated with logging can affect egg maturation rates, emergence timing, and fry size (Holtby 1988). Hatchery operations can also change community demographics. Planting pre-smolts into natural streams can change the relative abundance and size of species (Nickelson et al. 1986; Nielsen 1994). Establishing hatchery stocks from wild populations changes the temporal distribution of wild spawning. Historically, hatchery populations were established by collecting adults from the beginning of the spawning run until brood stock goals were met. This imposed strong artificial selection on spawning timing; adults that returned early had “zero” fitness. As a result, the peak spawning time of many wild populations is now later than when under natural selection alone.

The results of the habitat diversity-species diversity experiment are consistent with, and provide a mechanistic explanation for, observational evidence that heavily logged watersheds with simplified habitat have less diverse juvenile salmonid communities dominated by steelhead (Reeves et al. 1993). However, there are a number of explanations for this observation not directly related to interspecific interactions among fry. First, streams with low habitat diversity should also have low spawning gravel diversity. In particular, a lack of channel complexity should reduce the amount of low-velocity, well-sorted, small-gravel spawning habitat used by both coho and cutthroat (Smith 1973; Trotter 1989). Second, degraded habitats should have lower productivity due to the reduced number of coho carcasses (Bilby et al. 2001). Reduced productivity may reduce species diversity regardless of competitive interactions. The reduction in coho abundance should be especially detrimental to anadromous cutthroat that feed on coho eggs, fry, and smolts during adult life history stages.

The habitat selection experiment suggests that management activities that change the relative size and/or abundance of coho and steelhead will change competitive interactions, patterns of habitat use, and the degree of niche overlap. In basins where hatchery populations of coho were established by removing early migrating adults, their size advantage over steelhead in the remaining wild population would be reduced. The opposite would result if hatchery populations of steelhead were established using the same protocol. Similarly, planting large hatchery pre-smolts into wild streams could alter
interspecific interactions and patterns of habitat use. These demographic/ecological changes may have evolutionary consequences if habitat mediated juvenile growth rates influence life time fitness.

The effects of anthropogenic habitat alteration on interspecific interactions have the potential to persist for decades, if not centuries. Given the temporal scales of ecologically relevant processes, is safe to say that once degraded, the streams draining forested watersheds of northwestern North America will never return to pre-European conditions. Many of our ill-conceived hatchery practices have been addressed through closures and/or operational changes. The days of indiscriminately planting hatchery pre-smolts into streams have passed. My guess is that the negative effects of habitat degradation, overharvest, and hatchery propagation are more ecological than evolutionary. There is less habitat, less wild fish and more hatchery fish. Still, as we attempt to restore habitat, kill less fish, and use of hatcheries for conservation rather than propagation, it will be important to consider not just the numbers of wild fish remaining, but also the distribution of spawning times represented within and among species.


Everson, L. B. 1973. Growth and food consumption of juvenile coho salmon exposed to natural and elevated fluctuating temperatures. ms Thesis. Oregon State University, Corvallis, OR.


Gause, G.F. 1934. The struggle for existence. Williams & Wilkins, Baltimore, Maryland.


Glova, G. 1986. Interaction for food and space between experimental populations of juvenile coho salmon (Oncorhynchus kisutch) and coastal cutthroat trout (Salmo clarki) in a laboratory stream. Hydrobiologia 131:155-168.


Hartman, G. F., and C. A. Gill. 1968. Distributions of juvenile steelhead and cutthroat


USA 51:1207-1210.


Nickelson, T. E., M. F. Solazzi, S. J. Johnson, and J. D. Rodgers. 1992b. Effectiveness of selected stream improvement techniques to create suitable summer and winter rearing habitat for juvenile coho salmon (Oncorhynchus kisutch) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49:790-794.


