

AN ABSTRACT OF THE DISSERTATION OF

Brooke E. Penaluna for the degree of Doctor of Philosophy in Fisheries Science presented on September 12, 2013.

Title: New Insights on an Old Topic: Understanding the Effects of Forest Harvest on Trout in the Context of Climate

Abstract approved:

Jason B. Dunham

Studies of the effects of forest harvest on streams and fish have a long history in the Pacific Northwest. Results of this work have prompted development of new forest harvest practices that are more protective of these resources, but the effectiveness of these new practices has not been fully evaluated. Furthermore, the effects of contemporary forest harvest in the context of climate change are poorly understood. To address these issues, my overall research goal was to understand how water quality, water quantity, and instream habitat influence individuals and corresponding population dynamics of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*). My work was designed to complement field results from a new generation of watershed studies currently underway in western Oregon. I combined semi-natural experiments with modeling based on field observations to understand fundamental causes and processes influencing trout. This multifaceted approach provided a novel process-based perspective on issues related to forest harvest and climate. In Chapter 2, I evaluated individual- and population-level responses of coastal cutthroat trout to instream cover. Although the influences of forest harvest on stream flow, temperature, and turbidity are often the focus, instream cover may be strongly influenced by forest harvest. In addition, restoration of instream cover is now a common practice, but the importance of cover itself to stream-living fishes is still a major question. To address this issue, I conducted large-scale manipulative experiments in outdoor semi-natural stream units to approximate conditions experienced by trout in headwater streams in western Oregon. I determined that infrequent cover use by trout leads to emigration. Next, I built upon key ideas within stream ecology related to the importance of location within a landscape to aquatic biota, which have been explored and debated extensively. The variability in population responses across similar locations within a

landscape is less understood. My objective in Chapter 3 was to understand the variability in population biomass of coastal cutthroat trout across headwater streams by understanding of the relative roles of two general classes of variables that occur in headwater streams: dynamic environmental regimes and relatively fixed habitat structure. I provided evidence that environmental regimes contribute to biomass variability while also being constrained by the habitat structure, given the range of conditions that I was able to simulate. Although the effects of contemporary forest harvest and climate change occur simultaneously, they are not typically considered together, as they are in Chapter 4. Here, I tracked population responses of trout, including biomass, survival, growth, and timing of emergence during six decades across four modeled headwater streams using the same individual-based trout model as in Chapter 3. I modeled four scenarios: 1) baseline conditions (simulation of existing conditions); 2) effects of contemporary forest harvest; 3) effects of climate change; and 4) the combined effects of forest harvest and climate change. Differences among scenarios were tied to changes in flow and temperature regimes. Here, I found that there was a high degree of local variability in the responses that I simulated. Whereas localized responses to forest harvest have been observed, my findings contrast with the vast majority of work on species responses to climate change, most of which reports relatively synchronous or uniform responses. I highlighted the role of individual variability of trout and local variability of streams, which ultimately suggest that some individuals and populations of trout may be more vulnerable than others to the effects of forest harvest, climate change, or both processes together.

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New Insights on an Old Topic: Understanding the Effects of Forest Harvest on Trout in the
Context of Climate

by
Brooke E. Penaluna

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

Brooke E. Penaluna, Author

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I would like to dedicate my dissertation to Ivan-él sabe por qué.

New Insights on an Old Topic: Understanding the Effects of Forest Harvest on Trout in the Context of Climate

CHAPTER 1: GENERAL INTRODUCTION

The landscape of the Pacific Northwest is profoundly shaped by historical and contemporary forest harvest practices, which are intensively regulated to protect important fisheries. In this region, forests, fish, and clean water are highly valued socially and economically, and thus, their sustainability depends on our ability to understand linkages between these sometimes competing uses of land and water. Over longer time-frames, we must also understand how forests, fish, and clean water will respond to climate change. Concerns over the consequences of forest harvest on fishes have a long history, dating back almost eight decades (e.g., Northcote and Hartman 2004; Stednick 2008). This historical work has contributed a great deal to our understanding of how stream-living fish populations and stream ecosystems in general can respond to forest harvest. Historical work culminated in the development of the Northwest Forest Plan of 1994 and revised state practices for the protective contemporary forest guidelines that are currently in place (Everest and Reeves 2006). The questions we have today are centered on the influences of contemporary forest harvest on fish in the context of broader and longer-term influences resulting from a changing climate.

My dissertation is designed to complement field studies from a new generation of watershed studies currently underway in western Oregon. To address the classic questions about forestry and fisheries in the context of contemporary forest harvest and climate change, I applied new concepts and tools that are founded on an individual-based perspective of population dynamics. Population dynamics emerge from behaviors and interactions among individuals (Lomnicki 1988), and understanding individuals can provide a more insightful explanation of changes in the distribution and abundance of organisms. Whereas the logic of an individual-based

approach to studying ecology is compelling, the logistical constraints of studying individuals can be quite challenging. Here, I combine semi-natural experiments with modeling based on field observations to understand fundamental causes and processes influencing trout under contemporary forest harvest and climate change.

This multifaceted approach provides a process-based perspective to issues related to forest harvest under a changing climate that have vexed biologists for decades. My overall research goal was to understand changes in streams associated with the effects of contemporary forest harvest and climate change and examine whether those changes influence individuals and corresponding population dynamics of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*). I address my overall research goal with three chapters that together provide several lines of inquiry about the effects of forest harvest and climate change on trout.

In Chapter 2, I evaluate individual- and population-level responses of coastal cutthroat trout to instream cover. Although the influences of forest harvest on stream flows, temperatures, and turbidity are often the focus of studies, instream cover may be strongly influenced by forest harvest and its associated practices. This is particularly true in the context of historical forest practices, which led to loss of instream cover on a massive scale (Miller 2010). Restoration of instream cover is now common practice, but the importance of cover itself to stream-living fishes is still a major question (Allouche 2002). To address this issue, I use manipulative experiments to approximate conditions experienced by trout in headwater streams in western Oregon. Manipulative experiments provide a rigorous, empirical evaluation of cause-and-effect relationships under a limited range of conditions. In these western Oregon streams, seasonal low flows are associated with decreased survival (Berger and Gresswell 2009) and limited availability of instream cover that serves as hiding cover (Andersen 2008). Collectively, these studies suggest that instream cover should be important for trout, but direct evidence linking instream cover to individual- or population-level responses is lacking (Allouche 2002). In addition, instream cover has not previously been emphasized in studies examining the effects of historical forest

harvest on fish (Stednick 2008). Although it is known that animals use a suite of behaviors to avoid predation, such as grouping, emigrating, or using cover, it is not known under what conditions trout use these behaviors. Here, I examine cover use, emigration, grouping, and foraging activity of trout in large-scale experiments in outdoor semi-natural stream units (<http://www.dfw.state.or.us/fish/OHRC/>) during summer of 2009. I determine that infrequent cover use by individual trout leads to emigration and the ability to emigrate is a key driver of trout abundance.

Next, I build upon fundamental ideas within stream ecology related to the importance of location within a landscape (Vannote et al. 1980) and the heterogeneous environment (Townsend 1989) that occurs throughout a stream network (Benda et al. 2004). The importance to aquatic biota of location within a landscape has been explored and debated extensively, but the variability in population responses across similar locations within a landscape is less understood. My objective in Chapter 3 is to examine the variability in population biomass of coastal cutthroat trout across nearby headwater streams by understanding the relative roles of two general classes of variables that occur in headwater streams: dynamic environmental regimes and relatively fixed habitat structure. I simulate biomass in four streams using a detailed individual-based trout model (inSTREAM; Railsback et al. 2011) calibrated with actual field data for stream temperatures, flow, turbidity, habitat structure, and estimates of population abundances (see Trask Watershed study: <http://www.odf.state.or.us/trask/default.asp>) over a four-year period. Individual-based models allow for dissection of complex and interacting processes, as well as simulation of long-term responses that cannot easily be quantified in the field. Here, I provide evidence that environmental regimes contribute to population variability while also being constrained by the habitat structure, given the range of conditions that we are able to simulate. This chapter offers information about the role of habitat structure and it sets a foundation for the next chapter by exploring how trout responses are tied to dynamic and fixed elements of streams.

In my last chapter, Chapter 4, I synthesize ideas related to individual-based ecology, trend detection, and trajectory analyses to evaluate the independent and combined influences of forest harvest and climate change on trout. Although the effects of contemporary forest harvest and climate change occur simultaneously they are not typically considered together. In addition, most applications of individual-based models compare only final outputs of alternative scenarios from a representative stream. Here I track population responses of coastal cutthroat trout, including biomass, survival, growth, and timing of emergence during six decades, across four modeled headwater streams using the same individual-based trout model as in chapter 3. To account for baseline, forest harvest, climate change, and the additive effects of forest harvest and climate change, I manipulate actual flow and temperature regimes. Here I found that there is a high degree of local variability across trout populations in the responses that I simulated. Whereas localized responses to forest harvest have been observed (Murphy and Hall 1981; Bisson et al. 2008), our findings contrast with the vast majority of work on species responses to climate change, most of which reports relatively synchronous or uniform responses (e.g., Parmesan and Yohe 2003).

I integrate and synthesize several lines of inquiry to provide a more complete body of evidence in relation to influences of contemporary forest harvest and climate change on trout. There are many relevant insights that can be drawn from my results, and the overall message is that responses are highly localized. I hypothesize that this may be due to differences among local stream characteristics, namely the habitat structure. Accordingly, my work will have on-the-ground implications towards influencing major natural resource sectors in the Pacific Northwest—forests and fish.

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CHAPTER 2: AN EXPERIMENTAL EVALUATION OF THE ROLE OF INSTREAM COVER FOR STREAM-LIVING TROUT

2.1 Abstract

Instream cover is a potential driver of population dynamics in fish, but it has received less attention than food and space, more commonly accepted limiting factors. To address the role of instream cover for coastal cutthroat trout (*Oncorhynchus clarkii clarkii*), we experimentally manipulated cover availability in semi-natural outdoor streams where available food, space, and other potentially confounding covariates associated with cover were held constant. The proportion of cover use was directly linked to emigration because individuals were more likely to emigrate if they infrequently used cover. Cover availability controlled the magnitude of emigration, cover use, and grouping. Distinct behaviors were expressed depending on the ability to emigrate; trout grouped when streams were closed to emigration, whereas when streams were open to emigration, individuals that were less likely to use cover were more likely to emigrate. Foraging activity was elevated when streams were open to emigration, and resident individuals more intensively used cover, suggesting that these behaviors constrained time available for foraging. Our findings show that cover has important influences on trout behaviors and density.

2.2 Introduction

Food and space are among the most commonly invoked limiting factors for stream-living fishes (e.g., Chapman 1962; Grant et al. 1998; Hughes and Grand 2000), but other potentially limiting factors, such as cover (Berryman and Hawkins 2006) may be equally important. Cover, shelter, or refuge (hereafter cover) provides a place to avoid predators, evade competition, and circumvent harsh environmental conditions within a site (Allouche 2002; Orrock et al. 2013). It has long been acknowledged that cover enhances animal retention in streams (e.g., Tarzwell 1937; Gowan and Fausch 1996),

yet the role of cover alone as an influence of trout populations is less clear. Conditions that result in cover use by individuals are not known.

Here, we consider the role of cover on fish in small streams during seasonal low-flows, where vulnerability to terrestrial predators may be especially high (Steinmetz et al. 2003). For example, survival of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) is lowest during seasonal low-flows in late summer and fall (Berger and Gresswell 2009), when lower water levels naturally result in less instream cover. Under such conditions, fish may select reaches with instream cover (Andersen 2008), or perhaps emigrate if cover is inadequate or not available. If cover is less available and emigration is not possible, fish may adopt alternative behaviors such as schooling, shoaling, or grouping (hereafter grouping, reviewed by Krause and Ruxton 2002).

Our overall objective was to evaluate how instream cover availability influences the behavior, corresponding size structure, and density of coastal cutthroat trout. To this end, we chose to conduct an experiment in semi-natural streams, where cover availability could be manipulated, and where available food, space, and other potentially confounding covariates associated with cover were held constant. By adopting an experimental approach, we controlled and observed responses of trout to limited cover.

We examined predictions from several hypothesized influences generated from prior observations of coastal cutthroat trout, as well as observations of stream-living fish in general. We hypothesized that when cover was less available and emigration was not possible there should be greater proportion of cover use, because coastal cutthroat trout are strongly associated with cover (Andersen 2008). Under these same circumstances, we also hypothesize that there will be less grouping (Krause and Ruxton 2002) and more sharing of cover. Grouping may lead to increased per-capita foraging success if groups enhance information related to food detection (Ward and Zahavi 1973) or if social-dominance hierarchies are disrupted (Reinhardt 1999). However, when streams were open to emigration, larger, dominant individuals should

control access to cover and thus, we assumed that smaller fish might be more likely to emigrate (e.g., Chapman 1962; Keeley 2001; but see Dunham et al. 2000). Under these circumstances, trout rely more on cover, and thus we hypothesized that foraging time would be reduced (Grand and Dill 1997). Alternatively, other behavioral characteristics of trout, such as frequency of cover use, may influence which individuals emigrate, with trout that use cover more being less likely to emigrate. In cases where fish rely more on cover, we hypothesized that foraging time might be reduced (Grand and Dill 1997). Collectively, these results may provide a better understanding of the role of cover as a factor that may limit trout.

2.3 Methods

2.3.1 *Experimental setup*

Our experimental design approximated conditions experienced by coastal cutthroat trout during low-flow conditions in small streams in western Oregon, USA. Here, we conducted a realistically-scaled experiment using coastal cutthroat trout in a semi-natural setting where available food, space, and other potentially confounding covariates associated with cover were held constant, such as water depth (Power 1987; Lonzarich and Quinn 1995), turbidity (Harvey and Railsback 2009), and velocity (Bisson et al. 1988). Coastal cutthroat trout often are the only salmonid species, and sometimes the only fish species, naturally found in headwater streams, and are more strongly associated with cover than other salmonids (Trotter 1997; Behnke 1992). We conducted a manipulative experiment using outdoor streams at the Oregon Hatchery Research Center (<http://www.dfw.state.or.us/fish/OHRC/>). The stream units were located outdoors where the fear of predation for trout likely seemed real. Due to logistical and permitting complications, however, we excluded predators from entering the experimental area with a black mesh enclosure that was 3.5–6.0 m above ground level. In particular, in the area immediately surrounding the streams, many predators were observed during the experiment (e.g., American crow, *Corvus brachyrhynchos*;

bald eagle, *Haliaeetus leucocephalus*; belted kingfisher, *Megaceryle alcyon*), in addition to other known predators in the area (e.g., American mink, *Neovison vison*).

Our experiment had two phases. In the first phase, for 14 days, we measured behavioral responses (grouping, cover use, foraging) across two levels of cover availability (high, low) when emigration was closed. In the second phase, for 28 days, we measured all the same behaviors plus emigration across the same two levels of cover availability when emigration was open. We had 4 replicates for each stream unit (of either high or low, as are defined below)

We constructed these eight replicate experimental stream units (20 x 2 m), with continuous flow supplied from an adjacent stream. We routed through a 679,648 L settling pond. A stainless steel screen with 2-mm mesh filtered water entering the pond. Across the four existing channels, we created eight units by separating conjoined stream units with 3-mm square-mesh screens. Mean water temperature was $11.2 \pm 0.9^{\circ}\text{C}$ (SD). The stream flows steadily decreased over the course of the study (ranging from 33 to 23 L s^{-1}) and they were similar among stream sections. To ensure that depth would not be used for cover (Power 1987), we maintained water depth levels at < 30 cm.

We collected wild coastal cutthroat trout (9.4 to 23.4 cm fork length) by electrofishing from nearby streams during June of 2009. To uniquely identify individuals, we implanted each trout with a 2.3-cm half-duplex passive-integrated transponder (PIT) tag. Trout were acclimated on-site in darkened indoor tanks supplied with local stream water. After three days, we randomly assigned and moved 24 trout to each stream reach. These trout were acclimated to stream units for three additional days. We classified trout a-priori into three length classes, by dividing the length distribution of trout into thirds. Our groups included small- (9.4–14.9 cm), intermediate- (15.0–19.4 cm), and large-sized (19.5–23.4 cm) trout. The density of trout across our stream units was relatively high (0.4–0.6 trout m^{-2}) over the study period, compared to streams supporting coastal cutthroat trout in nearby Oregon coastal streams (0.2–0.6 trout m^{-2}) D. Bateman, Oregon State University, unpublished

data.). We wished to have densities that were high enough to potentially invoke density-dependent interactions among individuals in our experiments, but that were also within the range of those naturally observed.

We assigned statistical blocks to each pair of units along horizontal and vertical gradients, which essentially resulted in one block per corner of experimental area. Blocking allowed for us to account for dissimilar environmental conditions both horizontally from a natural stream and a small dirt road, and vertically from varying macroinvertebrate assemblages (up- or downstream position from stream water supply). Within each block, we randomly assigned a high- and low-density cover availability treatment. High-density stream units had 25 cover pieces, and low-density stream units had 5 cover pieces. Because trout in natural streams use cover pieces that are similar to their body length or longer (Andersen 2008), we designed covers to exceed the size of our largest trout (23.4 cm). A single cover consisted of a 30.5- by 30.5-cm cement paver top-piece with a 30.5- by 20.3-cm paver bottom-piece glued underneath in the center. This created two 5.1- by 30.5-cm equal-sized spaces on each end of the piece to provide trout cover positions. Hence, our high-density units had 50 covered positions and our low-density units had 10 covered positions. In each stream reach, cover were randomly distributed using a grid of 20 by 4 potential equally spaced locations. In sum, we had 24 trout in each stream reach, with either 50 cover positions (high) or 10 cover positions (low).

Trout could emigrate only when emigration boxes were open at both up- and downstream ends of each stream reach. (Note that trout in our stream units constitute a study population and may not be considered populations in the sense of populations in the wild, yet we use the term emigration to identify when trout are leaving the stream unit and study population.) These boxes were accessible to all trout, but were constructed so that individuals had to enter through a narrow white tube, which results in only motivated trout exiting (McMahon and Matter 2006). To determine when individuals left, we checked boxes for the presence and identification of individual trout daily between 0900 and 1100. If an individual trout was found three times in the

exit box, we physically removed it from the experiment and counted it as intending to emigrate. In this way, individuals making local exploratory movements were not considered as trying to emigrate (modified from Keeley 2001).

We examined stream shading across study reaches in a post-hoc exploratory measurement of tree canopy, because during our experiment we noticed unequal shading from nearby trees that may have influenced behavioral responses. To quantify stream shading, we took densiometer readings every 3 m along each reach between 1200 to 1300 hrs and summed the proportion of covered area in each cardinal direction.

2.3.2 *Behavioral responses*

We examined behavioral responses (grouping, cover use, sharing of cover, feeding) across two levels of cover availability (high, low) and we additionally measured emigration when emigration boxes were open. We recorded behavioral observations from behind a blind to avoid disturbing fish by our presence. We were not able to distinguish among individuals for grouping or feeding attempts and thus we recorded these responses as aggregate numbers of individuals within each stream reach.

We identified individuals using instream cover or emigrating with a hand-held PIT tag reader, allowing us to detect a link between these behaviors by identifying individuals. Each day throughout the experiment we recorded individuals that emigrated, and determined the proportion of trout that emigrated for each length class. We deliberately measured cover use with a hand-held PIT tag reader while in the stream, because this would encourage individuals to take cover, if they were going to use cover at all.

We measured cover use as a proportion by measuring the number of trout that used a cover position (defined above) divided by the number of trout present in each length class. We recorded cover use every fourth day throughout the experiment, with 5 observations before emigration was allowed and 7 observations after it was.

We also recorded trout sharing of cover positions to give detail about how they used cover. We measured trout sharing cover as a proportion by measuring the number of times, by length class, that multiple trout used any of the possible cover positions, divided by the number of cover pieces found in the experimental unit, either 10 (low cover stream units) or 50 (high cover stream units). We recorded sharing of cover at the same time that we measured cover use throughout the experiment.

We defined grouping behavior as observations where ≥ 3 individuals were within a standardized body-length (15 cm fork length) of each other. Then the number of groups was calculated per stream unit. We recorded grouping behavior with 3 observations before emigration was allowed and 4 observations after it was.

We quantified feeding behavior as the total number of nips at the water surface by trout, and reported it as proportion of nips per trout out of the number of trout remaining (Noakes and Baylis 1990). We recorded grouping measurements 3 times before emigration was allowed and 4 times after it was. We released 10 g (dry mass) of dry krill all at once in one spot at midday every other day in the upstream end of each reach, with 3 nip observations before emigration was allowed and 5 nip observations after it was. We allowed trout in each stream unit to feed on drifting krill to cessation, which was determined as 60 seconds of no feeding action beyond last nip at the surface. Krill that was not eaten by trout was removed from downstream nets immediately after feeding.

2.3.3 *Statistical analyses*

For all analyses, size class (small, intermediate, large), cover availability (high, low), and whether or not a stream reach was open to emigration were analyzed as categorical variables. We examined whether the proportion and timing of emigrating trout were a function of trout size class, cover availability, whether or not a stream reach was open to emigration, and interactions using a generalized linear mixed model (Bolker et al. 2008) for a binomial-like response, using the logit link. We accounted for blocks and repeated measurements of each stream reach (random effects). We fit a

model with cover availability and ability to emigrate as fixed effects, leaving out size class and interaction terms due to their statistical insignificance. We predicted that trout would emigrate more from low-cover stream sections, and that small-sized trout would emigrate more than larger trout due to territoriality and density dependence.

To evaluate whether the distributions of trout emigrants between low- and high-cover stream units were different, we compared their distributions using the two-sample Kolmogorov-Smirnov test. This test is sensitive to small sample sizes and small counts in a class for the expected frequency (Zar 1999), as was the case in our study, so we did not try to additionally account for blocks. We pooled the replicates of the number of emigrants for each cover type (low and high) to avoid zeros in our counts of a class, which in our case is number of emigrants per day, especially for high-cover stream units. We predicted that trout would emigrate sooner when cover availability was lower compared to when it was higher.

We tested whether proportion of trout using cover was a function of trout size class, cover availability, whether or not a stream reach was open to emigration, and their interactions using a generalized linear mixed model for a binomial-like response, using the logit link. We accounted for blocks and repeated measurements of each stream reach (random effects). We fit a model with size class, cover availability and whether or not a stream reach was open to emigration as fixed effects, leaving out their interactions due to statistical insignificance. We predicted that trout would be more likely to use cover when it was less available, that larger trout would dominate territories around cover, and that there would be less use when emigration was available.

We also analyzed whether proportion of trout sharing cover was a function of trout size class, cover availability, whether or not a stream reach was open to emigration, including interactions, using a generalized linear mixed models. We initially predicted that there would be more sharing when cover was less available. This model does not account for complex random effects (i.e., blocking, repeated measurements of each stream reach) or statistical interactions because these features

were of the lowest intrinsic biological interest and likely blocks had low variability among them due to being spatially located adjacent to one another (Ramsey and Schafer 2002; Bolker et al. 2008).

To examine a potential link between cover use and emigration, we examined the odds of using cover, out of the five times that cover use was measured when emigration was closed, for trout that eventually emigrated versus trout that remained. We predicted that emigrant trout might have used cover less often when compared to non-emigrant trout.

We evaluated whether group size was a function of cover availability and whether or not a stream reach was open to emigration with a mixed model using a normal response that accounted for blocking as a random effect. We fit a model with cover availability, whether or not a stream reach was open to emigration as fixed effects excluding interactions due to their statistical insignificance.

We tested whether feeding behavior (nips/trout) was a function of cover availability and the ability to emigrate with a mixed model using a normal response that accounted for blocking as a random effect. We fit a model with cover availability and whether or not a stream reach was open to emigration as fixed effects, leaving out their interactions due to lack of statistical significance. We predicted more grouping when availability of cover was lower and when emigration was closed. We performed all statistical analyses using SAS software 9.2.

2.4 Results

Cover availability enhanced the magnitude of the expression of emigration, grouping, and cover use behaviors. We found that experimentally lowering cover availability resulted in more individuals emigrating from the stream reach ($F_{1,19} = 32.76$, $P = 0.0001$; Fig. 1a,b), and consequently lower overall trout densities. The probability of trout emigrating from low-cover stream units was 3.5 times higher than from high-

cover stream units (95% CI: 2.22 to 5.56). Although there may be biologically-relevant emigration by intermediate-sized trout when cover opportunities are fewer, trout size was not a factor in emigration (Fig. 1b). The distribution of trout emigrants differed between low- and high-cover stream units (KS = 0.040, D = 0.080 α = 0.05; D > KS critical value so reject H_0 that distributions are equal) with emigration being 5d earlier and at a faster rate in low-cover units (Fig. 1a). One low-cover stream unit was an outlier in this day-to-emigrate analysis, because trout in this unit behaved more similarly to high-cover stream units. This outlier reach had more canopy cover (66%) than other stream units (22%, 16%, 0%, 0%, 0%, 38%, 47%) based on densiometer readings. The removal of this stream section maintains a similar level of statistical significance (KS = 0.040, D = 0.080).

In addition, trout group size was larger in stream units with low cover availability versus high ($F_{1,9} = 3.17$, $P = 0.10$; Fig. 3a). Average group size was estimated to be larger by almost three more trout in low-cover stream units than in high (95% CI: 0.74 to 6.18). The proportion of trout using cover in stream units with low cover availability was smaller than in high-cover units ($F_{1,40} = 23.76$, $P \leq 0.0001$; Fig. 2a,b), with 12.17 times less use by trout in low-cover stream units than high (95% CI: 4.32 to 34.30). However, there was no difference in feeding activity of trout between high- and low-cover units (Fig. 3b).

We found behaviors of individuals were strongly linked to the ability to emigrate. When stream units were open, trout either emigrated (Fig. 2.1a,b) or, for those that remained, they were more likely to use cover ($F_{1,40} = 6.08$, $P = 0.01$). The probability of cover use by trout was 34% times higher when stream units were open versus closed (95% CI: 0.14 to 0.83). However, when stream units were closed, trout group size was higher compared to when they were open ($F_{1,9} = 5.67$, $P = 0.04$; Fig. 3a). The estimated average group size was larger by two more trout in a group when units were closed than when units were open (95% CI: 0.11 to 4.45). We found evidence for selective emigration of individuals based on cover use. For example, out of the five times that cover use was measured while emigration was closed, 43% of

those trout that eventually emigrated were never observed to use cover, and none used cover 5 times (Table 2.1). In contrast, only 7% of non-emigrating trout never used cover and 37% used cover 5 times.

Behavioral changes associated with emigration also affected feeding activity by trout (Fig. 3b). Feeding activity was reduced in closed versus open units ($F_{1,57} = 8.63$, $P \leq 0.0040$) and average number of nips per trout was estimated to be 1.03 nips less in units closed to emigration versus open units (95% CI: -1.73 to -0.32). Collectively, when grouping dominated, trout exhibited lower feeding activity, whereas when emigration and more intense cover use occurred, feeding activity was higher.

The size of trout also played a role in the proportion of trout that used and shared cover ($F_{2,40} = 17.07$, $P \leq 0.00010$; Fig. 2a,b). Large trout exhibited the highest probability of use among the three size classes, with 40.9 times more cover use than intermediate (estimated probability of use at 15.9 with 95% CI: 6.23 to 40.70) or smaller-sized trout (estimated probability of use at 1.3 with 95% CI: 0.813 to 2.25). Small trout shared cover positions the most, with an estimated 14% more sharing than the other size classes (95% CI: 0.07 to 0.23; Fig. 2c,d). Intermediate-sized trout shared 3% of the time (95% CI: 0.01 to 0.09) and large trout essentially did not share (95% CI: 0 to 0.01).

2.5 Discussion

Here, we present experimental evidence demonstrating complex influences of cover use by trout on behaviors and local demography when other confounding covariates are held constant (Fig. 4). Among the factors held constant are overall space and food availability, two factors known to have strong influences on trout (Chapman 1962; Grant et al. 1998; Hughes and Grand 2000). Our findings show that when these factors are not variable, emigration is linked to cover use, with higher levels of emigration

associated with reduced availability of cover (and not trout size). The ability to emigrate, in turn, is also linked to altered behavioral expression in trout as seen by reduced incidence of grouping, greater probability of cover use, and increased feeding activity when emigration is not possible. More generally, these results suggest that cover availability is a key factor influencing trout behaviors and densities.

2.5.1 *Cover availability affects magnitude of behavioral expression*

Cover availability can modulate the degree to which given behaviors are expressed by trout. When cover availability is high, cover use is more likely because cover is more readily available and intraspecific interactions may be reduced. An individual that seeks a hiding place to avoid predation may come and go based on predation risk (Orrock et al. 2013), but also faces competition in efforts to obtain and maintain that cover position (Berryman and Hawkins 2006). When cover is less available, there may be more intense intraspecific competition for limited cover, and some individuals may be forced to employ alternative behaviors. In particular, results here indicate that when cover is less available, and emigration is not possible, there is an increase in grouping, but when emigration is possible, there is elevated emigration and cover use. We suggest that there is relationship between instream cover and trout behaviors even though we do not manipulate predation risk. Other studies have shown that as predation risk increases, so does emigration (spiders, *Tetranychus urticae*, Bernstein 1984), group size (Impala *Aepyceros melampus* Creel and Creel 2002), or use of habitat providing cover (juvenile lemon sharks, *Negaprion brevirostris* using inshore or mangrove lake area, Guttridge et al. 2012). Collectively, this may suggest that our findings result from a combination of perceived predation threats and limited hiding options due to reduced cover.

2.5.2 *The influence of emigration on trout behaviors and densities*

The ability to emigrate directly affects individual behaviors, densities of individuals, and when it occurs it can be linked to cover use. By isolating the ability to emigrate, we highlight how emigration alone decreases local densities. Emigration is a common response among mobile aquatic organisms and may occur for multiple reasons. For example, emigration has been linked to population density, food availability (Snider and Gilliam 2008), patch configuration (Andreassen and Ims 2001), and predator avoidance (Poethke et al. 2010). Here, we find that emigration can also depend on availability of cover. When emigration is not possible, trout that eventually emigrated were those that initially used cover less frequently than trout that remained in streams. This suggests that emigrants may because they are unable to access cover (e.g., intraspecific competition). It is also possible that individuals may be predisposed to invoke particular behaviors because they lack the capacity for alternative behaviors (individual specialization; Bolnick et al. 2003). Whether behaviors observed here were obligate or facultative, the loss of emigrants contributed to a loss of individuals that used cover less frequently, thus altering the behavioral composition of residents (individuals more likely to use cover).

The ability to emigrate is also linked to grouping, presumably representing an antipredator behavior that can be adopted when alternatives (e.g., cover use) are limited (Lima and Dill 1990). When emigration is possible, grouping essentially disappears (Figure 2.4). Although emigration is potentially risky due to unknown hazards in a new location, emigrants may also gain access to increased food or space. When trout emigrate, the local density decreases, resulting in an increase in per-capita cover availability for remaining residents. Following emigration, the smaller number of remaining individuals may also leave insufficient numbers of individuals to form effective groups. Although territorial behavior is pervasive for trout and other salmonids (Grant et al. 1998), it is conceivable that grouping may be important in many situations. These include populations that are closed to emigration because they are isolated by barriers (Morita et al. 2009), or those in locations that lack cover from

predators (Boss and Richardson 2002), from places or times when local densities are elevated (e.g., during periods of extreme low-flows). Comparing our results to those from similar studies suggests the importance of understanding context-specific influences of cover and emigration (McMahon and Matter 2006). Supporting our results, Harvey et al. (1999) observed increases in emigration by trout when cover is limited. Similarly, in support of our findings linking cover to emigration, in a broad-scale experiment, Gowan and Fausch (1996) found that habitat manipulation influenced trout movement. Other studies have reported no relationship between emigration and cover (Boss and Richardson 2002), or a stronger relationship between emigration and another factor, specifically food (Wilzbach 1985) or density (Mesick 1988). Accordingly, these results identify the importance of understanding the context-dependent circumstances that may play into them. Among many differences, we highlight two, including 1) different temporal time-frames used to measure emigration; and 2) selection of streams where cover may not have been limiting enough. For example, emigration was measured over a 7-day (Wilzbach 1985) compared to a 20- or 40-day timeframe (Boss and Richardson 2002), and for trout <130 mm, cobbles found in natural streams may have acted as cover, in addition to what cover was experimentally added (Boss and Richardson 2002; see also Andersen 2008). In summary, these results collectively point to context-specific conditions surrounding the relationship of instream cover and the ability to emigrate.

Based on prior studies showing size-biased emigration, smaller trout are more likely to emigrate (Chapman 1962; Elliott 1986; Mesick 1988; Lonzarich and Quinn 1995; Keeley 2001), leading us to believe that we should expect similar results (see also Peters 1983; Orrock et al. 2013). In our study, however, we do not find more small-sized trout emigrating, perhaps because each cover position is long enough for multiple trout to share. Accordingly, small trout in our study could remain in the stream reach sharing cover with a larger trout. Intermediate-sized trout, however, do not emigrate or use cover more than the other two size-classes. Size-based emigration

is based on the context-dependent circumstances from each study, and we need to further examine those conditions to understand all factors influencing emigration.

2.5.3 *Higher feeding activity associated with emigration and higher cover use*

Per-capita feeding is elevated when emigration is possible and resident trout more intensively use cover compared to when emigration is not possible and trout mainly group. This indicates that increased cover use by resident individuals may not constrain feeding activity as much as grouping. This pattern may be explained by intraspecific interactions, which are likely elevated during grouping, reducing an animal's propensity to perform another action, such as feeding (Krause and Ruxton 2002). Larger group sizes are generally associated with elevated feeding efforts (rainbow trout *Oncorhynchus mykiss* Johnsson 2003), thus it is possible that groups in our study are still small enough that total feeding activity is depressed. Theory suggests that there should be more feeding while grouping (Krebs et al. 1972; Creel 2011), but trout typically hold territories with dominance hierarchies (Chapman 1962), and rarely exhibit grouping behavior. Accordingly, it is possible that feeding while grouping for trout is lower than that of another animal that uses grouping as a standard tactic. Although grouping may constrain feeding opportunities for trout, the use of this behavior may increase the chances of survival through safety in numbers.

2.5.4 *Conclusions*

Consideration of multiple responses in our study provides insight into the complex interplay among context-specific behaviors underlying local cutthroat trout densities (Fig. 4). By considering individuals, we were able to link cover use to emigration through individual specialization of trout (trout that use cover more frequently are less likely to emigrate). Our results reveal that cover availability directly influences emigration of trout and that it can also influence the degree of behavioral expression

for other responses of emigration or grouping. The ability to emigrate has a dominant role in the behavioral repertoire of trout by driving which behaviors are expressed (i.e., emigration, cover use, and grouping). Essentially, more cover means less emigration by trout and, in turn, more retention of trout in the stream. Our study highlights the importance of intrapopulation variation to behaviors, our local study population, and ultimately population dynamics. Overall, our findings place cover availability for trout in a more central role among processes influencing local densities, such as food and space. This suggests that it merits serious consideration among key processes underlying populations, which could affect management and conservation of fish.

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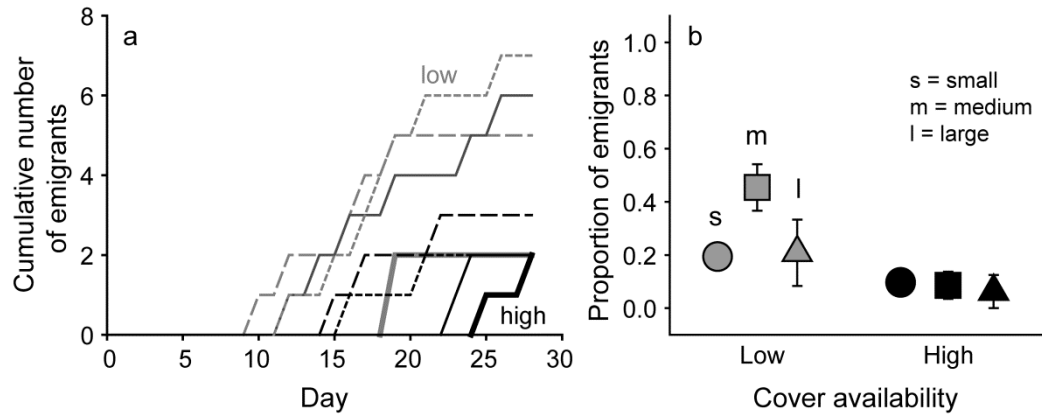
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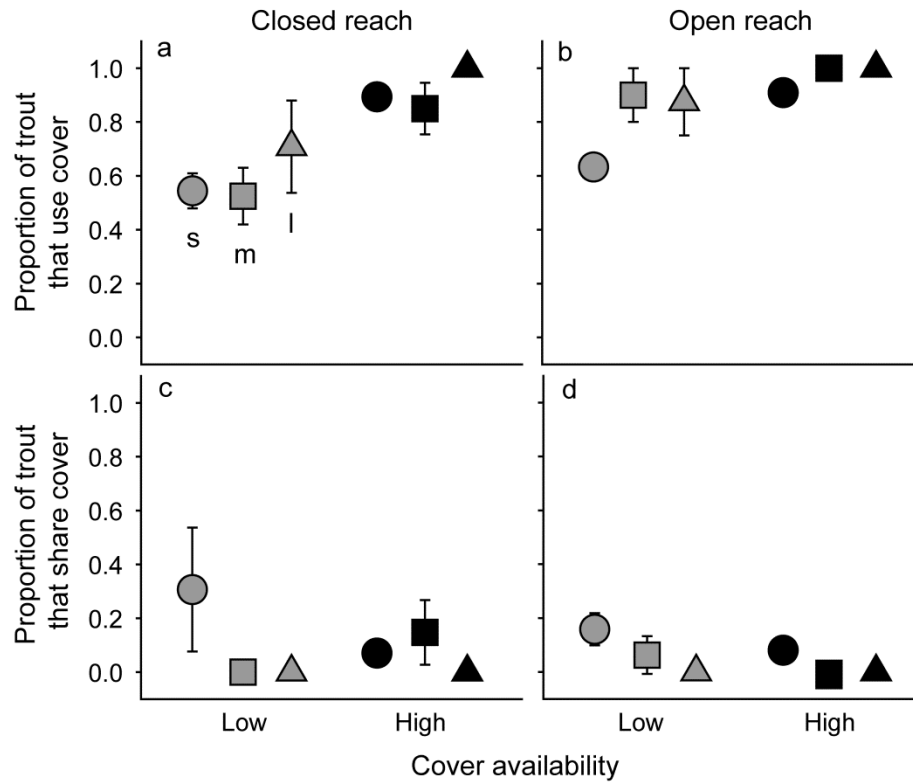
Table 2.1: Cover use by emigrant and non-emigrant coastal cutthroat trout (n = 192).

Refuge Use	% Trout Using Refugia		Odds Ratio*	95% CI for Odds Ratio
	Emigrant	Non-emigrant		
Never	43	7	10.00	3.11 to 32.15
Once	19	7	3.14	0.80 to 12.34
Twice	14	3	4.61	0.85 to 24.73
Three times	10	12	0.80	0.16 to 3.96
Four times	14	34	0.33	0.09 to 1.20
Five times	0	37	0	0

*The odds of cover use for a trout that eventually emigrates is estimated to be insert odds ratio value here number of times the odds of refuge use for a trout that remains.



1
2 Figure 2.1. a) Cumulative emigration by cutthroat trout (*Oncorhynchus clarkii clarkii*)
3 per day in high-density (black, n = 4) and low-density (gray, n = 4) instream cover
4 stream units. Different line types represent results from one of four stream units for
5 either high- or low- density cover and b) proportion of trout that emigrate by length
6 class small: 9.4–14.9 cm (circle); intermediate: 15.0–19.4 cm (square); large: 19.5–
7 23.4 cm (triangle) sized fish in high-density (black, n = 4) and low-density (gray, n =
8 4) instream cover stream units.



9

10 Figure 2.2. a) Proportion of cutthroat trout (*Oncorhynchus clarkii clarkii*) that use
 11 cover (mean \pm SE) when stream reach is either closed to emigration or b) open and c)
 12 proportion of trout that share cover (mean \pm SE) when stream reach is either closed to
 13 emigration or d) open by length class (small: 9.4–14.9 cm (circle); intermediate: 15.0–
 14 19.4 cm (square); large: 19.5–23.4 cm (triangle) in high-density (black, n = 4) and
 15 low-density (gray, n = 4) instream cover stream units.

16

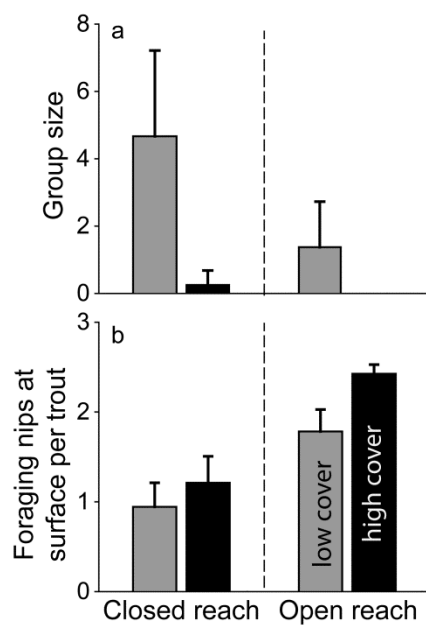


Figure 2.3. a) Group size (mean \pm SE) and b) feeding nips at surface per individual (mean \pm SD) by cutthroat trout (*Oncorhynchus clarkii clarkii*) in high-density (black, $n = 4$) and low-density (gray, $n = 4$) instream cover stream units separated by when the stream reach is either closed or open to emigration.

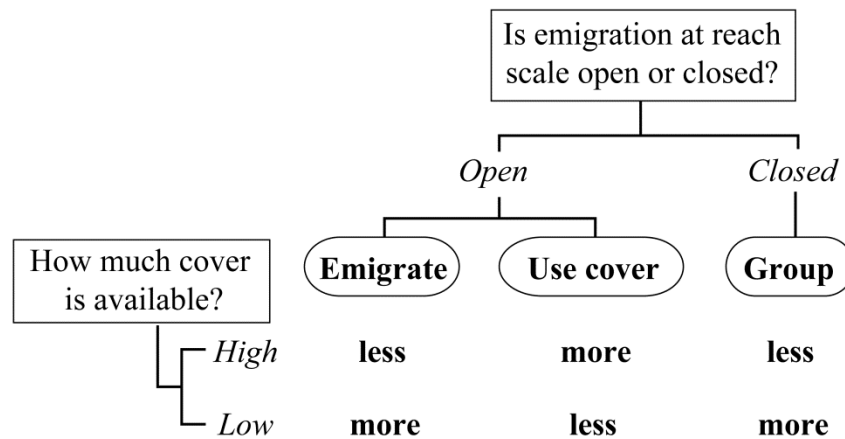


Figure 2.4. Conceptual model synthesizing study results highlighting that emigration determines which behavior is expressed, and cover availability affects the intensity of behavioral responses for cutthroat trout (*Oncorhynchus clarkii clarkii*). When stream units were closed to emigration, grouping behavior by trout was more prominent, with more grouping occurring when cover was less abundant. When stream units were open to emigration, grouping was replaced by both emigrating and increased use of cover by remaining trout, with more emigration and less cover use when cover were less abundant. Cover use by trout also depended on their size class (see Fig. 1).

CHAPTER 3: CAN ONE STEP INTO THE SAME STREAM TWICE? EXAMINING THE ROLE OF ENVIRONMENTAL REGIMES AND HABITAT STRUCTURE FOR TROUT POPULATIONS USING AN INDIVIDUAL-BASED MODEL

3.1 Abstract

The importance of location to biological processes in streams has been explored and debated extensively, but the variability in population responses across similar locations within a landscape is less understood. We used an individual-based model of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) to understand the heterogeneity in trout biomass across headwater streams networked within the same watershed. The model tracked individual trout through daily processes of spawning, movement, feeding, growth, and mortality for four years. We modeled four streams found in the field as well as 12 additional stream combinations where we replaced the environmental regime (i.e., flow, temperature, turbidity) of a given stream with those from each of the three adjacent streams, while keeping habitat structure (i.e., channel shape, instream cover, spawning gravel) fixed. We also performed single-parameter sensitivity analyses on the four modeled streams. Trout biomasses differed among modeled streams. This pattern held even when environmental regimes from nearby streams replaced local regimes. We also found that environmental regimes contribute to biomass variability. Collectively, these results provide evidence that trout biomass in our study system is fundamentally constrained by habitat structure, and that variability in biomass is influenced by environmental regimes. Hence, habitat structure merits attention when considering effects from land use and climate change because it may cause trout populations to respond differentially.

3.2 Introduction

The evolution of concepts in stream ecology has culminated in a collective recognition that location within a landscape influences aquatic biota (Hynes 1975; Vannote et al. 1980; Wiens 2002). In this perspective, streams are viewed as patchy and heterogeneous environments (Minshall et al. 1985; Perry and Schaeffer 1987; Townsend 1989) that vary across various spatio-temporal dimensions (Ward 1989; Ward and Stanford 1995) within a stream network (Benda et al. 2004). This heterogeneity is influenced by floodplains (Junk et al. 1989), riparian zones (Gregory et al. 1991), upslope processes (Montgomery 1999), surface- and groundwater interactions (Boulton et al. 1989), and low-frequency and high-magnitude events that are often regarded in the context of disturbance (Resh et al. 1988; Swanson et al. 1988; Reeves et al. 1995). The net result of these interacting processes is a distribution of conditions that varies in both space and time among locations within stream networks (Poole 2002; Arthington 2012). Multiple aspects of location are essentially confounded in practice, and disentangling the effects of general classes of factors on biota has proven challenging in their natural environment, which makes it difficult to have a comprehensive view of their role to population dynamics of aquatic biota (e.g., Wiley et al. 1997).

Variability among locations within streams is tied to dynamic environmental regimes of stream flow (Poff et al. 1997), temperature (Arismendi et al. 2013) and turbidity, as well as the relatively fixed habitat structure of streams including channel forms that create velocity shelters, hiding cover, and other forms of habitat. Given enough time, virtually any of these features may exhibit variability, but the daily, seasonal, and annual variability in stream flows typically far exceeds that of local habitat structure, which generally changes only in response to infrequent high-flow events (Frissell et al. 1986; Reeves et al. 1995; Benda et al. 2004). The literal interpretation of Heraclitus by stream ecologists (“You cannot step twice into the same river”) originates from the obvious influences of temporally variable stream flows and their attendant influences on ecosystem processes (Resh et al. 1988). These two fundamental features: habitat structure and environmental regimes are each tied to what may more generally comprise the influence of “location” in streams. Although there is a general understanding that location-related influences are essential to fish,

little information is available to explicitly contrast the relative influence of these factors in relation to one another. Given this, our objective in this study was to evaluate the role of fixed habitat structure relative to that of more dynamic environmental regimes in driving demographic responses of fish in headwater streams.

We considered the locations of four headwater streams networked within the same watershed that support coastal cutthroat trout (*Oncorhynchus clarkii clarkii*). Headwater streams provide an ideal setting because they are tightly coupled with terrestrial ecosystems and may be more responsive to their location than larger channels (Vannote et al. 1980; Benda et al. 2004). In addition, cutthroat trout are a widespread salmonid throughout the western United States, providing an interesting case study with the ability to generalize future hypotheses at a broader extent. To contrast location-related influences of habitat structure and environmental regimes, we employed an individual-based model of trout population dynamics (Railsback et al. 2011) parameterized with multi-year, daily measurements of stream flow, stream temperature, and turbidity, as well as field measurements of habitat. Comprehensive data on environmental regimes, habitat structure, and trout populations were collected in the field from 2007-2011 at 250-m reaches in each of the four streams. To calibrate the model, we compared size and abundance of simulated trout from the model by minimizing sum of squared deviations for all age classes to actual trout data estimated from mark and recapture at the corresponding field stream (J. Dunham, unpublished data).

We used a substitution/replacement approach that enabled us to evaluate whether trout populations were more responsive to dynamic environmental regimes or to the relatively fixed habitat structure, in a manner that would be difficult or impossible to replicate in a natural setting. We used an individual-based trout model in each of the four streams in their observed states (i.e., their local habitat structure and environmental regime), in addition to 12 simulations where we replaced the environmental regime (i.e., flow, temperature, turbidity) of a given stream with those from each of the three adjacent streams while keeping habitat structure (i.e., channel shape, instream cover, spawning gravel) fixed. We also performed single-parameter sensitivity analyses on the four modeled streams to understand how trout in each

headwater stream responded to specific factors linked to environmental regimes or habitat structure. In a broader context, this work is important for understanding how local variability in trout populations is tied to environmental regimes or habitat structure of streams, which has implications for species management and conservation.

3.3 Methods

3.3.1 Study sites

Our simulations were based on measurements from four streams in the headwaters of the Trask River watershed, in the Tillamook River basin of the northern Coast Range, Oregon, USA (Table 2.1). Model simulations were performed for a 200- to 250-m length of contiguous stream reach, named after the streams where these reaches were located: Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem. Precipitation in the headwater streams ranges from 2.75–2.83 m/year with most precipitation coming as winter rain (Daly et al. 1994). Stream temperatures are moderate (5–13°C) year-round, and turbidity is very low (4 NTU) except during winter storm events (up to 150 NTU; R. Bilby and S. Johnson, unpublished data). Rock and Pothole are located downstream in the watershed (336.6 m and 324.4 m respectively) with Gus Creek (468.7 m) and Upper Mainstem (609.2 m) being further upstream. Three streams have similar watershed areas (Gus = 302.1 ha, Upper Mainstem = 293.2 ha, Pothole = 325.4 ha) and one, Rock Creek, is twice as big (667.6 ha). The wetted area during seasonal low flows varies with Upper Mainstem (791.81 m²) being the smallest, followed by Pothole Creek (1010.0 m²), Rock Creek (1416.4 m²), and Gus Creek (1500.0 m²). Coastal cutthroat trout occur in all four headwater streams with some actual streams supporting sculpins (*Cottus* spp.) as well as steelhead (*O. mykiss*) and coho salmon (*O. kisutch*) juveniles.

3.3.2 The trout model

We used version 5.0 of inSTREAM, Lang, Railsback & Associates, Arcata, California, USA as our individual-based trout population model. This model is well documented (e.g., Railsback et al. 2009, 2011) and available at

<http://www.humboldt.edu/ecomodel>). InSTREAM simulates trout population dynamics in a realistic environment, and extensive model testing has shown it to reproduce trout population responses typically observed in nature for both individuals (Railsback and Harvey 2002) and populations (Railsback et al. 2002). Our intent in applying this model was not to predict or duplicate actual responses of trout in the field, however, but rather to evaluate how trout respond to environmental variability as related to influences of environmental regimes and habitat structure. In this sense the model is truly “valid” for our intended purpose (Rykiel 1996). Here we outline how the model works and focus on features relevant to the objectives of this study. As an individual-based trout population model, inSTREAM has population dynamics that emerge from individual trout responding to environmental conditions that vary spatially and temporally. Unless noted otherwise, we used the parameter values for cutthroat trout and small streams provided by Railsback et al. (2009). We changed the latitude of model streams to 45°N, which influences photoperiod.

In our application, inSTREAM represents habitat as “reaches” (each study stream is represented as one reach) that are made up of rectangular cells. Reach variables include flow, temperature, and turbidity. The cells within reaches represent units of microhabitat, with typical areas of one to several square meters and variables such as depth, velocity, area of velocity shelter for drift-feeding, and a characteristic distance to hiding cover. Trout are represented as individuals from when they emerge from redds; trout variables include length, weight, condition (the fraction of healthy weight for their length), sex, and which cell they feed in. The trout life cycle is completely represented in the model, beginning with redds, which are represented as objects with variables for the number of live eggs they contain and the eggs’ development status. The model operates at a daily time-step.

InSTREAM’s daily schedule of actions occurs in the following order. First, daily values of flow, temperature, and turbidity are taken from files of actual field observations. The depth and velocity of each cell is then calculated from the flow to allow for changing environmental conditions. The first trout action is spawning: female trout age 1 or older with fork length >10 cm spawn if conditions are within specified dates and environmental thresholds are met. When they spawn, female trout

move to cells with spawning gravel and construct a redd (nest). The number of eggs deposited in a redd increases with female fork length. The representation of spawning and redds is simplified in the model, but it enables the model to simulate the full life cycle and long-term population dynamics (Railsback et al. 2009).

Next, all trout select a cell for feeding by making a tradeoff between energy intake and mortality risk (Railsback et al. 1999; Railsback and Harvey 2002). The version of inSTREAM we used assumes that trout feed during daylight hours. Food intake is represented with a conventional drift-feeding approach, and net energy intake (growth) is calculated with a conventional bioenergetics approach. In the model, trout select habitat as a function of size, and larger trout deplete food and cover available to smaller trout, resulting in a length-based hierarchy (see ideal despotic distribution, Fretwell 1972). Generally, the habitat selection method causes individuals to choose available feeding habitats not already occupied by a larger individual, which minimizes risk while avoiding weight loss (Railsback and Harvey 2002). Next, daily growth or weight loss is determined from the net energy intake provided by the selected cell. The final trout action is survival. InSTREAM represents mortality due to several factors, including predation by terrestrial animals, trout predation, and starvation. The daily probability that a trout will survive depends on individual attributes (length, weight) and variables of its cell, as well as vulnerability to stochastic events. Lastly, redd actions include updating its developmental stage (a function of temperature), determining how many eggs die due to processes such as temperature stress and disease, scouring, or desiccation. When a redd is fully developed, recruitment of new trout results as a function of surviving eggs.

Input. Measurements of habitat structure were collected to parameterize the model for each stream. During seasonal low-flow in 2009, measurements of channel shape were made and used to delineate cells. For each cell, we measured availability of velocity shelter and spawning gravel as well as distance to hiding cover. Depth, velocity, and water surface elevation of each cell were measured over a range of low, medium, and high flows from 2009–2010. We computed daily mean stream flow, stream temperature, and turbidity from field measurements recorded every 10 minutes from March 2007 to September 2011 for each stream. Mean turbidity was measured

using an instream nephelometer, which measures the scatter of a focused light beam by suspended solids. Following standard procedure to minimize initialization effects (Railsback 2009, 2011), we simulated eight years by repeating the four years of data for environmental regimes and analyzed results from the last four years only.

Calibration. Following Railsback et al. (2009), we calibrated inSTREAM to each stream by varying four parameters: concentration of drift-food, concentration of benthic food that trout search for, risk of terrestrial predation, and risk of trout predation, to find a combination of values that closely reproduced estimated trout densities and size by age class from the field data in September from 2007–2009. We compared size and abundance of simulated trout from the model by minimizing sum of squared deviations for all age classes to actual trout data estimated from mark and recapture at the corresponding field stream (J. Dunham, unpublished data). We classified resident cutthroat trout into five age classes (i.e., age 0, age 1, age 2, age 3, age ≥ 4).

Scenarios. We modeled trout biomass in relation to conditions within each stream (their local habitat structure and environmental regime), and then conducted a substitution of condition among streams, replacing the dynamic environmental regimes (stream flow, stream temperature, turbidity) of a given stream with those from each of the three adjacent streams while keeping habitat structure (channel shape, instream cover, spawning gravel) fixed. This resulted in 16 scenarios for both summer and winter during a 4 year-period. This substitution and replacement process was continued until all possible combinations of environmental regimes and habitat structures were examined. During the substitutions, we did not adjust the environmental regimes for proportional differences in watershed area or other features (Table 2.1) because there are complex links among stream flow, temperature, and turbidity that would be lost if such changes were made.

Population-level responses and data analysis. We set up the model to generate biomass every 10 days during the 4-year study. We averaged biomass for each of the five age classes for both summer (July and August) and winter (January and February) for the 16 scenarios every year.

We captured the complexities within a population among the 5 age classes of trout from all modeled scenarios using nonmetric multi-dimensional scaling (NMS), a nonparametric ordination technique (Kruskal 1964; Mather 1976). To calculate the similarity matrix, we used the square root transformation of the Euclidean distance among biomass values for each age classes to reduce the influence of highly influential age classes (Clarke 1993; McCune and Grace 2002). In the end, we had a matrix of 128 rows (16 scenarios for both summer and winter during a 4 year period) x 5 trout age classes, for a total of 640 values. To understand which age class was driving the ordination on each axis, we correlated the ranks of the axis scores with biomass by age class with Kendall's τ . We used multi-response permutation procedures (MRPP) of Euclidean distances ($\alpha = 0.05$; Mielke and Berry 2001) to examine the hypothesis of no difference among stream or environmental regime between pairs of modeled streams (Gus vs. Pothole, Gus vs. Rock, Gus vs. UM, Pothole vs. Rock, Pothole vs. UM, Rock vs. UM) and between seasons (winter vs. summer) using. MRPP is a nonparametric procedure for testing the hypothesis of no difference among pairs or groups (McCune and Grace 2002). To further describe patterns, we additionally examined dispersion, defined as the spread in multivariate space among streams for trout biomass, measured as the area of a convex hull. We analyzed all data using PC-ORD software (MjM Software Design, Gleneden Beach, Oregon), except for dispersion where we used software R ver. 2.11.1 (R Development Core Team 2005) with the *siar* package.

Sensitivity analysis. We evaluated sensitivity of the model to key factors that are considered to be especially important to adult stream-living trout populations: base flow, drift food, hiding cover, piscivory risk, redd scour, spawning gravel, summer temperature, velocity shelter, and winter temperature (Railsback et al. 2011). We performed a sensitivity analysis for each of the four headwater streams with their own environmental regimes. A sensitivity analysis provides an assessment of the relative effect of model parameters with respect to parameter uncertainty by running the model multiple times using a wide range of values for one factor. The analysis used inSTREAM's "limiting factors tool" (Railsback et al. 2011), which automates the generation of input files for sensitivity scenarios because they fit our streams. The

exception was the minimum base flow, which we set to 0, as well as the low range of gravel availability, velocity shelter, and hiding cover, which we set to 0.25 because headwater streams in the Trask watershed are so small in size. The range of values for the analyzed inputs was consistent among the 4 streams, around 5–75% above and below the standard value. Results were analyzed using linear regression analyses where the influence of inputs is indicated by larger slopes and R^2 values. Only older (\geq age-1) trout were considered for the sensitivity analysis because of the wide range of annual variability associated with age-0 trout.

3.4 Results

Biomass of trout showed no overlap in the ordination among headwater streams for simulations using environmental regimes that corresponded to each stream (Fig. 3.1a; Table 2.1). Biomass increased with increasing values of axis 1 from a lowest overall biomass in Pothole Creek to higher biomass in Rock, Upper Mainstem, and Gus Creeks, in that order (Fig. 3.1a; Fig. 3.2). In addition, as biomass increased by stream there was a general increase in dispersion in biomass with each stream as measured by the convex hull area (Pothole Creek = 0.04; Rock Creek = 0.18; Upper Mainstem = 0.16; Gus Creek = 1.86).

A similar pattern of differences in trout biomass among streams was observed when environmental regimes were replaced by regimes from nearby streams. Although biomass in streams stayed in their same general position (Fig. 3.1b; Table 3.1), there was an increase in overlap among data points with alternative environmental regimes expanding biomass boundaries by stream (Fig. 3.1a vs. 1b). Convex hull area also increased for trout biomass under scenarios of alternative environmental regimes when compared to streams modeled with their own environmental regimes (Pothole Creek = 0.04 to 0.41; Rock Creek = 0.18 to 0.46; Upper Mainstem = 0.16 to 0.99; Gus Creek = 1.86 to 6.51). Model output further supported these general patterns, showing an increase in mean trout biomass by stream (Fig. 3.2). It also suggested that differences in biomass among streams are greater than year-to-year variability in summer.

Application of the environmental regime from Rock Creek led to projected biomass values higher than those generated by the application of regimes from other streams for all study streams (Fig. 3.1c; Table 3.1). There were significant seasonal differences in the NMS ordination as seen by the seasonal separation along axis 2, with summer being marked by higher biomass of younger trout (Fig. 3.3; Table 3.1).

Biomass was consistently sensitive to baseflow input in all streams in the model with higher baseflows resulting in a greater biomass of adult trout (Table 2.2). Food (drift and benthic) was another sensitive input for three streams (except Rock Creek), especially in Upper Mainstem where it was most important (represented by a higher R^2 value of 0.52 versus 0.29 for baseflow). For the three streams where food was influential in the model, greater food availability led to higher biomass of adult trout. Elevated summer temperatures resulted in reduced biomass of adult trout in Gus Creek, but not for the other three modeled streams. Elevated piscivory risk led to reduced biomass of adult trout in Rock Creek, but not the other three modeled streams. Hiding cover and redd scour from high flows were sensitive parameters in the model for Pothole Creek. When sensitive, fewer redd-scour events from high flows resulted in higher biomass of adult trout, as well as more hiding cover resulted in elevated biomass of adult trout.

3.5 Discussion

In stream ecology, there is a long history of research to understand which factors influence local variability of trout (e.g., Wiley et al. 1997; Lisi et al. 2013). In practice, location-related effects on fish populations are tied to multiple factors that are often confounded in nature and thus cannot be independently evaluated (Wiley et al. 1997). By employing a simulation approach, we were able to disentangle two classes of factors that can drive the influence of location: habitat structure and environmental regimes. Our findings show that habitat structure plays a dominant role in determining the variation of trout biomass. The ordination polygons (Fig. 3.1) for each stream remain in the same general space when alternative environmental regimes are applied.

Environmental regimes also contribute to the variability in biomass, however, because the boundaries of the ordination polygons for each stream expand considerably when alternative environmental regimes are applied. When streams are subjected to single-parameter sensitivity analysis, we find that environmental regimes can affect variation in trout biomass, however. This is due in part to the fact that the sensitivity analysis examined a range of conditions that exceeded the range of variation observed among our study streams in nature. Collectively, these results provide evidence that trout biomass in our study system is fundamentally constrained by habitat structure and that variability in biomass is influenced by environmental regimes.

Habitat structure locally controls biomass variation in these modeled streams as illustrated by the spatial stability of ordination polygons for each stream when alternative environmental regimes are applied (Fig. 3.1). Habitat structure defined herein describes the physical environment of a stream, and is composed of two types of instream cover (hiding cover and velocity shelter for drift feeding), spawning gravel, and depth of each cell which is set by daily stream flow. These factors may independently or interactively influence trout. For example, in Pothole Creek, sensitivity analysis indicates that hiding cover is an important constraint on biomass, but in other streams hiding cover is considerably less important. Another example is the trout population in Gus Creek, which consistently had the highest estimates of population biomass as well as the greatest degree of variability in these estimates. Elsewhere, greater variation in abundance estimates has been linked to greater habitat heterogeneity (e.g., Anderson et al. 2006), and hence, we hypothesize that streams with more heterogeneity in habitat structure can support a population structure with multiple age classes.

The scale at which trout experience environmental regimes (stream reach) and habitat structure (cells within reaches) is fundamentally different. In the model, environmental regimes are composed of stream flow, stream temperature, and turbidity, which are attributed to an entire modeled stream reach. This, as well as their highly dynamic nature, distinguishes environmental regimes from the habitat structure, although the latter can interact with flow in producing local (among cells within a stream reach) hydraulic variability. Environmental regimes seem to be anchored in

habitat structure because they contribute to biomass variability, as seen by the ordination polygons for each stream expanding considerably when alternative environmental regimes are applied. However, turbidity can reduce the reactive distance to prey and corresponding feeding success of trout (Sweka and Hartman 2001), as well as the risk of predation (Gregory and Levings 1998). The levels of turbidity seen in these modeled streams were likely not extreme enough to influence trout responses (Harvey and White 2008). Similarly, based on responses of cutthroat trout to temperatures in the laboratory (Meeuwig et al. 2004; Bear et al. 2007), variability in temperatures in our system was not extreme enough to produce strong biological responses, at least in terms of survival or growth, which ultimately contributes to biomass. Within a stream reach, stream flow influences the total amount of wetted habitat available, in volume, area, or both, which may influence the number of fish present as well as the body size of individuals (Chapman 1966; Bohlin et al. 1994; Dunham and Vinyard 1997). As with turbidity and temperature, however, the range of variability in stream flows in our system was not broad enough, relative to the local influences of habitat structure, to shift biomasses very dramatically, except for the environmental regime from Rock Creek. When the Rock Creek environmental regime was applied to any stream, the highest biomass for each trout population occurred, likely because its flow was the highest of all the local regimes, allowing trout more wetted area. Further, we observed that trout were especially sensitive to seasonal low flows, when flows were manipulated further via sensitivity analysis (Berger and Gresswell 2009).

Interactions among variables in the model environment may play a stronger role than individual variables. The local hydraulic environment in the model represents an interaction between habitat structure and stream flow. Accordingly, the same flows in streams with different habitat structure can produce radically different environments and thus the localized responses of trout that we observed (Statzner et al. 1988). Local hydraulics influence three key factors in the model: food availability, the importance of velocity shelters, and the depth of each modeled cell. These factors can strongly influence positions selected by trout in streams (Fausch 1984) and habitat selection rules in the model are designed to reflect this (Railsback et al. 2011). Food can be

particularly important to stream-living fish (Chapman 1966). Here, because three of the four streams had the same food concentration values based on the calibration process, food is not contributing to the differences in biomasses among streams.

Our study has valuable implications for management because nearby streams found within the same watershed have different biomass due to their different habitat structures. This suggests that trout populations from different ‘places’ may be more sensitive to climate and land use changes due to their habitat structure alone (e.g., Jeffress et al. 2013). In a management context, this suggests that providing uniform standards to manage species runs the risk of ignoring the importance of natural variability (Bisson et al. 2009). Although the importance of local variability adds complexity to managing streams and stream-living fish, it provides a new way of thinking about the issues, many of which have a long and on-going history in applied ecology. Essentially, if we can better understand the natural variability of stream-living trout populations, then we gain the ability to better manage both streams and stream-living trout. Although we show in our study that habitat structure has the greatest influence on trout biomass in the short term, over the longer term, alterations to environmental regimes may be large enough to overwhelm the effects of habitat structure. Nonetheless, our work shows that habitat structure can be a dominant factor influencing fish in headwater streams, but that this influence is likely dependent on both variability of environmental regimes, and the time scale over which the physical dynamics of streams are considered.

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Ecosystem Science Center. The use of trade or firm names here is for reader information only and does not constitute endorsement of any product or service by the U.S. Government.

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Table 3.1. Description of environmental (ENVR) regimes, physical stream features, and calibration values for four headwater streams in Trask Watershed, OR. Streams are Gus, Pothole, and Rock Creeks, and Upper Mainstem (UM). Winter is January and February and summer is August and September. Environmental regimes display average values with standard deviation values in parentheses for March 2007 to September 2011. Distance to hiding cover, and availability of velocity shelter and spawning gravel are averaged values (total/no. of cells in stream). Higher distance to hiding cover values represent less overall hiding cover availability.

Model input	Factor	Headwater stream			
		Gus	Upper Main	Rock	Pothole
ENVR regimes	Winter stream temp (°C)	4.8(1.4)	4.7(1.1)	5.8(1.2)	6.4(0.9)
	Winter stream flow (m ³ /s)	0.51(1.22)	0.26(0.24)	0.73(0.74)	0.37(0.48)
	Winter turbidity (NTU)	11.6(39.6)	11.8(17.3)	7.7(18.6)	17.6(52.1)
	Summer stream temp (°C)	11.1(1.3)	10.5(1.1)	11.3(1.0)	10.9(0.7)
	Summer stream flow (m ³ /s)	0.03(0.02)	0.04(0.02)	0.03(4.10)	0.03(0.00)
	Summer turbidity (NTU)	9.9(8.1)	10.5(8.9)	4.9(0.0)	3.6(2.1)
Habitat structure	Distance to hiding cover (m)	2.40	1.06	1.75	2.30
	Velocity shelter *	0.40	0.32	0.88	0.36
	Spawning gravel *	0.14	0.17	0.10	0.06
	Cells (no. per stream)	35	32	31	35
Calibration	Drift food (g)	1.5x10 ⁻⁹	6x10 ⁻¹⁰	1.5x10 ⁻⁹	1.5x10 ⁻⁹
	Benthic food (g)	5x10 ⁻⁷	8x10 ⁻⁷	5x10 ⁻⁷	5x10 ⁻⁷
	Aquatic predation **	0.900	0.960	0.900	0.900
	Terrestrial predation **	0.990	0.985	0.990	0.990

*factor is estimated as a percentage of cell area with that characteristic

**factor is estimated as probability of occurrence ranging 0-1

Table 3.2. Multi-response Permutation Procedure results of population data outputted from our model for four headwater streams in the Trask Watershed, OR where alternative environmental regimes were substituted among local regimes while habitat structure from a stream remained fixed. We examined the hypothesis of no difference among stream or environmental regime between pairs of modeled streams and between seasons. Streams are Gus, Pothole, and Rock Creeks, and Upper Mainstem (UM). Significant p-values indicate differences within the pair in question and are indicated in bold (alpha = 0.05). A is chance-corrected within group agreement and it is a measure of effect size ($A = 1 - (\text{observed delta}/\text{expected delta})$).

Scenarios grouped by:	Pairwise comparisons	A	P
Stream	Gus vs. Pothole	0.25	<0.001
	Gus vs. Rock	0.33	<0.001
	Gus vs. UM	0.11	<0.001
	Pothole vs. Rock	0.02	0.05
	Pothole vs. UM	0.20	<0.001
	Rock vs. UM	0.32	<0.001
ENVR regime	Gus vs. Pothole	0.00	0.40
	Gus vs. Rock	0.01	0.05
	Gus vs. UM	0.01	0.09
	Pothole vs. Rock	0.04	<0.001
	Pothole vs. UM	0.01	0.10
	Rock vs. UM	0.06	<0.001
Season	Winter vs. Summer	0.04	<0.001

Table 3.3. Sensitivity analysis of key factors that may affect age 1+ coastal cutthroat trout population biomass (g) in four headwater streams in Trask Watershed, including Gus, Pothole, and Rock Creeks, and Upper Mainstem (UM). Population data were analyzed using linear regression analyses with positive or negative slope values indicated. Factors are more important when they have higher slope magnitude and R^2 . We have bolded factor/stream combinations that have $R^2 > 0.05$. Hiding cover is measured as distance to nearest hiding cover.

		Headwater stream			
		Gus	UM	Rock	Pothole
Baseflow (m ³ /s)	slope	123,134	26,999	466,529	115,131
	R^2	0.68	0.30	0.86	0.96
Benthic and drift food (g)	slope	11,797	4,566	34	2,229
	R^2	0.34	0.52	<0.001	0.15
Summer temperature (°C)	slope	4,963	93	1,286	747
	R^2	0.15	<0.001	0.03	0.01
Hiding cover (m)	slope	809	186	1,051	1,137
	R^2	0.01	<0.001	0.04	0.06
Piscivory risk *	slope	-458	-167	-1,609	-122
	R^2	<0.001	0.01	0.09	0.00
Redd scour *	slope	-91	0	0	-2,178
	R^2	<0.001	<0.001	<0.001	0.13
Spawning gravel *	slope	56	16	17	147
	R^2	<0.001	<0.001	<0.001	0.00
Velocity shelter *	slope	-518	-12	-160	-688
	R^2	<0.001	<0.001	<0.001	0.03
Winter temperature (°C)	slope	2,333	75	104	287
	R^2	0.04	<0.001	<0.001	0.01

*factor is estimated as probability of occurrence ranging 0-1

**factor is estimated as a percentage of cell area with that characteristic

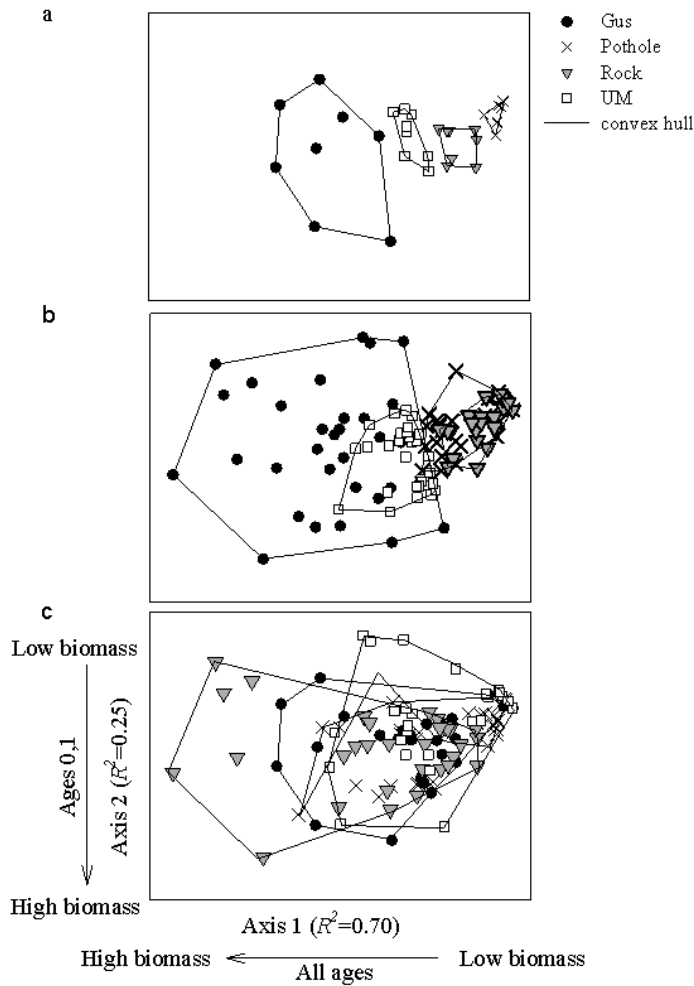


Figure 3.1. Nonmetric multidimensional scaling ordination of average biomass of coastal cutthroat trout (a) in four modeled streams (stress = 2.20) observed in the Trask Watershed including Gus, Pothole, and Rock Creeks, and Upper Mainstem (UM). The solid line represents convex hull area for each stream. The four modeled streams are again plotted in (b) and (c) in addition to the 12 stream combinations where we replaced the environmental regime (i.e., flow, temperature, turbidity) of a given stream with those from each of the three adjacent streams (stress = 5.90). The ordination in (b) is coded by habitat structure of the stream used with the solid line indicating the convex hull area. The ordination in (c) has the same points as in (b), but this time we have coded for environmental regime of stream. Influential age classes for (b) and (c) are indicated for biomass with arrows indicating positive or negative correlations for each axis (all $|r| \geq 0.6$).

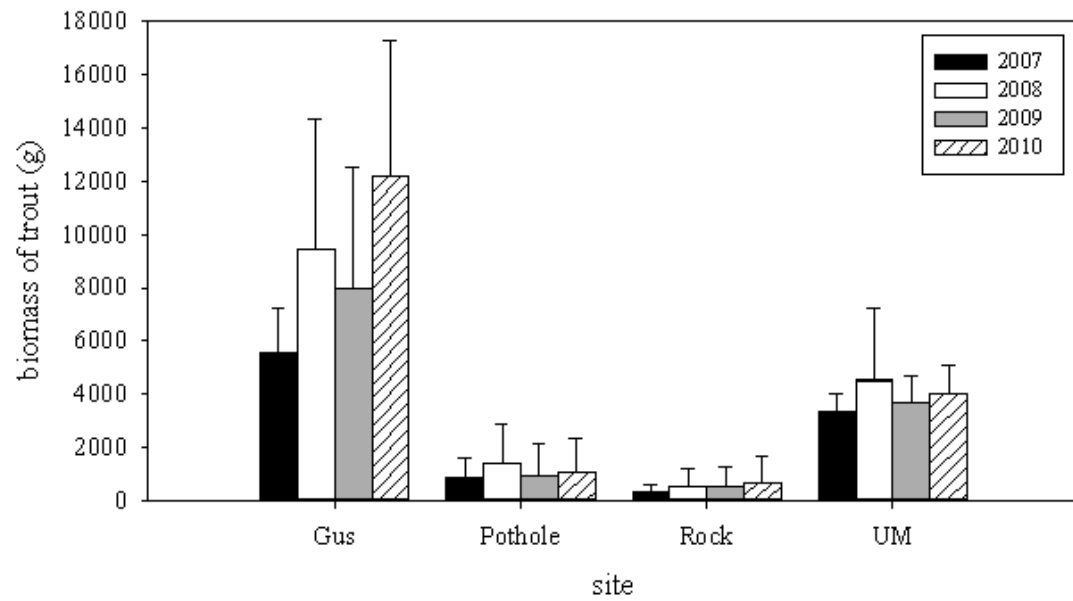


Figure 3.2. Example average biomass (+1SD) of coastal cutthroat trout during summer from four headwater streams in the Trask Watershed, Gus, Pothole, and Rock Creeks, and Upper Mainstem (UM). Standard deviations represent variability among years. All age classes are combined.

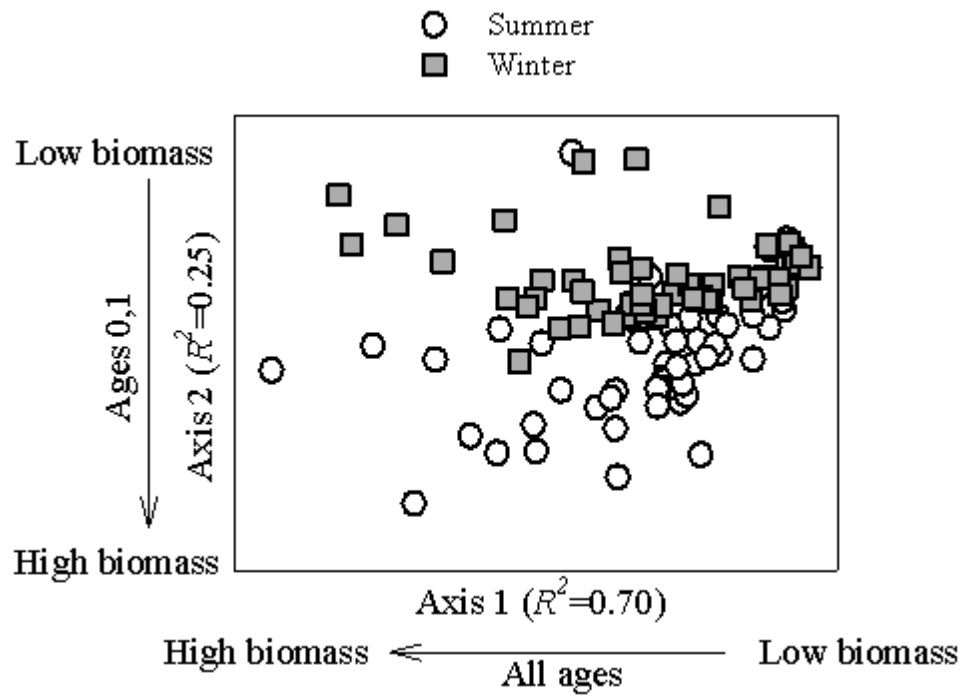


Figure 3.3. Nonmetric multidimensional scaling ordination of average biomass of coastal cutthroat trout in both the four modeled streams actually found in the Trask Watershed including Gus, Pothole, and Rock Creeks, and Upper Mainstem (UM) in addition to the 12 stream combinations where we replaced the environmental regime (i.e., flow, temperature, turbidity) of a given stream with those from each of the three adjacent streams (stress = 5.90). The ordination has the same points as in Figure 1b and 1c, but here we have coded by season to explain the variability along axis 2. Influential age classes are indicated for biomass with arrows indicating positive or negative correlations for each axis (all $|r| \geq 0.6$).

CHAPTER 4: LOCAL VARIABILITY EXPLAINS VULNERABILITY OF TROUT POPULATIONS TO LAND USE AND CLIMATE CHANGE

4.1 Abstract

Climate change occurs simultaneously with land use change, creating a range of conditions that have no historical analog. Studies examining the combined effects of these factors have considered the problem at a broad extent, but local variability may play a key role in understanding actual population responses. Here we use an individual-based model of coastal cutthroat trout population dynamics parameterized with daily measurements of stream flow, stream temperature, and turbidity over multiple years, as well as, field measurements of both the habitat structure and trout population estimates. We tracked the independent and combined effects of contemporary forest harvest and climate change in four headwater streams networked within the same watershed over 63 years by manipulating stream flow and stream temperature regimes. Although we applied identical independent and combined effects of contemporary forest harvest and climate change scenarios across modeled streams, we found a high degree of local variability in trout responses to both forest harvest and climate change. Among the biotic responses we evaluated, timing of emergence was the most consistent among streams, with trout emerging earlier in response to warmer temperatures. Other responses (growth, survival, and biomass) were highly variable among the four streams we studied and scenarios considered. Climate change had greater effects than forest harvest on the timing of emergence, survival, or growth of age-0 trout across streams, but, those composite effects did not consistently translate into a change in overall population biomass. Even though forest harvest had minimal effects on parameters underlying population demography, when it did, these effects were more likely to arise at the population level. Localized responses to forest harvest have been observed, but our findings contrast with the vast majority of work on species responses to climate, most of which reports relatively uniform responses. Ultimately, these findings suggest that there is a high degree of local variability in

trout responses, implying that some stream-living trout populations are more vulnerable to the effects of forest harvest, climate change, or the combination of the two processes than others.

4.2 Introduction

The interactive effects of land use and climate change can produce ecological conditions that have no historical analogs (Vitousek et al. 1997; Williams and Jackson 2007). Climate change alone has been identified as a key driver of ecological change whereas land use change has been suggested to have an even larger influence (Sala et al. 2000). Regardless of the relative magnitudes of influences from either, it is clear that land use and climate change cannot be considered independently in evaluating the future. Many studies examining the combined effects of climate and land use change have considered the problem at a very broad extent by projecting range contractions for multiple species (e.g., Jetz et al. 2007). Such perspectives can provide valuable insight, but local variability (both spatial and across time) may play a key role for understanding actual species' responses to the independent and combined effects of climate and land use change (e.g., Jeffress et al. 2013).

Here we consider the case of local impacts of contemporary forestry in the context of climate change. Our focus is on the Pacific Northwest, USA, where historical forest practices led to dramatic losses of habitat for both terrestrial and aquatic species, prompting development of more protective contemporary forest harvest practices (Everest and Reeves 2006). Unlike climate change, forest harvest occurs at a local scale. Furthermore, due to regrowth of the forest following harvest, effects are more likely to be episodic in nature, such that conditions seem to be altered by forest harvest for a few years, and may eventually return to pre-harvest conditions (e.g., Jones and Post 2004). We focus on how forestry influences conditions in streams, notably short-term increases in stream temperatures (Johnson and Jones 2000;

Groom et al. 2011) and altered stream flows (Hicks et al. 1991; Moore and Wondzell 2005; Jones and Post 2004; Surfleet and Skaugset 2013). Both temperatures and flows in streams in this region have been linked to climate as well, with documented long-term increases in stream temperatures (Arismendi et al. 2012) and decreases in fall and winter low-flows (Luce and Holden 2009; Safeeq et al. 2013). Compared to the more episodic effects of forest harvest (e.g., Johnson and Jones 2000; Jones and Post 2004), climate effects on stream temperatures and flows are expected to result in continuous and irreversible changes over millennial time-frames.

Detecting potential effects of contemporary forest harvest and climate change on fish populations can be challenging because the signal of each response can be difficult to detect in the context of the wide range of natural variability observed in fish populations. Most studies examining the effects of traditional and contemporary forestry on trout have been designed to measure population parameters including abundance, biomass, or density among different ages of trout (Hall et al. 1978; Hartman & Scrivener 1990; Gregory et al. 2008; Bisson et al. 2008). These demographic parameters, however, have many interacting and less-well studied underlying processes (e.g., survival, growth) that can drive population dynamics (van Horne 1983) making it difficult to understand why a population change has occurred, if a change can be identified at all (Bisson et al. 2008). Furthermore, in the context climate change, changes in the timing of biological events (i.e., phenology) may be particularly relevant (Parmesan and Yohe 2003; Root et al. 2003; Jonsson and Jonsson 2009; Thackeray et al. 2010).

Our overall objective in this work was to track the independent and combined effects of contemporary forest harvest and climate change on trout in four nearby headwater streams found within the same watershed over 63 years by manipulating stream flow and stream temperature regimes. We selected coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) as our species of interest as it is a widespread salmonid throughout the Pacific Northwest and often the focal species in studies of fish and forestry in the region (Northcote and Hartman 2004; Stednick 2008). Our approach in

evaluating both forestry and climate change was to employ an individual-based model of trout (Railsback et al. 2009, 2011), parameterized with multi-year, daily measurements of stream flow, stream temperature, and turbidity, as well as field measurements of both the habitat structure and trout population estimates. In each of the four study streams, we collected extensive data on environmental regimes, the habitat structure, and trout populations at 250-m reaches in the field from 2007–2011. Although most applications of individual-based models compare only final outputs of alternative scenarios from one stream, we examine populations through time and among streams to understand spatial variability in responses of trout populations to forest harvest and climate change scenarios. Our process-based model also contrasts with climate envelope models that are typically used to understand the effect of climate change on a species by mapping the geographic shift in a species range. The approach we adopt here allows us to conduct alternative simulation experiments (e.g., apply exactly the same forest harvest and climate scenario across streams), while representing key mechanisms linking populations to flow and temperature by virtue of using a well-published model (Railsback et al. 2009, 2011) that is strongly parameterized with field data. We chose to examine responses of trout that represented those commonly tracked in field studies, or believed to be particularly relevant to the specific impacts of forest harvest or climate change, including biomass, survival, growth, and timing of fry emergence.

Modeled effects of forest harvest were based on those observed in recent studies of contemporary forest harvest practices (Johnson and Jones 2000; Groom et al. 2011; Moore and Wondzell 2005; Surfleet and Skaugset 2013), and climate effects were based on observed trends in stream flows and temperatures within the region (Arismendi et al. 2012; Safeeq et al. 2013). Although a broad range of scenarios could be simulated, we chose to begin with those that have been recently observed in the region. We evaluate results from these simulation experiments to better understand how climate and land use interact to influence multiple responses of trout, as well as how these responses can vary locally (i.e., among streams) and through time. In light

of the fact that land use and climate change are simultaneously occurring, anticipating population responses to independent and combined effects of forest harvest and climate change is critical to the guidance of management, policy, and conservation efforts to mitigate their effects. Thus, our results provide a relatively comprehensive perspective on anticipated responses of trout to environmental change.

4.3 Methods

4.3.1 Study sites

We simulated four headwater streams representing field sites with fish populations under study in the Trask River watershed, located in northwest Oregon, USA (Fig 4.1; J. Dunham unpublished data). Stream flows in this region are dominated by wet winters, with a mix of snow and rain at higher elevations and rain at lower elevations (2.75–2.83 m/year; Daly 1994). These climatic conditions, combined with steep terrain and low aquifer and soil permeability, lead to flow regimes characterized by flashy winter flows linked to winter storms, followed by declining flows in spring and an extended low-flow period in late summer and early fall (Safeeq et al. 2013, Wigington et al. 2013). Stream temperatures are moderate year-round (6–12°C; R. Bilby and S. Johnson, unpublished data). These streams are dominated by coastal cutthroat trout *Oncorhynchus clarkii clarkii*, with sculpins *Cottus* spp., steelhead *O. mykiss*, and coho salmon juveniles *O. kisutch* also occurring at few sites.

4.3.2 The trout model

The individual-based trout model we used was version 5.0 of inSTREAM, Lang, Railsback & Associates, Arcata, California, USA (Railsback et al. 2011). This model is fully described, with parameter values (e.g., Railsback et al. 2009, 2011) and is publically available (<http://www.humboldt.edu/ecomodel>). Unless noted here, we

used the parameter values for cutthroat trout and small streams provided by Railsback et al. (2009) and Chapter 2. Model calibration in streams studied herein is explained in detail in Chapter 2.

As an individual-based trout model population dynamics in inSTREAM are consequences from the fates of individual trout responding to environmental conditions that vary spatially and temporally. InSTREAM models trout population dynamics in a realistic environment resulting in its ability to reproduce responses for individuals (Railsback and Harvey 2002) and populations (Railsback et al. 2002). Our intent in applying this model was to evaluate how trout respond to changes in stream flow and temperature under different scenarios of contemporary forest harvest and climate change, and hence, the model is “valid” for our intended purpose (Rykiel 1996).. Here we briefly describe how the model works (see also Railsback et al. 2009, 2011).

InSTREAM captures many complexities of real streams. In inSTREAM, each study stream is represented as a reach that is broken into a network of rectangular cells. Reach-scale variables include flow, temperature, and turbidity, which are constant over the entire reach, but vary daily for each stream. Each cell represents a unit of microhabitat from one to several square meters in area that has a specific depth, velocity, area of velocity shelter for drift-feeding, area of spawning gravel, and distance to hiding refuge. Trout are represented as freely feeding individuals from when they emerge from redds. Each trout is attributed with a length, weight, condition, sex, and assigned to cell within which it feeds in for a given day. Because trout are modeled as individuals, population dynamics emerge from consequences of individuals and the consequences those behaviors. The complete trout life cycle is represented in the model (redds, egg, fry, juvenile, adult). Redds are represented as objects containing both the number of eggs they have and the eggs’ development status.

InSTREAM operates at a daily time-step following a schedule of actions. At the start of each day, daily values of stream flow, temperature, and turbidity are taken

from files of actual field observations. The flow sets the depth and velocity for each habitat cell, and ultimately the stream wetted area for each reach. Hence, these daily updates allow for changing environmental conditions corresponding to each scenario.

The first trout action is spawning. Female trout spawn if conditions are met, spawning once per year depending on the date, flow and temperature thresholds, and female size. When allowed, female trout move to a cell with spawning gravel and create a redd (nest). The number of eggs deposited increases geometrically as a function of fork length. The timing of spawning is important because egg mortality is a result of flow and temperature fluctuations. Each breeding adult (female and male) incurs a weight loss of 20% to represent energy loss due to reproduction. All trout select a cell, a velocity shelter within the cell, and feeding activity to maximize short-term (90 d) fitness, which is a function of growth and survival (Railsback and Harvey 2002). The version of inSTREAM we used assumes that trout feed during daylight hours, and they have access to a set amount of food. Food intake is represented with a conventional drift-feeding approach, and net energy intake (growth) is calculated with a conventional bioenergetics approach. In the model, habitat selection is prioritized as a function of fish size, with the largest fish occupying the most profitable cells first resulting in a length-based hierarchy. Daily growth or weight loss is determined based on the net energy intake provided by selected cell. The last trout action is survival. InSTREAM represents mortality due to several factors, including predation by terrestrial animals, trout predation, disease, and starvation. The daily probability that a trout will survive is conditioned on individual attributes (length, weight) and attributes of its cell.

The developmental stage of eggs within a redd is a function of temperature. Each day the model updates developmental stage, determining how many eggs die due to processes such as temperature stress and disease, scouring, or desiccation. When a surviving egg in a redd is fully developed, there is the conversion of each egg into a new trout, analogous to emergence and first feeding in nature.

Input. We parameterized the model for each stream with field measurements of habitat structure recorded during seasonal low-flow (August-September) in 2009. We measured availability of velocity shelter and spawning gravel as well as distance to hiding cover (Railsback et al. 2011). Depth, velocity, and water surface elevation of each cell were measured at fixed transects over a range of low, medium, and high flows from 2009-2010. Transects were spaced to correspond with the boundaries of low-flow channel units (see Railsback et al. 2009, 2011). We computed daily mean stream flow, stream temperature, and turbidity from measurements recorded every 10 minutes from March 2007 to September 2011 from continuous long-term gaging stations (<http://watershedsresearch.org/Trask/>) located just downstream from each reach.

We evaluated multiple years of simulated data under each scenario (i.e., baseline, forest harvest, climate change, combined) for each stream. Because we had observations from only 2007-2011, we randomly selected the environmental regimes from one of those initial years every year for 67 years (we were limited by the capacity of our 32-bit system to 67 years). This ordering became the baseline scenario and the basis for modifications for all alternative scenarios, all of which are described below for each stream. We chose to ‘cut the forest’ under both the forest harvest and combined scenarios in year 5 (due to the elimination of the first 4 years of data to remove initialization effects; see Railsback 2009, 2011). We used a total of 63 years of data to evaluate under each scenario set forest harvest to year 1.

Scenarios. We designed this study to mimic changes in stream temperature and flows associated with independent and combined effects of contemporary forest harvest and climate change. In addition to these changes, we modeled a baseline scenario that mimicked natural variability in stream flows and temperatures observed from 2007-2011 at each stream. Hence, we have four different scenarios (baseline, forest harvest, climate change, and combined) that we applied to each stream. In the baseline scenario, we ran the first four years in their natural order, and then randomly

selected temperature and flow conditions from one of those four years for each additional year. Although the sequencing of years may matter to whether a population crashes, all trout populations under this scenario persisted for the entire study period. With these baselines established, we modified conditions to mimic effects of contemporary forest harvest and climate change, as well as the additive effects of both.

To model the effects of contemporary forest harvest, we cut the forest in year 1, which would result in increased summer temperatures and altered flows for a brief period of time following simulated harvest to mimic temporary effects noted in the literature. We elevated stream temperatures for 15 years (Johnson and Jones 2000) with the first five years having the greatest effect followed by a gradual decrease to baseline (Beschta and Taylor 1988). Specifically, for each of the first five years, daily mean stream temperature post-harvest increased by 0.37°C , as seen from industrial forest lands in Oregon (Groom et al. 2011), for a total increase of 1.85°C . Then, we linearly decreased the daily mean stream temperature by 0.037°C each year, reaching baseline values in year 16 post-harvest because that is when the forest canopy should be restored, providing shade to the stream. During these same 15 years, we shifted summer regimes earlier by 10 days (Johnson and Jones 2000) by advancing regime values for stream flow, temperature, and turbidity from July to begin on June 20. We changed stream-flow regimes for 25 years (Hicks et al. 1991; Stednick and Kern 1992; Stednick 2008) by manipulating storm events and seasonal low flows. We increased daily water yield by 20% on the days when each storm event persisted that exceeded 2 SD above the observed annual mean because although water yield increases from forest harvest are highly variable they generally increased by around 20% (Moore and Wondzell 2005). We increased summer (July-September) daily mean flows by 45% above baseline for five years (Jones and Post 2004; Surfleet and Skaugset 2013), then decreased summer mean flows from the elevated 45% by 2.25% per year for 20 additional years until baseline was reached in year 26 post-harvest because as the forest regrows, water is used by trees.

We generated the climate change scenario by increasing year-round stream temperatures and decreasing fall and winter flows. We steadily increased mean stream temperatures by 0.06°C annually based on stream temperature trends occurring in the Pacific Northwest over the past 50 years (Arismendi et al. 2012), reaching an additional 3.78°C higher than baseline at the end of the study period (63 years). We decreased mean fall flows by 0.25% (October-December) and winter mean flows by 0.49% (January-March) annually (Safeeq et al. 2013) resulting in a gradual decrease over time reaching 15.75% below baseline for fall flows and 30.87% below baseline for winter flows at the end of the simulation. Because streams of Coastal Oregon generally have single-peaked hydrographs key changes from climate change are occurring during peak winter months from decreasing rain (Safeeq et al. 2013) and not during summer as seen in heavily snow-dominated systems (Luce and Holden 2009; Safeeq et al. 2013).

We combined the additive effects of contemporary forest harvest under a changing climate (both stated above) for the combined scenario because they occur simultaneously in the natural world. We first made the changes from forest harvest, then added alterations from climate change on top of those.

Responses of trout. We set up the model to generate response outputs every 30 days during the 63-year study. Under the different scenarios, we evaluated population biomass (g), growth (cm/month; fork length), and survival (proportion of total that survived in each age class) by season each year as well as timing (Julian date) of fry emergence. Seasons include summer (July, August) and winter (January, February). Age classes during winter were restricted to ages 1+ because the model assigns an additional year to each trout on January 1st every year (in keeping with convention in fisheries biology), thus there are no age-0 trout in winter. For biomass, growth, and survival, we used averages responses for each response in each trout age class (ages 0, 1, 2, 3+). Timing of fry emergence was evaluated as the date each year on which the

median value of the population emerged and estimated using MATLAB code from Warren et al. (2012).

4.3.3 *Statistical analyses*

To provide an overall view of differences among streams and scenarios, we examined summer and winter responses of median biomass, growth, and survival for each age class among all four scenarios (baseline, forest harvest, climate change, and combined) across all 63 simulation years using Kruskal-Wallis one-way analysis of variance on ranks. In cases of significant differences ($p \leq 0.05$) indicated by these analyses, we evaluated pairwise comparisons among the four scenarios using a non-parametric Tukey's test on ranks. We focused these tests on deviations of responses from a stream's specific baseline scenario to responses observed for that stream related to forest harvest, climate change, and combined scenarios (i.e., baseline vs. other scenarios). When the scenario for a stream deviated significantly from its own baseline, we also examined the direction and magnitude of the observed differences.

Annual trends in both biomass and the median date of fry emergence for each stream were evaluated using the Mann-Kendall test (Mann 1945). This rank-based test is robust to outliers and non-linear trends (Hirsch et al. 1982; Esterby 1996). To minimize potential serial correlation effects, we corrected the p-values by modifying the Mann-Kendall trends using the package FUME for R. We evaluated annual trends of biomass and fry emergence over the duration of the study (63 years) for all scenarios. In addition, for both the forest harvest and combined scenarios, we examined additional dates of years 15, 20, and 25 to capture the time period when forest harvest may have the greatest impact (see scenarios section above).

The Kruskal-Wallis and Mann-Kendall analyses were analyzed using software R ver. 2.11.1 (R Development Core Team 2011).

Trajectories. A trajectory, as considered here, is a vector that describes direction and distance in multi-dimensional space (McCune and Grace 2002). Our objective was to apply trajectories to more fully evaluate collective responses of age classes of trout in different scenarios with respect to biomass, growth, survival, and fry emergence. In particular, we were interested in the long-term trajectory of population responses to understand the route that each scenario follows over time in relation to baseline. To this end, we applied nonmetric multi-dimensional scaling (NMS), which is a nonparametric ordination technique (Kruskal 1964; Mather 1976). For the time period of interest over 63 years, the NMS ordination condensed information on all age classes for each response into two coordinates that represented a metric in a 2-dimensional space for each scenario and stream. We averaged and grouped values for all responses every five years (e.g., Coulibaly and Burn 2005; Arismendi et al. 2013). This allowed us to evaluate longer-term patterns of responses (e.g., 5-year increments of biomass) and to evaluate a large enough number of events within the span of 63 years to visualize trajectories for each scenario in each stream. We used Euclidean distance to calculate similarity matrices for this analysis. For each stream in summer, we had a matrix of 52 rows (13 five-year time periods for 4 scenarios) x 4 trout age classes for a total of 208 values and for each stream in winter, we had a matrix of 52 rows x 3 age classes (no age 0 trout in winter because birthdays of fish occur on January 1st) for a total of 156 values.

The NMS results were displayed in a 2-dimensional plot with the proximity of two points (metrics) representing the degree of similarity between them. This allowed us to follow the trajectories of a response variable in different scenarios and streams at 5-year intervals over the simulation period (63 years). The direction of the trajectory was calculated as the long-term trend in the Euclidean distance for each scenario relative to baseline each year. The distance of each trajectory is the distance between the scenario and baseline for each response. Thus, the long-term trajectory of the distances provided a visual representation of this similarity. We performed our NMS analysis using PRIMER software 6.1.5 (Plymouth Marine Laboratory, UK), and then

calculated the Euclidian distances for each scenario over time in relation to baseline from the coordinates generated by the NMS analysis using Microsoft Excel. We analyzed the relationship between the rank of each scenario and each response variable (biomass, growth, survival, and fry emergence) for each stream using Spearman's correlation analyses ($\alpha \leq 0.05$).

4.4 Results

Our simulations revealed no differences under the contemporary forest harvest scenario compared to baseline for any trout ages in any stream with respect to their survival, growth, and biomass values in summer over the duration of the study (Table 4.1). Survival, growth, and biomass of trout under the climate change and combined scenarios, however, depended on season, stream, and age of trout. During winters, survival, growth, and biomass of trout were not different for any of the streams under the climate change and combined scenarios compared to baseline values, except biomass of age-1 trout at Gus Creek that increased 22% (353 g above baseline) under the climate change scenario and age-3+ trout that decreased 44% (-1933 g) under the climate change scenario and 37% (-1638 g) under the combined scenario.

During summers, biomass for any age class of trout was not different under the climate change and combined scenarios compared to baseline values, except at Gus Creek where ages 0, 2, and 3+ trout were reduced (Table 4.1). Summer survival and growth of age-2 and 3+ trout under the climate change and combined scenarios not different from baseline values. Survival and growth of age-1 trout in summer responded to the climate change and combined scenarios, but this varied among streams. Age-1 trout in Upper Mainstem showed reduced growth under the climate change scenario, age-1 trout in Pothole Creek had reduced survival under the climate change scenario, and age-1 trout in Rock Creek had reduced survival under the combined scenario. Among all streams, age-0 trout most consistently showed reductions in growth or survival compared to their baselines. Summer survival of age-

0 trout at Gus Creek, Pothole Creek, and Rock Creek were reduced compared to their baselines under climate change and the combined scenarios whereas summer survival of age-0 trout in Upper Mainstem was not different. Summer growth of age-0 trout at Pothole Creek and Rock Creek were reduced when compared to their baselines for both climate change and the combined scenarios, whereas summer growth of age-0 trout was only reduced for the combined scenario at Upper Mainstem when compared to its baseline. Summer growth of age-0 trout for Gus Creek was not different under alternative scenarios.

Our trend analysis showed earlier median timing of fry emergence over the 63-year duration of the study for climate change by 24 to 55 days (4–9 days/decade) and the combined scenario by 11 to 24 days (1–4 days/decade) for all streams (Table 4.2; Fig 4.2). The trend in magnitude for the median timing of fry emergence for contemporary forest harvest was also earlier at Pothole Creek by 10 days in year 20, even though it was not earlier in any other stream or for any other time period. The trend in magnitude for the median timing of fry emergence for the combined scenario was earlier at Pothole Creek and Rock Creek in years 20 (by 8 and 19 days respectively) and 25 (by 9 and 15 days), but not in the other two streams or in year 15. There were no significant trends for the median timing of fry emergence from the baseline scenario over the study period for any stream.

The total biomass of all ages grouped together in summer depended on stream and scenario (Table 4.3; Fig 4.3). Summer total biomass of trout was not different for trout in Gus or Rock Creek over any time period. Total biomass of trout in Pothole Creek was reduced under forest harvest, climate change, and the combined scenarios in summer. In addition, there was suggestive evidence ($p = 0.06$) that total biomass of trout decreased under the forest harvest scenario in Pothole Creek in year 20. Total biomass of trout in Upper Mainstem was reduced under the climate change and combined scenarios over time. It was also reduced under the forest harvest scenario in year 15.

The trajectories of trout populations under contemporary forest harvest, climate change, and the combined scenario indicated that none of the populations return to baseline after 63 years (Fig 4.4). Trajectories depended on season, stream, scenario, and trout response. Of all the scenarios, contemporary forest harvest was, on average, closest to baseline for all streams and responses during summer (Fig 4.4). There are exceptions to this trend when, for example, climate change was closest to baseline (summer biomass and survival at Upper Mainstem and summer biomass at Rock Creek) or when the combined scenario was closest (winter biomass and survival at Rock and Upper Mainstem). Climate change and the combined scenario resulted in trajectories that are negatively related to baseline for all streams, except Upper Mainstem where only climate change was negatively associated.

4.5 Discussion

Our results suggest that trout within individual streams, located within the same local watershed, responded very differently to the effects of land use and climate change. Among the biotic responses we evaluated, timing of emergence, which in the model depends on when trout spawn and temperature input, was remarkably consistent among streams, with trout emerging earlier in response to warmer temperatures. Other responses (growth, survival, and biomass—which arise from several inputs and processes in the model, including behavior) were highly variable among the four streams we studied and scenario considered. Overall, it is clear that the impacts of climate change were greater than forest harvest on the timing of emergence, survival, or growth of age-0 trout across streams, but at the population-level when considering biomass over time they have arguably similar effects (Fig 4.3). It may have been expected that forest harvest would have minimal effects on certain responses, emergence, survival, and growth, underlying population demography across streams, given the shorter-term nature of environmental changes related to forest harvest where influences of temperature and flow returned to baseline conditions within 16 and 26

years, respectively. In considering effects of climate and forest harvest in winter or summer, we found that trout were most sensitive to simulated environmental changes during summer. Collectively, these results point to a high degree of local variability in the responses we simulated. Whereas localized responses to forestry have been observed in other studies (see reviews by Hall et al. 2004; Bisson et al. 2008) our findings contrast with the vast majority of work on species responses to climate, most of which reports relatively synchronous or uniform responses (Walther et al. 2002; Parmesan and Yohe 2003; but see Walther 2010), including fishes (Bunnell et al. 2010; Overland et al. 2010; but see Schindler et al. 2010). Below we discuss each simulated scenario (forest harvest, climate change, combined effects) in more detail to better interpret the complex and variable responses we modeled.

4.5.1 Forest Harvest Scenario

A wide range of variability has been observed in trout population responses to historical forest harvest practices (Murphy and Hall 1981; Reeves et al. 1997; Hall et al. 2004; Bisson et al. 2008). Part of this observed variability can be explained by differences in the details of how forestry was carried out and how physical factors, such as temperature and flow, were influenced in each setting (Moore et al. 2005; Moore and Wondzell 2005; Pollock et al. 2009). Related to this is the challenge of imposing the classic rules of experimental design (e.g., Hurlbert 1984) in a study of forest harvest. Typically, replication in studies conducted at broad extents ($>10^3$ m) is limited, and there can be tremendous natural variability among experimental units that may confound or obscure ecological inferences (Hargrove and Pickering 1992; Groom et al. 2011). By adopting a simulation approach based on characteristics of natural stream channels, environmental regimes, and trout population characteristics, we were able to conduct manipulative experiments with a high degree of control and realism. Overall, our results indicate that the simulated effects of contemporary forest harvest on trout were relatively minimal. In comparison to historical forest practices, which

are not designed to be protective of streams or aquatic biota (Hall et al. 2004; Everest and Reeves 2006; Bisson et al. 2008).

Although the effects of contemporary forest harvest were limited on the timing of emergence, survival, or growth of age-0 trout compared to the effects of climate change, there were some notable responses. In particular, though temperature and flow regimes under the forest harvest scenario go back to baseline values at years 16 and 26, respectively, trout responses continue to deviate from their baselines for an additional 38 years within the time frame of our simulations (Fig 4.4). This could signify some degree of population momentum (Koons et al. 2006) occurring after impacts of forest harvest have subsided. Hence, the legacy of alternative population structures for the trajectories under each scenario may be a real response for trout populations to change (Figure 4.4). Among the streams we studied, Gus Creek appeared to be the least responsive to forest harvest, and a characteristic feature of Gus Creek was a much greater proportion of older and larger trout (Chapter 2), which may have contributed to the demographic stability of this population. Of the other streams, only one (Pothole Creek) exhibited a decline in biomass associated with effects of forest harvest (Fig 4.3), which is likely due to earlier emergence that coincided with warmer temperatures linked to forest harvest, because other response changes in this stream were minimal (Fig 4.2). Earlier fry emergence in Pothole Creek was likely also influenced by the fact that winter stream temperatures there were initially warmer than the other three streams, and thus any additional warming would have a greater biological response (Chapter 2). Supporting our finding of an earlier timing in fry emergence following forest harvest is an empirical study that also identifies earlier fry emergence of salmon following forest cutting (Scrivener and Andersen 1984).

4.5.2 Climate Change Scenario

Under the climate change scenario, the most consistent response among the four streams was an advance in the timing of fry emergence (see also Jager 1999). Warmer

water temperatures accelerate the development of eggs, resulting in earlier emergence timing (Shapovalov and Taft 1954) which could lead to larger size in advance of winter (Scrivener and Andersen 1984), and higher over-winter survival (Berger & Gresswell 2009). Survival and growth of age-0 trout in summer (by definition, there are no age-0 trout in January-February) were also sensitive to the effects of climate change. Interestingly, the effects of climate change on the timing of emergence, survival, or growth of age-0 trout did not consistently translate into a change in overall population biomass. This may be expected if the equilibrium density of trout is limited by availability of food and body size of trout, and that growth and mortality of younger age classes represents a pattern of density dependence or self-thinning commonly observed in stream-living trout (Bohlin et al. 1994; Elliot 1994; Dunham and Vinyard 1997) and within the model we applied (Railsback et al. 2002). Two streams had changes at the population level with reductions in biomass over time, one of which also saw reduced biomass levels due to forest harvest (Pothole Creek). In the other case, the modeled trout population declined to local extirpation after 40 years of influences from climate change (Upper Mainstem, Figure 4.3). Examination of the results revealed that individuals were not able to successfully spawn or emerge from redds in the modeled scenario because model thresholds were not met. Under natural conditions, local failure to recruit may be balanced by immigration from adjacent reaches, unless the system is isolated (Tsuboi et al. 2013). Alternatively, trout may be able to actually respond with more flexibility in spawn timing or emergence than the current formulation of the model allows (e.g., Jonsson and Jonsson 2009).

4.5.3 *Combined Scenario*

Combining the influences of climate change with those anticipated with forest harvest revealed a wide range of responses among our study streams. For example, when considering response trajectories in summer, the combined scenario resulted in essentially additive effects in Gus Creek for winter survival, whereas the timing of fry

emergence mirrored the influences of climate change alone. In contrast, the timing of fry emergence in Pothole Creek was more influenced (i.e., slower earlier emergence rate) in the combined scenario due to the effects of both influences than in the climate change scenario without effects of forest harvest (i.e., faster earlier emergence rate). These contrasting outcomes likely result from non-linear responses of trout to multiple factors in the model that, in turn, depend on characteristics of each stream (e.g., Chapter 2; Koch et al. 2009; Walther 2010). As with other scenarios, the combined influences of climate change and forest harvest on biomass were not consistent. Two trout populations showed reductions in biomass under the combined scenario. One (Pothole Creek) showed reductions that exceeded those observed from forest harvest or climate change alone, and a second (Upper Mainstem) showed lower reductions in biomass relative to climate change alone, likely because there was no effect from forest harvest alone. In spite of the variability we simulated in trout responses to the combined scenario, overall it is clear that the impacts of climate change were greater than forest harvest on the timing of emergence, survival, or growth of age-0 trout across streams, but at the population level they have arguably similar effects (Fig 4.3).

4.5.4 *Conclusions*

In this simulation, we applied identical independent and combined effects of contemporary forest harvest and climate change scenarios across modeled streams that resulted in us finding a high degree of local variability in trout responses. Climate change had greater effects than forest harvest on the timing of emergence, survival, and growth of age-0 trout across streams; however, interestingly, those composite trout responses did not consistently translate into a change in overall population biomass. Rather, only two populations had reductions in biomass at the population-level from climate change (Pothole Creek and Upper Mainstem). Although climate change influenced more responses of trout that underlie population dynamics (emergence, growth, and survival), its effects at the population level were still not as

dramatic as they may be given more time, or in streams where populations are living closer to the margins of their environmental tolerances. Forest harvest, in contrast, had minimal effects on the timing of emergence, survival, or growth of age-0 trout for any modeled stream. When the timing of emergence was earlier under the forest harvest scenario, however, it led to reductions in biomass at the population-level, even if only for one stream (Pothole Creek). Contemporary forest harvest practices in the Pacific Northwest have been designed to minimize influences on streams and fish (Everest and Reeves 2006). In other studies where land use regulations and practices are not in place, the effects from land use may be much greater than we modeled (e.g., Foley et al. 2005). The importance of local variability seen in our study is not unexpected, considering that across the Pacific Northwest, effects of stream temperatures and flow from climate change and forest harvest are observed in a non-uniform manner (e.g. for temperature see Moore et al. 2005; Arismendi et al. 2012; for flow see Moore and Wondzell 2005; Safeeq et al. 2013). There are two explanations for this, the second being the most likely. First, there is variability in how forest harvest or climate change affects flow and temperature in the natural world. Second, there is variation in physical habitat structure, as well as food supply or predation risk, among streams that likely accounts for the differences. We also suggest that trend detection of populations, which may be the case in some cases here, may be more of an issue of population momentum (Koons et al. 2006) than simply statistical power (e.g., Bisson et al. 2009). Hence, the legacy of alternative population structures for the trajectories under each scenario may be a real response for trout populations to change that has not had enough time to transpire into changes in population biomass. Nonetheless, this suggests that some stream-living trout populations are more vulnerable to the effects of forest harvest, climate change, or a combination of the two, than others due to the local variability of stream conditions. It is possible, then, that populations that remain connected to one another may be able to offset the effects of climate change by supplementing abundances from nearby population sources. Our approach using a process-based model allows us to identify a

change in population, and we can establish where the change came from, and potentially what caused it. Hence, by understanding both local variability and processes underlying population dynamics, we stand to gain a more comprehensive view of the role of various factors to trout, which allows us to more accurately identify the effects of forest harvest and climate change on trout.

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Table 4.2. Trends for the median day of fry emergence of trout for only the forest harvest (FH) and combined (FH + CC) scenarios in four modeled streams, including Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem (UM). Annual trends in fry emergence (days/yr) were analyzed using the Mann-Kendall test and p-values were corrected for serial correlation for dates of years 15, 20, and 25 to capture the time period when forest harvest may have an impact. Different scenarios include manipulations to stream flow and temperature regimes (see Methods for detail). Significant p-values in bold ($\alpha \leq 0.05$) represent increasing or decreasing trends. Magnitude is the Sen slope (days/decade) over time.

stream	scenario	year 15			year 20			year 25		
		tau	p-value	slope	tau	p-value	slope	tau	P-value	slope
Gus	FH	-0.03	0.91	-2.4	-0.02	0.94	-4.5	-0.03	0.87	-3.2
	FH+CC	-0.15	0.50	-4.5	-0.16	0.36	-4.9	-0.17	0.28	-3.8
Pothole	FH	-0.36	0.08	-5.3	-0.19	0.05	-5.1	-0.12	0.51	-3.5
	FH+CC	-0.05	0.70	-2.8	-0.19	0.01	-4.2	-0.23	0.01	-3.6
Rock	FH	0.30	0.15	4.8	0.25	0.14	5.1	-0.02	0.90	-0.9
	FH+CC	-0.22	0.99	-4.1	-0.38	0.02	-9.5	-0.31	0.03	-6.0
UM	FH	0.43	0.23	12.7	0.44	0.12	10.1	0.39	0.09	9.7
	FH+CC	-0.02	1.00	0.2	-0.03	0.91	-1.2	0.18	0.32	3.5

Table 4.3. Trends for total biomass (g) of trout for only the forest harvest (FH) and combined (FH + CC) scenarios in four modeled streams, including Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem (UM). Annual trends in total biomass (g/yr) were analyzed using the Mann-Kendall test and p-values were corrected for serial correlation for dates of years 15, 20, and 25 to capture the time period when forest harvest may have an impact. Different scenarios include manipulations to stream flow and temperature regimes (see Methods for detail). Significant p-values in bold ($\alpha \leq 0.05$) represent increasing or decreasing trends. Magnitude is Sen slope (g/yr) over time.

stream	scenario	year 15			year 20			year 25		
		tau	p-value	slope	tau	p-value	slope	tau	p-value	slope
Gus	FH	-0.09	0.46	-90.09	0.04	0.82	-9.63	0.09	0.56	25.96
	FH+CC	0.05	0.84	41.41	0.09	0.58	41.41	0.02	0.86	-1.07
Pothole	FH	-0.07	0.77	-28.54	-0.26	0.06	-31.40	-0.15	0.29	-17.35
	FH+CC	-0.03	0.92	-2.83	-0.21	0.21	-23.32	-0.22	0.13	-23.57
Rock	FH	0.10	0.62	96.80	0.21	0.21	42.59	0.05	0.76	13.27
	FH+CC	-0.05	0.84	-5.05	0.13	0.46	22.00	-0.09	0.53	-5.41
UM	FH	-0.35	0.04	-91.66	-0.27	0.10	-51.77	-0.16	0.27	-20.88
	FH+CC	0.07	0.77	-6.42	0.29	0.18	53.00	0.30	0.10	50.78

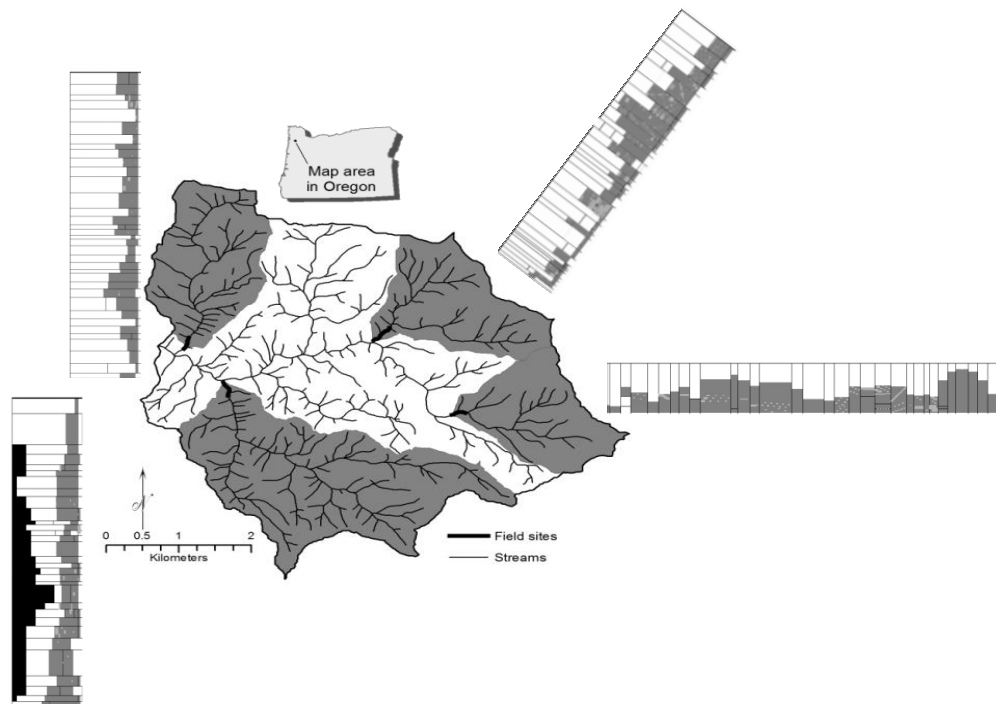


Figure 4.1. Map of Trask Watershed, OR, USA, identifying sub-basins of Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem in gray. Stream reaches representing actual field sites are in bold and modeled streams for each field site are next to corresponding sub-basin. The gray shade in modeled streams is water, white represents cells that may have water in higher flows, and black is riparian habitat that is above floodplain.

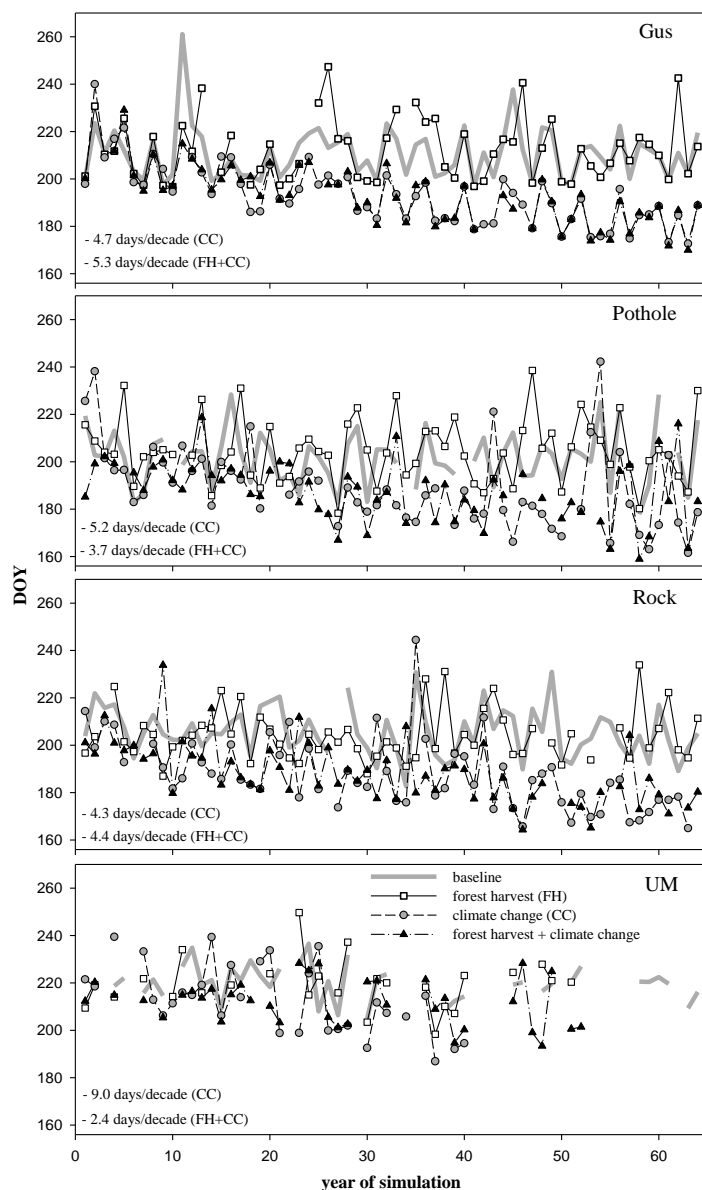


Figure 4.2. Day of year (DOY) when median number of modeled fry had emerged over time in Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem (UM). Scenarios include manipulations to stream flow and temperature regimes (see methods narrative for detail). Only significant trends ($P < 0.05$) over time are listed and include the slope of the trend (days per decade). Negative values represent early fry emergence. Gaps in data are due to years with no emergence because model thresholds were not met.

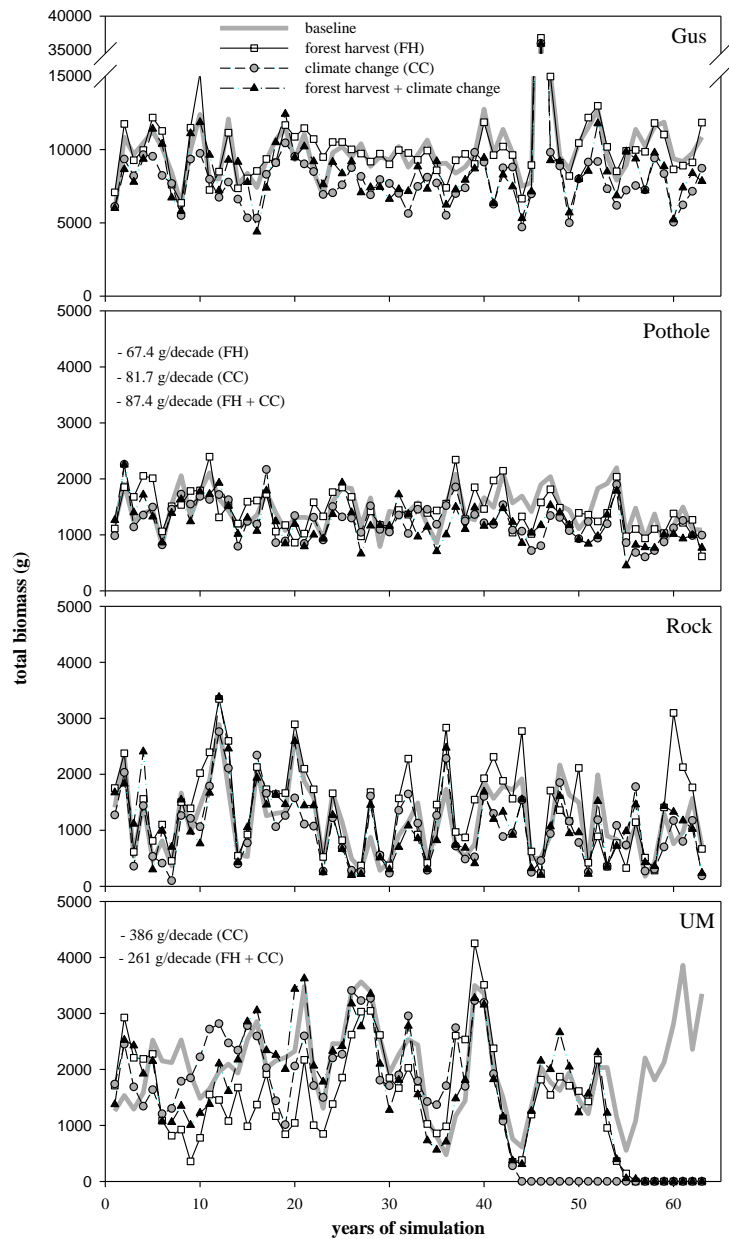


Figure 4.3. Total biomass (g) in summer for all trout ages grouped together over time in Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem (UM). Different scenarios include manipulations to stream flow and temperature regimes (see methods narrative for detail). Only significant trends ($P < 0.05$) are shown with the slope of the trend (g/decade).

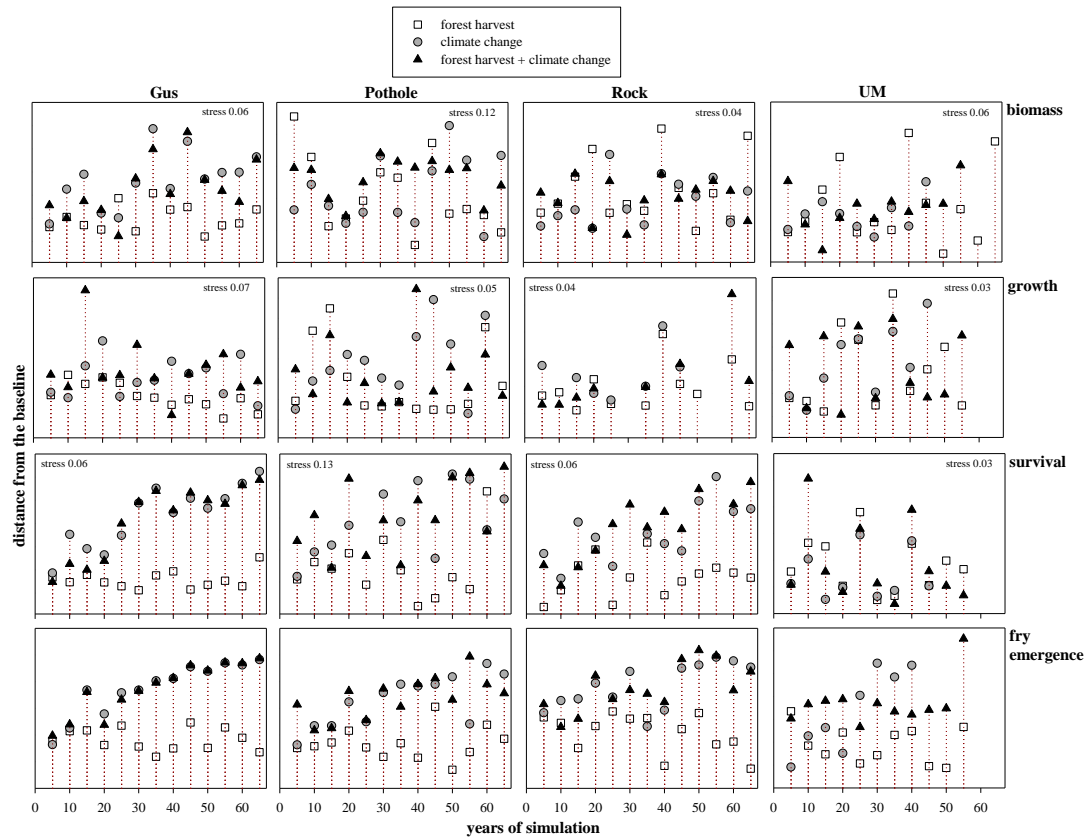


Figure 4.4. Difference in trajectories of trout populations in summer in relation to baseline for forest harvest, climate change, and combined (forest harvest + climate change) scenarios for biomass (g), growth (cm/month), survival (proportion of total in that age class that survive), and fry emergence (median date for population) over time in Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem (UM). Different scenarios include manipulations to stream flow and temperature regimes (see methods narrative for detail). Values have been averaged and grouped every five years.

New Insights on an Old Topic: Understanding the Effects of Forest Harvest on Trout
in the Context of Climate

CHAPTER 5: GENERAL CONCLUSIONS

My overall research goal was to understand changes in streams associated with the effects of contemporary forest harvest and climate change and examine whether those changes influence individuals and corresponding population dynamics of coastal cutthroat trout. By coupling manipulative experiments with modeling, I had the ability to evaluate a complete range of conditions with control over the study system. Such approaches inherently lack the realism that is present in observational studies conducted under fully natural conditions, but they provide greater insights into system behaviors without the usual array of confounding conditions that are always operating in nature (Resetarits and Bernardo 1998). Although behaviors or other characteristics of individuals do not always influence population dynamics (e.g., McPeck et al. 2001), such was not always the case in my work. In Chapter 2, individual behaviors were linked to patterns of habitat (cover) use, as well as the tendency to emigrate in conditions where cover was limited, thus driving local dynamics of experimental populations of trout. The importance of cover to the behaviors of individuals and ultimately population dynamics has been the topic of much debate in stream fishes (Allouche 2002), as well as more generally in contrast to food and space as limiting ecological factors (Berryman and Hawkins 2006). To further evaluate the importance of habitat structure (instream cover is one component of structure), in Chapter 3, I employed individual-based models (Railsback et al. 2011) that were parameterized with field data from four different streams that support trout in the Trask River watershed, northwest Oregon. I conducted a simulation experiment and sensitivity analysis that identified habitat structure as the key factor driving differences in trout biomass among streams. In Chapter 4, I extended the model to simulate anticipated impacts of contemporary forest harvest and climate change on instream conditions,

and trout. Overall, these simulations found that trout responses to changes in stream flow and stream temperature associated with forest harvest and climate change were highly localized. In other words, each stream responded differently to identical changes in stream flow and temperature. Furthermore, whereas the diverse responses of trout to climate change were most evident in young-of-year trout, this was not the case for forest harvest. Dynamics of individuals within this young-of-the-year age class, however, did not always translate into more aggregated responses of sequential age classes or the population, such as overall biomass. Hence, responses of trout that are inferred from changing environmental conditions cannot be simply understood by understanding a single stream, a single life stage, a single factor, or a single biological response.

The lessons learned from my work have a variety of important implications for understanding long-debated issues concerning fish and forestry, as well as an emerging body of work on effects of climate change on fish and aquatic ecosystems. In particular, whereas localized responses to forest harvest have been observed (Murphy and Hall 1981; Bisson et al. 2008), our findings contrast with the vast majority of work on species responses to climate change, most of which reports relatively synchronous or uniform responses (e.g., Parmesan and Yohe 2003). My research suggests that certain trout populations may be more vulnerable to forest harvest and climate change than others. In addition, results of my experimental study suggest that instream cover merits serious consideration next to more widely accepted population drivers of trout, such as food and space (e.g., Chapman 1966; Grant et al. 1998). Due to the importance of instream cover shown here, I suggest that the lack of instream cover may have played a role in the response of coastal cutthroat trout populations to historical forest harvest. Although there is no clear reason to explain the depressed response of coastal cutthroat trout to historical forest harvest (Bisson et al. 2008; Gregory et al. 2008), a hypothesis has been presented for coastal areas suggesting increased competition with other salmonids due to decreased pool habitat

complexity, in particular less instream cover habitat (e.g., as hypothesized by Reeves et al. 1997). Alternatively lack of cover could result in lowered survival, as hypothesized by Berger and Gresswell (2009), based on their analyses of survival of trout in relation to stream flows (see also Andersen 2008).

There are many relevant insights that could be drawn from the results of simulating population dynamics of trout in relation to influences of contemporary forest harvest and climate change, but the overall message is that responses are highly localized. This finding poses challenges for designing broad-scale studies of the effects of environmental changes on stream fishes, as finding replicates or suitable streams to serve as controls may prove extremely challenging at best. In a management context, this suggests that providing uniform standards to manage species, such as coastal cutthroat trout, runs the risk of ignoring the importance of natural variability (Bisson et al. 2009). Although the importance of individual and local variability adds extra complexity to managing streams and stream-living fish, it opens doors to new ways of thinking about the issues, many of which have a long and on-going history in applied ecology. If we can better understand the natural variability, then we gain the ability to better manage streams and stream-living fish to provide more locally adapted solutions to benefit multiple resources. Collectively, this work represents a small step in new directions to address old issues that will need all of the tools, technologies, and perspectives that we can bring to bear as we look forward into learning how to manage the natural resources that we value now well into the future. With the conclusion of this dissertation, I look forward to the opportunity to continue in this line of inquiry and build on the lessons learned herein. May the trout swim on...

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