THE ECOLOGY OF JUVENILE STEELHEAD (*ONCORHYNCHUS MYKISS*): DETERMINANTS OF POPULATION DYNAMICS AND INDIVIDUAL PERFORMANCE ACROSS A HETEROGENEOUS STREAM ENVIRONMENT

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AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of Knut Marius Myrvold, submitted for the degree of Doctorate of Philosophy with a major in Water Resources and titled "The ecology of juvenile steelhead (*Oncorhynchus mykiss*): determinants of population dynamics and individual performance across a heterogeneous stream environment", has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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ABSTRACT

Identifying the processes by which populations are governed and the conditions under which they are operant is a primary interest in ecology and has obvious relevance for management. Anadromous Pacific salmonids represent a particularly imperiled taxon with large conservation interest, especially in the Columbia River Basin, USA. This project concerned the juvenile rearing stage of a population of threatened Snake River steelhead (*Oncorhynchus mykiss*) in the Lapwai Creek watershed, Idaho. The system is characterized by hot and dry summers, heterogeneous habitat conditions, and substantial differences in densities both within and among tributary streams. The primary goal of this research was to identify mechanistic linkages between individual- and population-level demographic parameters and their environment, and to understand how population processes operate to shape individual performance.

The results showed that temperature-induced energetic costs posed constraints on individual growth, suggesting that energetic cost can offset the competitive advantages of large body size when food is a limiting factor. Secondly, density-dependent regulation of cohort size occurred under certain conditions but was not ubiquitous, suggesting population sizes below carrying capacity. The strength of the regulation was explained by environmental conditions and temperature. Thirdly, despite overall low densities, density dependence was manifested in depressed individual growth rates. Growth rates in both cohorts were negatively related to the total population densities, but were inconsistently affected by the densities of the other cohort. Fourthly, habitat-based controls on densities were operant across spatial scales. Whereas watershed topography and discharge regime best described the variation in subyearling densities, yearlings were better described by channel hydraulics. Finally, site fidelity was overall low, suggesting that a large proportion of the individuals were not territorial, and that the propensity to stay was better predicted by habitat factors than biotic factors.

In conclusion, these results show an overall strong abiotic control on juvenile steelhead abundance in the study system, but the strength of these controls to vary substantially across time and space. The subsequent strength of the density-dependent processes depended on these abiotic controls. The combined effects of these abiotic and density-dependent controls constrained and shaped individual growth performance and movement decisions.

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DEDICATION

In loving memory of

Sonja E. Olsson (1926-2012)

Katja S. Rützel (1977-2013)

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1: INTRODUCTION, STUDY SYSTEM, AND PROBLEM STATEMENT

Knut Marius Myrvold

INTRODUCTION

In its simplest form, ecology is the study of the distribution and abundance of organisms and the processes responsible for these patterns. It spans three levels of biological organization, from the individual organism, to the population, to the community. At the individual level, ecology deals with the relationship between the individual organism and its environment. At the population level, ecology concerns the distribution, abundance, trajectory of a particular species. There are two ways to study the population: as an entity with quantitative characteristics in its own right, or as a heterogeneous group made up by a combination of individuals with individual traits. Finally, community ecology concerns the structure of communities and the flow of energy, nutrients, and chemicals through them (Begon et al. 1996).

The unit for classification and management is most commonly the population, or some segment of a larger population, and most of the efforts by ecologists revolve around identifying which factors govern abundance and distribution. Populations are limited by external or environmental factors such as weather that act independently of population size, and regulated by density dependent factors, that is, when the per capita growth rate of the population depends on its own density (Sinclair and Pech 1996). Which of the two that is more important has been the focus of long standing debate (Nicholson 1933, Andrewartha and Birch 1954), but there is general consensus that populations are governed by a combination, rather than one or the other (Begon et al. 1996, Leirs et al. 1997, Karels and Boonstra 2000). Their relative importance varies by population, depending upon abiotic conditions, community organization, and the population's size and –trajectory, all of which are dynamic in time and space (Begon et al. 1996).

In most cases, however, other factors than population processes and their interactions with the natural environment also govern the distribution and abundance of organisms. Global change (referred to as the sum of climate change, societal change, and land use changes) affects species abundance and distribution directly through alterations to their habitats and their management, and indirectly via alterations to the climate and nutrient cycles (Vitousek 1992, 1994, Parmesan and Yohe

2003, Thomas et al. 2004). These impacts can occur at almost any spatial and temporal scale, and the effects on abundance and distribution depend on both the nature of the impacts as well as the life history characteristics of the species. Explicitly accounting for these factors in any ecological study is hence of great importance.

Although few biomes and ecosystems remain unimpacted by global change, some are more severely impacted than others. Freshwater ecosystems, large or small, flowing or still, are among the most altered ecosystems worldwide due to human dependence on water for consumption, power generation, transportation, and recreation (Carpenter et al. 1992, Dynesius and Nilsson 1994, Allan 1995, Poff and Zimmerman 2010). In the case of running water, dams and diversions alter the flow regime by means of the magnitude, frequency, duration, timing, and rate of change in streamwater flow, with the result that very few streams function as uninterrupted continua (Stanford and Ward 2001). This has important consequences for physical habitat configuration and temperature to mention some, and obviously these changes to the physical template affect the biological communities that can inhabit the stream.

The consequences of global change and flow alterations are particularly evident in anadromous salmonids. Pacific salmon and steelhead have disappeared from about 40% of their historical range in California, Oregon, Washington and Idaho over the last century, and remaining populations are often greatly reduced from historical levels (Nehlsen et al. 1991, Gustafson et al. 2007). The Columbia River has shown some of the most severe declines in salmon populations along the Pacific Coast, where steelhead and salmon numbers have declined dramatically since the 1870s. From a historical return of 8-10 million fish to the Columbia River alone, the annual returns are down to 10-20 % of those numbers today (Chapman 1986), with the majority of the individuals having begun their lives in hatcheries (NRC 1996).

Anadromous salmonids have complex life cycles, and utilize a wide range of habitats throughout their life (Quinn 2005). Attributing the declines to any particular factor was therefore a challenge in early investigations, oftentimes confounded by remediation measures and limited by technological shortcomings. The early declines of anadromous salmonids in the Columbia River Basin have largely been attributed to overexploitation and habitat modification (Chapman 1986), and later to the construction of hydropower dams on the mainstem rivers, which impacted all upstream stocks (NRC 1996). It was not until the seminal paper by Nehlsen et al. (1991), however, that a unified approach to understanding the status and trajectories of Pacific salmon, and setting regulatory goals for their recovery, were initiated.

With the resultant growing concern over the effects of these changes and an increased willingness to protect and restore the remaining populations, several populations of salmon and steelhead in the Columbia River Basin were listed under the Endangered Species Act in 1997. Because multiple, often site-specific factors have contributed to the declines of all populations, a critical step on the road to recovery was to identify the ecological and anthropogenic factors by which each population is affected.

In addition to the importance of investigating the limiting factors for population viability, ecological studies in impacted systems provide an opportunity to study ecological processes and test ecological theory. The great plasticity of individual traits (DeAngelis and Mooij 2005), feedback and compensatory mechanisms in population regulation (Murdoch 1994, Sinclair and Pech 1996, Hixon et al. 2002), and relationships with the physical environment (MacArthur and Pianka 1966, Rosenzweig 1981, Gaillard et al. 2010) might not appear as evidently in populations that are at or close to their quasi equilibrium. However, following some change or perturbation to the population or its habitat, these very mechanisms allow for the population to rebound towards former size (Turchin 1999). Perturbations that create gradients of biotic response, such as varying densities, hence provide a good opportunity to study the relationships between individual responses and population processes along the resultant density gradient.

One such situation is found in the Lapwai Creek watershed in North-Central Idaho, United States, where competing demands for stream water has caused declines in a population of steelhead, *Oncorhynchus mykiss*. The population was listed as threatened under the Endangered Species Act under the initial listing process in 1997, which prompted monitoring of the population trend and investigations of its limiting factors. This introductory chapter reviews key aspects of the initiation of my research in the Lapwai Creek watershed by highlighting its societal, legal, and technical context. The purpose is to provide a thorough background and introduction to the population that is used as the study system for my dissertation.

The chapter has three main objectives. First, I will highlight the listing process of Snake River steelhead under the Endangered Species Act, and the actions that were prompted as a result of this determination. Secondly I will introduce the study system, the water diversion infrastructure, the potential impacts that the operations can have on flow and fish habitat, and the following Biological Opinion, which concern the effects of the operation on steelhead population viability. Finally, I will conclude this introductory chapter with a statement of the research problem for my dissertation and a description of how the dissertation is structured.

SNAKE RIVER STEELHEAD

Due to the declines in salmonid abundances in general, and steelhead in particular, the National Marine Fisheries Service (NMFS) received in 1994 a petition to list steelhead throughout its range in California, Oregon, Washington, and Idaho under the Endangered Species Act (ESA). The Endangered Species Act establishes a national program to conserve threatened and endangered species of fish, wildlife, plants, and the habitat on which they depend. The ESA defines an endangered species as one that is in danger of extinction throughout all or a significant portion of its range, and a threatened species as one that is likely to become endangered in the foreseeable future throughout all or a significant portion of its range (ESA sections 3(6) and 3(20), respectively).

Section 4(a)(1) of the ESA and the listing regulations (50 CFR part 424) establish procedures for listing species. The Secretary of Commerce must determine, through the regulatory process, if a species is endangered or threatened based upon any one or a combination of the following factors: (1) the present or threatened destruction, modification, or curtailment of its habitat or range; (2) overutilization for commercial, recreational, scientific, or educational purposes; (3) disease or predation; (4) inadequacy of existing regulatory mechanisms; or (5) other natural or human-made factors affecting its continued existence.

In 1996, NMFS completed a comprehensive status review of West Coast steelhead populations in Washington, Oregon, Idaho, and California, and identified 15 Evolutionarily Significant Units (ESUs; see below) within this range. This resulted in a final rule to list two ESUs as endangered and three as threatened under the ESA on August 18, 1997 (NMFS 1997). Snake River steelhead was one of the threatened ESUs in that initial listing. Because of legal and other issues (see below), all listings were reaffirmed and/or revised on January 5, 2006 (NMFS 2006a). The 2006 listing included a total of nine threatened and one endangered ESUs of West Coast steelhead, some of which had previously been listed. Because the ESA warrants protection for the species as well as their habitat, critical habitat for 10 West Coast steelhead ESUs was designated by NMFS on September 2, 2005 (NMFS 2005). The rule identified 33 201 km of streams in the Pacific Northwest of importance to threatened or endangered anadromous salmonids, of which the Lapwai watershed was one of the designated areas for Snake River steelhead.

Only certain populations, or groups of populations that exhibit some common traits, known as distinct population segments or evolutionary significant units, were listed. Section 3 of the ESA defines “species” as including “*any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature*.” A group of Pacific salmon populations is considered an “*evolutionarily significant unit*” (ESU) if it is substantially reproductively isolated from other conspecific populations, and it represents an important component in the evolutionary legacy of the biological species (NMFS 1991). Further, an ESU is considered to be a “*distinct population segment*” (and thus warranting protection as a species) under the ESA (NMFS 2006a). A group of organisms is discrete if it is “*markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, and behavioral factors*.” Significance is measured with respect to the taxon (species or subspecies) (NMFS 2006a).

The initial listing in 1997 warranted protected status only for the anadromous form of *O. mykiss*, or steelhead, and this decision was reaffirmed in 2006. NMFS noted that there were uncertainties about the relationship of resident and anadromous forms of *O. mykiss*, but concluded that the two forms are part of a single ESU where they have the opportunity to interbreed. The US Fish and Wildlife Service, which has the jurisdiction over resident *O. mykiss*, or rainbow trout, disagreed and advised against the inclusion of resident *O. mykiss* in the ESU. Following a public hearing on the topic (see review in NMFS 2006a), NMFS noted that the resident and anadromous forms are “*markedly separated*” due to “*physical, physiological, ecological, and behavioral factors*” (NMFS 2006a), hence warranting the delineation as separate DPSs.

Multiple drivers have contributed through numerous mechanisms to the decline of West Coast steelhead. Although all the categories identified in section 4(a)(1) of the ESA have contributed, NMFS identified destruction and modification of habitat (category 1), overutilization for recreational purposes (category 2), and other natural and human-made factors (category 5) as being the primary reasons for the decline of both West Coast steelhead and Snake River steelhead (NMFS 2006a).

Salmonid populations persist over time as a function of life history characteristics unique to that population and adjacent populations. ESUs typically behave as metapopulations, at least over evolutionary timescales, in that there is some level of gene flow between populations (e.g. through straying), which contributes to the long term persistence of those populations (Hanski 1999). This spatial structure complicates the assessment of extinction risk (NMFS 2011) because the persistence of a population is contingent not only on its own status, but also on the status of adjacent populations (Schindler et al. 2010). Consequently, in planning and monitoring their recovery, the metapopulations structure has to be accounted for. NMFS adopted a two-step risk assessment approach according to certain criteria, first at the population level and secondly at the ESU level, to assess the viability of each. The criteria, known as Viable Salmonid Population (VSP) criteria consist of abundance, growth rate/productivity, spatial structure, and diversity (McElhany et al. 2000). Individual populations are assessed according to the criteria, and ESUs are assessed as the sum of individual populations. These larger-scale issues include total number of viable populations, geographic distribution of these populations (to ensure inclusion of major life history types and to buffer the effects of regional catastrophes), and connectivity among these populations (to ensure appropriate levels of gene flow and recolonization potential in case of local extirpations) (McElhany et al. 2000).

Infrastructure owned by the federal government represents a main cause of declines of steelhead in the Columbia River Basin. Section 7(a)(2) of the ESA requires Federal agencies to consult with U.S. Fish and Wildlife Service or NMFS to ensure that their actions are not likely to jeopardize the continued existence of endangered or threatened species or adversely modify or destroy their designated critical habitats. Section 7(b)(4) requires the provision of an incidental take statement (ITS) that specifies the impact of any incidental taking and includes reasonable and prudent measures (RPMs) to minimize such impacts (NMFS 2010).

Snake River steelhead constitutes an ESU and a DPS that occupies the Snake River Basin of southeast Washington, northeast Oregon and Idaho. Although the physical characteristics vary greatly over this range, the Snake River flows through terrain that is warmer and drier on an annual basis than the upper Columbia Basin or other drainages to the north (NMFS 1997). Geologically, the land forms are older and much more eroded than most other steelhead habitat. The eastern portion of the basin flows out of the granitic geological unit known as the Idaho Batholith. The western Snake River Basin drains sedimentary and volcanic soils of the Blue Mountains complex. Collectively, the environmental factors of the Snake River Basin result in water that is warmer and more turbid, with higher pH and alkalinity, than is found elsewhere in the range of inland steelhead. As most inland steelhead Snake River steelhead are summer steelhead which enter fresh water from June to October and spawn in the following spring from March to May (NMFS 1997).

The Snake River steelhead Distinct Population Segment consists of six major population groups (MPG), characterized by major river basins, and 24 independent populations, representing groups of tributary drainages or distinct areas within each basin (Figure 1). Lapwai Creek belongs to the Clearwater Lower Mainstem population of the Clearwater River major population group. Although the Clearwater Lower Mainstem is referred to as a population under the VSP criteria, I will refer to Lapwai Creek as a population in the following. The Clearwater Lower Mainstem consists entirely of A-run steelhead (steelhead that spend one year in the ocean before returning to spawn), which is found in relatively small tributaries such as Lapwai, Potlatch and Big Canyon creeks (NMFS 2005). The Lapwai Creek watershed is the westernmost and lowest elevation population in the entire major population group, and represents by such an important spatial diversity component.

Section 4(c)(2) of the ESA directs the review of the listing classification of threatened and endangered species at least once every five years to determine if any species should be 1) removed from the list; 2) have its status changed from threatened to endangered; or 3) have its status changed from endangered to threatened. The five year review following the 2006 reaffirmation concluded that Snake River steelhead had not met recovery criteria (NMFS 2011).

In their status analysis of the Clearwater River major population group, NMFS concluded there is "*insufficient data on natural spawning abundance to determine productivity for the five populations in this MPG. The overall abundance and productivity risk rating therefore was identified as high for all populations, except for the Lower Mainstem Clearwater River which was identified as moderate*" (NMFS 2011). *Spatial structure and diversity* risks currently are rated low for the Lower Mainstem Clearwater, Selway River, and the Lochsa River. The South Fork Clearwater River and Lolo Creek have moderate risk ratings for spatial structure and diversity. Four of the populations in the Clearwater MPG have an overall *viability* rating of high risk (South Fork Clearwater, Lolo Creek, Selway River and Lochsa River). The Lower Mainstem Clearwater River has an uncertain overall viability rating of "maintained", referring to an extinction risk of 6 % to 25 % in 100 years. Therefore, due to these population viability ratings, the Clearwater MPG is not viable and remains listed as threatened under the ESA (NMFS 2011).

In summary, West Coast steelhead and salmon have declined in numbers, distribution, and genetic composition due to a number of factors over the last century. Most notably, overfishing, and habitat destruction or -modification have been primary reasons for the declines. With growing concern over these declines, several distinct population segments of steelhead (corresponding to major river drainages) were listed under the Endangered Species Act between 1997 and 2006. Snake River steelhead was one of the population groups listed under the initial 1997 assessment. Major population groups within the Snake River segment share the common limitations of mainstem Snake and Columbia passage, but vary according to subbasin characteristics and population demographics. Further variation can be found within the major population groups at the scale of watersheds or drainages

LAPWAI CREEK AND THE LEWISTON ORCHARDS PROJECT

Lapwai Creek watershed

The 694 km^2 Lapwai watershed is situated southeast of Lewiston in North-Central Idaho. There are four major tributaries in the watershed that together form the 4th order Lapwai Creek which empties into the Lower Clearwater River, 237 m.a.s.l. The streams drain the north slopes of Craig Mountain (1530 m.a.s.l.) and carve steep canyons through the landscape. The predominant geology in the watershed is Columbia River basalt, with a band of Idaho Batholith in the upper, high elevation portion. The plateau above the escarpment is overlain with loess, and the predominant land use is dry land grain crops, which covers 34% of the entire watershed. Coniferous forests cover 29%, primarily at higher elevations above the prairie, and grasslands dominate the steep canyon sides and valley floors. The grasslands are utilized primarily for livestock grazing. Less than 5 % of the area is classified as developed for housing and infrastructure (Homer et al. 2007).

Because the Lewiston Orchards irrigation project was initiated over a century ago (see below), and logging, grazing, and agriculture have been widespread for even longer, little or no information is available on the hydrology prior to settlement. From a natural baseline it is however characteristic that runoff can be very flashy due to the local climate and the topography. First, mean annual precipitation is 490 mm, with larger amounts falling at higher elevations, and most of it in winter and spring. With the interior Columbia Basin climate of relatively rapid temperature fluctuations around freezing in winter, rain-on-snow events can cause rapid snowmelt and flashy runoff. Secondly, the catchments are high elevation and large relative to the steep and confined canyons through which they drain, with naturally limited meandering. The volume and velocity of the water during flooding by such has the capacity and competence to transport material downstream.

Historically, Craig Mountain has acted as a reservoir of water stored as snow, which gradually melted off during spring and early summer. In the recent century regional shifts in precipitation regimes and decreased foliage and forest cover due to logging have changed the runoff patterns. First, as with other interior Columbia drainages, regional climate change patterns have changed the precipitation regime in the elevation ranges found in the Lapwai watershed from a snow-dominated to a rain-dominated regime (Mote et al. 2003, Barnett et al. 2004). Secondly, logging and grazing practices on Craig Mountain have reduced the forest cover and structure. In turn, this leads to earlier and faster snow melt once temperatures are above freezing in late winter (Mote et al. 2003).

The stream gradients follow a shallow gradient on the plateau, followed by high gradients in the confined reaches below the escarpment. The stream gradients are lower below the confluences among the tributaries, but flood control levees and infrastructure (roads and railroad) have channelized the lower tributary and mainstem reaches (Richardson and Rasmussen 2007) and prevent connectivity with the floodplain (Williams 2011). The simplification of the stream channels has led to increased bed erosion and channel incision where the streams are confined and heavy deposition of gravel in unconfined reaches. During periods of low discharge, the widened channels resulting from the lack of channel forming processes exacerbate heat transfer and limit potential pool habitats (Poole and Berman 2001). The substrate is highly mobile in the lower reaches where deposition occurs, with most of it being cobble sized.

Habitat quality in the Clearwater River Lower Mainstem Area is largely in poor or non-functioning condition, or in streams with naturally low potential due to steepness or high water temperature. Common problems limiting fish production have been attributed to high summer temperatures, low summer discharge, flashy response to runoff, and moderately to severely degraded channels (NMFS 2006b). However, anecdotal evidence of stranded fish during a flash flood, and operation of a traditional steelhead snag fishery on Mission Creek (Johnson and Stangl 2000) suggest that streams in the Lapwai Creek watershed produced larger numbers of anadromous fish in the past (NMFS 2006b). Sweetwater Creek is fed by Lake Waha through groundwater seeps at the Twenty One Ranch spring, which made for a steady supply of cool temperature water. Lake Waha was formed by a slope failure which filled in the canyon of the West Fork Sweetwater Creek with rock and soil material. There are no natural outlets except through the seeps. The stable temperatures likely created favorable conditions for steelhead by buffering against high temperatures in summer and low temperatures in winter (NMFS 2010). NMFS (2010) concluded in the environmental baseline that the Lapwai Creek drainage has high potential for steelhead production if degraded habitats were restored, and it is an important source of A-run steelhead production.

Water diversions and canal infrastructure

Located within the Lapwai Creek watershed is the Lewiston Orchards Project (LOP), which consists of a series of water storage reservoirs, diversion dams, and canals that provide irrigation water to the town of Lewiston. The diversion system was established as a private enterprise in 1906 to provide a steady water supply for domestic use and food production during the hot and dry summer months. The initial irrigation system provided a timber flume and a canal to carry water from Sweetwater Creek to Reservoir A (Mann Lake), but was later expanded (see below). Due to limited longevity of the early wooden flumes, extensive and frequent repairs were necessary to limit water loss. In 1939, the Irrigation District, aided by the Works Projects Administration, launched a program for replacing the wooden flumes with concrete bench flumes. To ensure reliable water supply irrigation and industry, the LOP was authorized in 1946 (60 Stat. 717, Public Law 79-569), and in 1948 the irrigation district deeded the entire collection, reservoir and distribution system, and the water rights, to BOR.

The diversion system captures much of the water that would naturally be feeding Webb and Sweetwater Creeks, the two westernmost streams in the Lapwai Creek watershed. The project facilities include four diversion structures (Webb Creek, West Fork Sweetwater Creek, Sweetwater, and Captain John Creek), feeder canals, three small storage reservoirs (Soldiers Meadow, Reservoir A (Mann Lake), and Lake Waha), a domestic water system including a water filtration plant which is no longer in use, and a system for distribution of irrigation water (Figure 1). The current use of the diverted water is for irrigation purposes, primarily of suburban residential land use, covering some 15.8 km^2 of the area known as Lewiston Orchards (BOR 2009).

Water from the Webb Creek and Captain John Creek drainages is collected at Soldiers Meadow Reservoir. This water is released, when needed, and diverted into Sweetwater Creek by the Webb Creek Diversion Dam and Webb Creek Canal. Water from the West Fork Sweetwater Creek is stored in the offstream Lake Waha, which is fed by Lake Waha Feeder Canal. The stored water is pumped from Lake Waha back into the creek during the irrigation season. The water taken for irrigation purposes is diverted from Sweetwater Creek into Sweetwater Canal, which empties into Reservoir A. The system has the capacity to divert 0.91 m^3s^{-1} (32 cfs) through the Sweetwater Canal, and 0.57 m^3s^{-1} (20 cfs) through the Webb Canal (BOR 2009), and is operated from February through October.

Effects of the water diversion system on flow and fish habitat

The diversion system directly affects flow and access to habitat in both the Lapwai and Captain John watersheds. For the Lapwai Creek watershed, surface flow is impacted most directly in Webb and Sweetwater creeks, and to a lesser extent in mainstem Lapwai Creek below the Sweetwater confluence. Flows in over 8 miles of Sweetwater Creek, 9 or more miles in Webb, and over 6 miles in Lapwai Creek within anadromous reach are impacted during the irrigation season. Further, the diversions presumably preclude upstream passage to another 11 miles of stream that contain resident *O. mykiss* (Chandler and Parot 2003, NMFS 2010), which means that this section could likely support anadromous *O. mykiss* as well. Captain John Creek is affected by the diversion of water from an intermittent headwater tributary which diverts water into the Webb Creek drainage. The lower reaches of Captain John Creek, which empties into the Snake River, serve as spawning and rearing habitat for steelhead and Chinook salmon. It is designated as critical habitat for these two ESUs, and as Essential fish habitat for Chinook and coho salmon, but the effects are smaller than in Lapwai Creek watershed.

Prior to 2006, LOID and BOR were allowed unrestricted withdrawal of water from Sweetwater, Webb and Captain John creeks. The timing and amounts varied widely from year to year depending on the amount of precipitation, air temperature, runoff, and demand for irrigation and domestic water (NMFS 2010). Streamflows below the diversions depended on the influx of groundwater and the availability of surface water in excess of what was diverted. It is likely that the operations have eliminated most rearing habitat in Webb and Sweetwater, and to a lesser degree in Lapwai below the Sweetwater confluence, by drying the streambeds in summer (NMFS 2010). The duration, extent, and timing of the drying likely varied from year to year according to the precipitation and runoff regime. When the LOP diverted all surface flows the usable habitat were found largely as disconnected pools and in reaches where groundwater surfaced. Collectively, this habitat had poor quality.

With the process of minimizing take of steelhead (see below), minimum flow requirements were established, which require LOID and BOR to spill a minimum amount of water past the diversions during the irrigation season. The streams are however still affected as the amount of water is different than what would be the case in absence of the operations.

An action area is defined under the ESA as "*all areas to be affected directly or indirectly by the Federal action and not merely the immediate area involved in the action*" (50 CFR Part 402). The affected streams include designated critical habitat for the Snake River Basin Steelhead DPS, and are designated as Essential Fish Habitat (EFH) for Chinook salmon and coho salmon. Based on this, NMFS (2010) defined the action area to "*…consist of the following streams: (1) Captain John Creek from the headwaters of the North Fork to its mouth; (2) all portions of the Webb and Sweetwater Creek drainage systems where flows are altered by the LOP; (3) Lapwai Creek from its confluence with Sweetwater Creek, downstream to its mouth at the Clearwater River, and (4) the mainstems of the Clearwater River downstream of Lapwai Creek, the Snake River downstream of Captain John Creek to its confluence with the Columbia River, and the Columbia River downstream of the Snake River to the Pacific Ocean*".

Flow is the primary factor affected by the LOP, but the diversions also affect other physical variables that in turn affect channel forming processes. A channel is in equilibrium when the amount of sediment delivered to the channel equals the amount transported out. Both the delivery of sediments and the stream's capacity to transport sediments are factors that matter in this equation, both of which are affected by the LOP. First, sediments are trapped behind the diversion dams, leading to excess scour downstream of the diversions. Secondly, lower discharge below the diversions decreases the stream's ability to transport sediments. In sum these two factors can offset each other to some extent under conditions typically encountered in the irrigation season and when looking at the stream as a whole.

In summary, from a natural baseline the Lapwai Creek watershed spans a wide physiographic gradient despite its limited size. Compared to other systems in the Clearwater Lower Mainstem, the streams in Lapwai provide cool temperatures due to a relatively high elevation watershed and groundwater seeps. The low-elevation reaches of the tributaries and the mainstem Lapwai Creek are confined by infrastructures, and upland land uses largely affect runoff regimes and sediment and nutrient inputs to all the tributaries. Further, the two westernmost streams in the watershed have altered flow regimes due to water diversions. Because there is little or no data on the flow, habitat, or steelhead from the period before the operations started, it is impossible to know what conditions would be like in absence of the LOP. However, because the LOP withdraws water from critical habitat for ESA listed Snake River steelhead, the dam operator and owner (BOR) was required to quantify the impacts of the continued operations on steelhead population viability.

Biological Opinion of the future operation of the diversion system

Following the listing of Snake River steelhead under the Endangered Species Act in 1997, BOR initiated consultation with NMFS in 1998 at BOR facilities in the Snake River Basin upstream of Lower Granite Dam. BOR owns the LOP diversion infrastructure in the Lapwai watershed, which hosts listed Snake River steelhead and is designated critical habitat and Essential Fish Habitat. Each federal agency has an obligation to ensure that any action it authorizes, funds, or carries out is not likely to jeopardize the continued existence of any endangered or threatened species or destroy or adversely modify its critical habitat unless that activity is exempted (50 CFR 402.03). In short, the process consists of a Biological Assessment developed by the entity responsible for potential harm to reduce the impact, and a Biological Opinion of that assessment by the responsible authority. Under regulation 50 CFR 402.12(f), the "*contents of a biological assessment are at the discretion of the federal agency and will depend on the nature of the federal action*".

The "*nature of the federal action*" in this case is the continued operation of the LOP, which is also referred to as the *proposed action*. Proposed actions are defined as "*all activities or programs of any kind authorized, funded, or carried out…by Federal agencies*" (50 CFR 402.02). Because the project withdraws water from streams that are designated as critical habitat for a listed species, and because BOR is a federal entity, BOR was required to consult with NMFS under section 7 of the Endangered Species Act and section 305(b)(2) of the Magnuson-Stevens Fishery and Conservation Act (MSA) to minimize the impact of the operation of the project on steelhead. With the Biological Assessment, the BOR formally requested NMFS, the authority with jurisdiction over federally listed species, to give a Biological Opinion of the proposed action. Section 7(b)(4) requires the provision of an incidental take statement that specifies the impact of any incidental taking and includes reasonable and prudent measures to minimize such impacts (NMFS 2010).

The Magnuson-Stevens Fishery and Conservation Act warrants protection for designated Essential Fish Habitat. The Pacific Fishery Management Council (1999) designated essential fish habitat for Chinook and coho salmon in Idaho, and the LOP action area falls within this zone. Because this dissertation focuses on steelhead, I will not review the MSA process in much detail here. In conclusion, NMFS (2006b, 2010) found that Essential Fish Habitat in the Clearwater River, Snake River, Columbia River, and Captain John Creek is not adversely affected by the proposed action. Chinook and coho salmon were deemed adversely affected within the Lapwai Creek part of the action area (i.e. excluding Captain John Creek); coho through the same mechanisms as steelhead, and Chinook as described in the BiOp (NMFS 2010). Note that although the conservation measures under the MSA are similar to, they are not identical to those set forth under the ESA.

The following consultation history is long and will not be reviewed in great depth here. Instead, the reader is referred to NMFS (2006b:2-6, 2010:3-8) for details. The process was concluded with a revised Biological Assessment (BOR 2009) in which the key scientific and operational criteria had been discussed by the parties involved. The main points of relevance for streamflow were 1) collection of field data along Sweetwater and Webb Creeks, 2) finalization of ramping rates, sediment removal, and gravel replacement plan, 3) development of hydrologic and operational analysis tools to test the feasibility, reliability, and potential tradeoffs associated with candidate flow regimes, and 4) provisions for additional summertime flows under given hydrologic and storage conditions. The BOR proposed to spill all water in the months of November to January as the irrigation canals are not operated during the winter. For the months of February to April, the minimum flow provided for Sweetwater is 7.8 cfs and 4.0 cfs for Webb. For the month of May the rates are 3 and 1.5, respectively, and for June through October the rates are 2.5 and 1.0, respectively.

In response to this, NMFS concluded that the proposed action was not likely to jeopardize the continued existence of steelhead in the Lapwai Basin and beyond, or result in the destruction or adverse modification of designated critical habitat for listed species in the same area (NMFS 2010). Although continued persistence was not deemed jeopardized, the action was expected to cause incidental take of steelhead. Section 9(a)(1) of the ESA prohibits the taking of endangered species without a specific permit or exemption, and section 4(d) extends the prohibition to threatened species such as Snake River steelhead. *Taking* is defined as "*an action that harasses, wounds, or kills an individual of a listed species or harms a species by altering habitat in a way that significantly impairs its essential behavioral patterns*" (50 CFR 222.102). *Incidental* take refers to takings that result from, but are not the purpose of, carrying out an otherwise lawful activity conducted by the Federal agency or applicant (50 CFR 402.02). Adult fish use the streams in the action area primarily during high flows and/or prior to the operation of the diversion canals, and the LOP is hence not likely to cause any incidental take of adult steelhead. NMFS further stated that "*When the proposed action provides flows that are lower than those that would occur in the absence of the LOP, incidental take is likely to occur under the following circumstances: (1) Steelhead embryos and alevins may be killed when reduced surface flows either dewater redds or cause insufficient intergravel flows during the incubation period through the time when alevins would emerge from the gravels; and (2) stream flows artificially constrain steelhead abundance, growth, or survival due to reduced carrying capacity, high water temperatures or other stresses caused by flow reductions*" (NMFS 2010). The incidental take exempted by this statement is the loss of steelhead from these two circumstances.

Directly quantifying the take resulting from the action is impossible, and hence NMFS relied on habitat indicators that were related to the mechanism of take. There are critical uncertainties about the effects of the operation. Although several potential mechanisms occur, they can be not be readily distinguished from the natural baseline (i.e. in absence of the operations), be directly attributed to the operation, or remain infeasible for monitoring purposes. The Biological Opinion discussed the shortcomings of relying on various parameters (water temperature, fish density) instead of others (flow, connectivity), and concluded that flow would be the best quantifiable habitat parameter, as low flows are the primary cause of take in the action area.

Because the action has the potential to take steelhead, BOR was required to implement certain *reasonable and prudent measures*. Reasonable and prudent measures are non-discretionary measures to minimize the take for the take exemption under section 7(o)(2). The 2006 Biological Opinion identified seven reasonable and prudent measures that were required to meet the incidental take statement, of which point 3, "*the BOR shall monitor stream flows and any ancillary biological indicators necessary to determine if the extent of take exempted by this Incidental Take Statement is exceeded*" (NMFS 2006b) was the most important for the recovery monitoring.

In summary, because the LOP takes water from critical habitat for a listed species, the BOR was required to come up with a plan to minimize the impacts. BOR consulted with NMFS which has authority over anadromous salmonids. The technical and scientific discussion was concluded after 8 years, and resulted in several measures to minimize impacts. Among these measures, minimum flow requirements were the most important, and close monitoring of the effects was mandated.

PROBLEM STATEMENT

Identifying the factors by which a population is limited, and at what densities it is regulated, is of primary importance when setting goals for recovery and planning remediation measures to ensure viability of wild fish populations. As comes clear from the above review of the listing process, the key is to understand the mechanisms by which populations are governed and the conditions under which they are operant.

At the same time as solving an applied problem as the one in Lapwai Creek, we can also use the effort to learn something of fundamental value to ecology, hence making an applied solution applicable to other systems. The primary goal of this research is to identify mechanistic linkages between individual- and population-level demographic parameters and their environment, and to understand how population processes operate to shape individual performance.

The study concerns primarily the abiotic and biotic conditions in the Lapwai watershed, where adults spawn and juveniles rear. These conditions are dynamic across space and time, meaning that their controls over individual performance and population demographic parameters vary in their absolute and relative importance. This research does not directly cover the conditions encountered throughout the rest of the life cycle, such as mainstem migration, estuarine transitioning, and ocean migration and foraging. Although these phases are just as important for the overall persistence of an anadromous population, freshwater spawning and rearing habitat is a critical factor that controls the numbers and condition of sea-migrating smolts. In addition, it is the only environment that the resident form of the species ever encounters, and the conditions can hence influence their most central life history decision of residency or anadromy.

To understand these ecological processes and the patterns they create, and making the findings applicable to other systems, we developed a series of studies to test ecological hypotheses. The resultant manuscripts (listed below) are included in the following as chapters in this dissertation. They are written as stand-alone pieces that test specific ecological hypotheses, using the Lapwai Creek watershed as the study system. Consequently there is going to be certain repetition among the chapters, depending on the questions asked. The dissertation will be concluded with a summary- and synthesis chapter at the end. Supplemental data on sampling dates, individual growth rates, densities, hydrology, temperature, and habitat that pertain to all chapters are given in appendices 3 – 14.

My analysis philosophy follows that of Chamberlin (1890) and Burnham and Anderson (2002). In short, this means using multiple hypotheses that describe plausible processes that each has the potential to create the observed pattern; confronting these models with the data; and rank their relative support using information-theoretic criteria, which optimize the variance-bias tradeoff of statistical models. This method is based on a relative rank, and only concerns the models specified in the candidate set. We therefore identified the most important factors to each problem beforehand, and were explicit with regards to the processes each model depicted. Where appropriate, absolute goodness-of-fit statistics were used and reported.

List of chapters in this dissertation

Chapter 2: Interactions between body mass and water temperature cause energetic bottlenecks in juvenile steelhead. Myrvold, KM and BP Kennedy, *Ecology of Freshwater Fish* (in press)

Chapter 3: Metabolic constraints and physical habitat characteristics explain the spatial variation in the strength of self-thinning in a stream salmonid. Myrvold, KM and BP Kennedy, prepared for submission to *Journal of Animal Ecology*

Chapter 4: Age-specific density dependence and its impact on individual growth rates for a stream salmonid. Myrvold, KM and BP Kennedy, prepared for submission to *Oikos*

Chapter 5: A combination of watershed characteristics and in-stream habitat factors explain the spatial variation in densities of juvenile steelhead. Myrvold, KM and BP Kennedy, prepared for submission to *Transactions of the American Fisheries Society*

Chapter 6: Estimation of salmonid abundance based on single-pass electrofishing in small streams. Myrvold, KM and BP Kennedy, prepared for submission to *North American Journal of Fisheries Management*

Chapter 7: Patterns and processes of site fidelity in a stream salmonid. Myrvold, KM and BP Kennedy, prepared for submission to *Functional Ecology*

Chapter 8: Summary and synthesis. Myrvold, KM.

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FIGURES

Figure 1.1

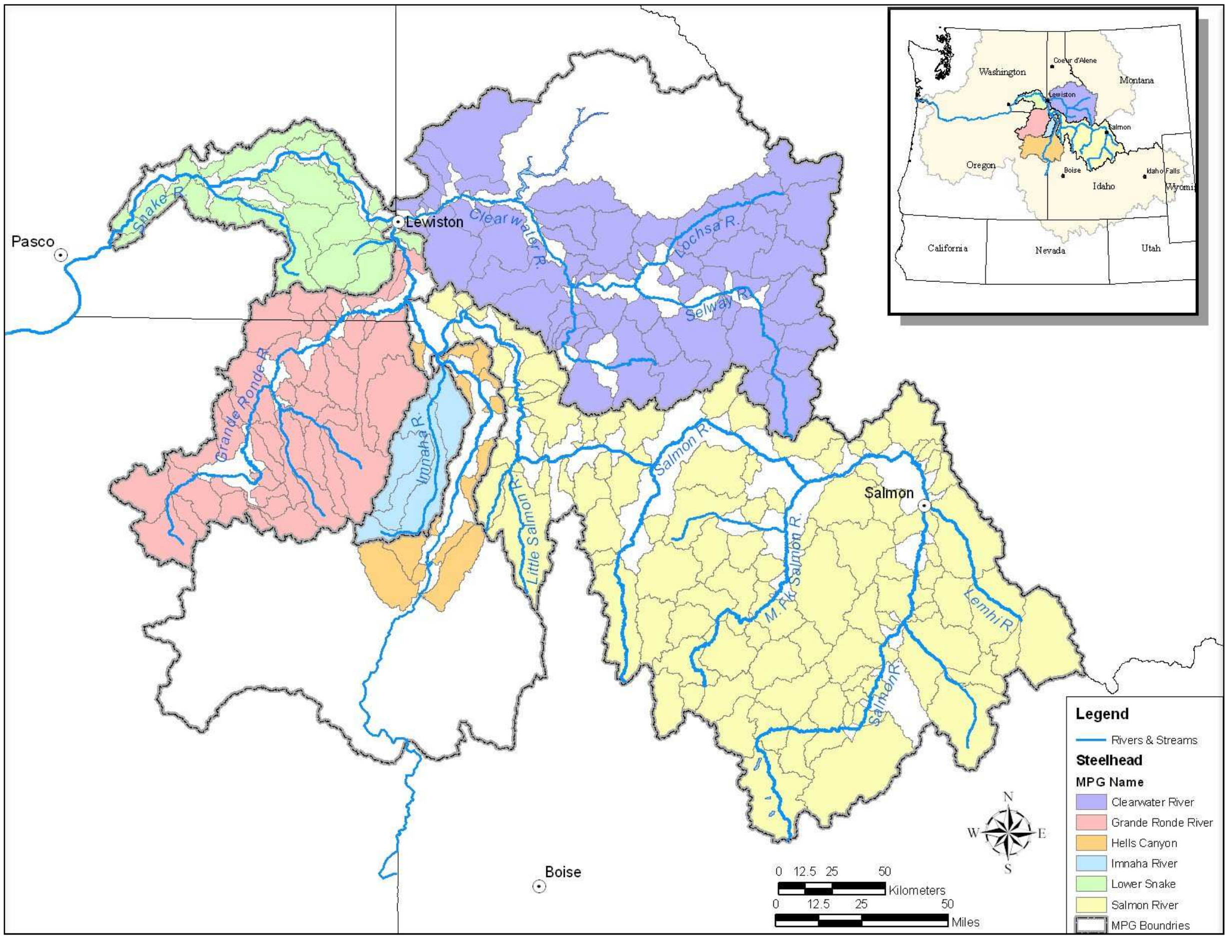

Figure 1.1. The map shows the six major population groups of Snake River steelhead, and their location within the Columbia River Basin (insert). The Lapwai Creek watershed is part of the Clearwater River Major Population Group. Adopted from NMFS (2010).

Figure 1.2

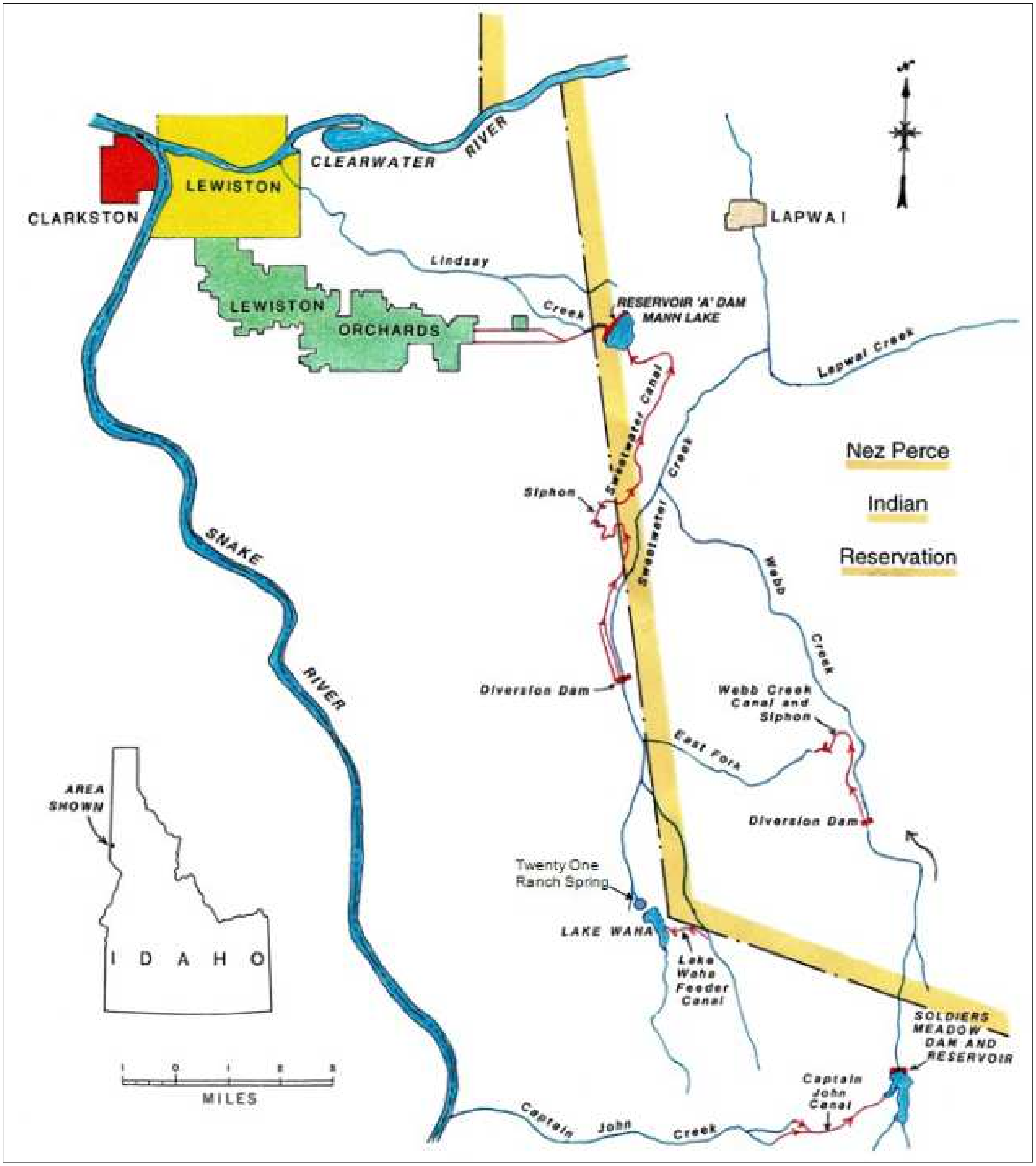

Figure 1.2. Overview of the diversion and water storage system of the Lewiston Orchards Project. From NMFS (2010).

CHAPTER 2: INTERACTIONS BETWEEN BODY MASS AND WATER TEMPERATURE CAUSE ENERGETIC BOTTLENECKS IN JUVENILE STEELHEAD

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ABSTRACT

Across taxa, it is generally accepted that there are fitness advantages to rapid growth early in life. For stream dwelling salmonids, however, high temperatures and associated energetic costs during the summer growing season might offset or even prevent the competitive advantage of large body size. Our overall objective was to understand the relative importance of factors that can cause variation in growth rates in an age-0 cohort of wild steelhead (*Oncorhynchus mykiss*) in Idaho, USA, where temperatures approach, and temporarily exceed, their tolerance level. For individually tagged fish inhabiting the same stream reach, we found that growth rates were negatively related to fish mass (slopes of the two best approximating models were both -0.024). Comparing growth rates from 16 different stream reaches throughout the watershed, we found that temperature-induced metabolic cost was the single best approximating model (AIC w_i = 1.0) of the variation in individual growth rates. The bioenergetics model showed that mass-specific metabolic costs decreased with mass, but the absolute energetic demands increased over the same size range. Because temperature had a multiplicative effect on metabolic cost, our results suggest that the effect of food limitation increased with fish size. We conclude that high water temperatures pose energetic bottlenecks and can be a

potentially strong mechanism limiting growth in juvenile salmonids in summer, particularly as streams in the region experience warming trends.

INTRODUCTION

Individual growth plays an important role in shaping the evolution and demography of fish populations because body size determines several fitness components (Sogard 1997, de Roos et al. 2003). In juvenile stream salmonids, growth rate has been shown to be a significant factor in determining ontogenetic status, life-history strategies, and ultimately, survival of individuals (Ward et al. 1989, Holtby et al. 1990, Metcalfe 1998, Kahler et al. 2001, Satterthwaite et al. 2010). Because these parameters are central determinants of both individual lifetime fitness and population viability, it is of great importance to understand the underlying processes that influence growth variation in salmonid populations (Rose et al. 2001, Quinn 2005, Crozier et al. 2008).

In its simplest form, growth is determined by the difference in energy intake and expenditures, and factors that are affecting either or both sides of the equation could thus directly or indirectly govern the growth rate. A number of factors affect growth in salmonids, ranging from individual behavior and characteristics (Abbott & Dill 1989, Orpwood et al. 2006, Reid et al. 2011) and population processes (Imre et al. 2005, Lobón-Cerviá 2009, Hartson & Kennedy 2014), to fish community structure (Tinus & Reeves 2001), habitat (Höjesjö et al. 2004, Kennedy et al. 2008), and temperature (Elliott 1976a, Boughton et al. 2007, Hayes et al. 2008). Water temperature is a particularly important factor regulating both energy intake potential as well as expenses (Brett 1971), and this further depends on the size and ontogenetic stage of the fish (Elliott 1994).

The effects of these factors are highly context dependent and dynamic across space and time (Gibson 2002). Individuals within the same stream reach all experience similar external factors, so that the individual's rank in the social hierarchy is the primary reason for differences in growth trajectories (Abbott et al. 1985, Nicieza & Metcalfe 1999, Höjesjö et al. 2002). At the level of the stream network, differences in productivity, thermal regime, abiotic environment, and biotic communities further produce spatial and temporal variation in growth potential and survival (Gibson 2002, Kennedy et al. 2008). Whereas some studies have documented fitness advantages (Holtby et al. 1990), recent studies have found the associated energetic costs to reduce or reverse the competitive advantage (Reid et al. 2011, 2012).

We were interested in testing the relationship between individual growth performance and body mass in a system where daytime temperatures approach and temporarily exceed the thermal tolerance of a coolwater salmonid, and where other abiotic and biotic conditions vary across time and space. The study took place in a tributary to the Clearwater River in Idaho, USA, which is designated critical habitat for wild steelhead. Our first objective is to test the relationship between mass and growth rate among subyearling individuals that experience the same environment. Our second objective is to test the relative importance of biotic and abiotic factors in explaining the variation in growth rates across the watershed. We employ a bioenergetic model to account for differences in body size and thermal regime, and compare the metabolic expenses incurred by the variation in stream temperatures.

MATERIAL AND METHODS

Study area and population

The Lapwai watershed is situated in North-Central Idaho and drains an area of 694 km^2 (Figure 1). The four main tributaries drain the north slopes of Craig Mountain (1530 m) through steep canyons before emptying into the Clearwater River (237 m). The predominant geology in the watershed is Columbia River basalt, with a band of Idaho Batholith in the upper, high elevation portion. The plateau above the escarpment is overlain with loess, and the predominant land use is dry land grain crops, which covers 34% of the entire watershed. Coniferous forests cover 29%, primarily at higher elevations above the prairie, and grasslands dominate the steep canyon sides and valley floors (Homer et al. 2007). Mean annual precipitation is 490 mm, with higher amounts falling at higher elevations.

Other fish species include, in order of abundance, longnose dace (*Rhinichtys cataractae*), sculpin (*Cottus* spp.), bridgelip sucker (*Catostomus columbianus*), redside shiner (*Richardsonius balteatus*), northern pikeminnow (*Ptychocheilus oregonensis*), and chiselmouth (*Acrocheilus alutaceus*). In recent years juvenile coho salmon (*Oncorhynchus kisutch*) have been stocked as part of a supplementation program in lower reaches of the system, but are generally not sympatric in space or time with steelhead. No hatchery supplementation exists for steelhead in the watershed.

We defined the study sites using a hierarchical stratified random approach (Frissell et al. 1986) to capture a gradient of physiographic (topography, geology, and land cover) and land use conditions within and across the four streams in the Lapwai watershed. At the largest spatial level, a general area (typically one stream-kilometer in length) was identified informed by *O. mykiss* occurrence (Chandler & Parot 2003), distance to other study reaches, tributary inputs, and known spring inputs. Within these sections we further narrowed the search by means of dividing the general area into as many representative 100 m reaches as possible, informed by land use, land cover, and channel constraints such as levees and channelization. We randomly chose one of these reaches and kept it as a study site for the duration of the study.

Sampling methods and material

Steelhead growth and densities

We started fish sampling when the flows were low enough to allow for efficient electrofishing in late June, and visited each site once per month until early November. We set block nets to ensure a closed population and conducted three-pass depletion electrofishing using a Smith-Root LR-24 backpack electroshocker (Smith-Root Inc., Vancouver, WA). To reduce the stress of capture and handling on fish, we conducted the sampling during early morning hours when the water temperatures did not exceed 18 ^{o}C. We set the voltage, frequency, and duty cycle within 20% of their mean values of 350 V, 30 Hz, and 15%, respectively. We held the juvenile steelhead in buckets filled with aerated stream water at ambient stream temperatures. Prior to any handling we anesthetized the fish with tricaine methanesulfonate (MS-222). We measured fork length in millimeter and weight to the nearest decigram. Steelhead were scanned for PIT tags using a FS-2001F-ISO reader (Destron Fearing, St. Paul, MN) and data on the individuals were recorded in program P3 (PIT-Tag Information System for the Columbia Basin). For untagged individuals 65 mm and larger we inserted 134.2 kHz PIT tags (Biomark Inc., Boise, ID) into the ventral body cavity posterior to the tip of the pectoral fin. Prior to release, fish were first allowed to recover in buckets with aerated water and were then moved to a live-well placed in the stream channel outside the sampling reach. Upon completion of sampling, we removed the blocknets and released fish back to the study reach. All fish sampling and handling procedures were permitted as part of the Section 7 consultation for the Lewiston Orchards Biological Opinion (NMFS 2006), and reviewed by the Idaho Department of Fish and Game (permit F-07-05-10) and the University of Idaho Institutional Animal Care and Use Committee.

Growth rates for recaptured individuals were calculated and expressed as percent change in body mass per day between capture and recapture. Densities were calculated using Carle & Strub's (1978) weighted maximum likelihood estimator of *K*-pass removal data. Due to the small size of these streams we obtained very high capture probabilities (season average ± SD was 0.63 ± 0.14) and consequently narrow confidence intervals around our population estimates. We expressed the population densities as the estimated number of subyearling steelhead per 100 m^2.

Temperature, discharge, and flow velocity

We had HOBO TidbiT v2 temperature loggers (Onset Computer Corporation, Pocasset, MA) installed at each site recording water temperatures ($^o C$) every 30 minutes. We used daily averages of temperature as the basis in the bioenergetics modelling.

Discharge (ls^{-1}) was calculated by taking approximately 15 depth and velocity readings spaced evenly along an established transect in the sampling reach. Velocity was measured at 60 % of the depth using a Marsh McBirney Flo-Mate Velocity Meter (Hach Company, Loveland, CO).

We quantified the average flow velocity (ms^{-1}) at each site during the second visit. We established transects perpendicular on the channel spaced 5 meter apart throughout the entire sampling reach. The transects were then split into 5 sections of equal width, and at each of the approximately 100 points we measured the flow velocity. A sample of these data for the months of July and September is shown in Table 1.

Steelhead diet and bioenergetics

In order to parameterize the prey energy density term in the bioenergetics equations, we collected stomach samples using non-lethal gastric lavage of up to 15 individuals per visit, covering the entire size range of steelhead. We acquired stomach samples from fish caught during the first pass in order to minimize time discrepancies or biases in gut content representation (i.e. fish analyzed for gut content analysis were not disrupted by previous electrofishing passes). We examined a total of 215 subyearling stomach samples and 216 yearling stomach samples. For each sample we identified the prey composition to the lowest taxonomic level, down to family in the invertebrate phyla and to species in vertebrate fauna.

We used values from the literature as shown in Appendix S1 to obtain energy density values and dry-to-wet weight ratios of the various prey groups. In instances where a study or multiple studies reported a range of energy density values for a single family, we averaged across the reported range to obtain a single value for the taxon of interest. In the events where we could not determine the life stage (denoted *any*) we averaged the values between larva and adult for the appropriate taxonomic level. For families with missing values we either averaged or borrowed values based on taxonomic grouping. We calculated the dry-to-wet ratio of both aquatic and terrestrial Insecta and aquatic and terrestrial Arthropoda based on the average ratios across our taxonomic list, and used this value (*.214*) as the substitute value where borrowing occurred on the class level. We assigned the value for sculpin to all fish. For spiders we used the general values for terrestrial Arthropoda. The energetic contribution of each prey group in a stomach sample was weighted by its wet mass. By summing these groups we obtained the average energy density of the stomach sample. Subyearling and yearling diets were similar (within 1% of each other in energy density). To allow for direct comparison between the individuals, and because diet samples at the individual level can be biased at high temperatures (Finstad 2005), we used the average value of 4324 J/g wet weight in the following bioenergetic analyses.

We used Fish Bioenergetics 3.0 (“Wisconsin model”; Hanson et al. 1997) to calculate consumption rates. Bioenergetic models are comprised of a set of mass-balance equations that link basic fish physiology with the environment. We specified the model with Thornton & Lessem’s (1979) consumption equation, Kitchell et al.’s (1977) respiration equation, Elliott’s (1976b) waste losses equation, and predator energy density equation number 2 in the package (Hanson et al. 1997) with a predator energy density of *5763* J/g wet weight (Glova & McInerney 1977). The model was parameterized using reported values as specified in Appendix S2. In all cases we used the site specific thermograph, and varied the growth scenarios as listed below.

First, to calculate the ration necessary to maintain body mass over a given time period with a given temperature regime, we controlled for allometric effects by keeping body mass constant at the start value over that time period (Hewett & Kraft 1993). By such we could compare the *maintenance metabolic costs* (i.e. from basal metabolism and wastes) across sites, expressed as J/g fish/day. Second, to express the percentage of the consumed energy that was allocated towards growth, we first separated the metabolic costs (maintenance ration) from the total consumption (maintenance plus growth from time t to t+1). The difference between the two was then divided by the total consumption to obtain the weighted quotient (to allow for comparison across a size range), and we denoted it the *fraction* allocated to somatic growth.

Candidate models and statistical analyses

Due to the clustered design and repeated measures we had to account for non-independence in the data to avoid pseudoreplication. The non-independence was induced by correlation in the grouping factors. The mixed effects model permits the data to exhibit correlation and non-constant variability, and consists of both fixed and random effects (Littell et al. 2006). The fixed effects variables set up the overall model structure whereas the random effects allow for site- and time-level variation in the relationship (as sites have differing productivity and physical habitat characteristics that also vary over time). In matrix notation it can be represented as

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}\gamma + \varepsilon,$$

where $\boldsymbol{y}$ denotes the vector of the observed values, $\mathbf{X}$ is the known fixed effects design matrix, β is the unknown fixed effects parameter vector, $\mathbf{Z}$ is the known design matrix for random effects, γ is a vector of the unknown random-effects parameters, and ε is an unknown random error vector whose elements are not required to be independent and homogenous (Pinheiro & Bates 2000).

We built model structures *a priori* to test hypotheses of the relationships between mass and growth and energy allocation, respectively (objective 1), and between growth rate, density, discharge, flow velocity, and maintenance metabolic cost (objective 2). For each fixed effects model structure we specified three types of random effects (random slope, random intercept, and random slope and intercept), each constituting a unique model (Table 2). In all but the flow velocity models the grouping factors were space (site) and time (visit). We truncated the data set to only include sites with 5 or more recaptured individuals per visit to avoid bias (Burnham & Anderson 2002). We used

SAS v.9.2 Proc MIXED (SAS Institute, Cary, N.C.) specified with the Kenward & Roger (1997) approximation of denominator degrees of freedom in the model, and maximum likelihood as the estimator. The null model likelihood ratio test was significant for all models ($P < 0.0001$) and we hence specified an unstructured covariance structure (SAS Institute 2008).

We used an information-theoretic criterion to assess the relative plausibility of these candidate models (Akaike 1973, Burnham & Anderson 2002). Information-theoretic data analysis is based on Kullback-Leibler information, which is the information lost when statistical models are used to approximate full truth. Akaike's information criterion (AIC) is given as

$$AIC = -2\ln\left(\ell\left(\hat{\theta}\middle|data\right)\right) + 2K,$$

where $\ln\left(\ell\left(\hat{\theta}\middle|data\right)\right)$ is the value of the maximized log-likelihood over the unknown parameters, given the data and the model, and K is the number of estimable parameters in that model. The model with the lowest AIC value is the best approximating model of the data. The models i were ranked using the simple AIC differences, Δ_i, given as $\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{min}$. To make interpretation and inference easier, we normalized the likelihood functions of the models so that they sum to 1. The probability of model i being the best approximating model in the set is called the Akaike weight (w_i), and is given as

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_i\right)}$$

We performed one comparison for the growth-mass models (class 1a), the fraction-mass models (1b), and the growth-abiotic/biotic factor models (2). The rank of the various models depends on the comparison made, and these are displayed with their Akaike weights in Table 2. For each comparison we provided parameter estimates for models with strong relative support (i.e. $w_{max}/w_i < 2$). For these models we present the estimated total variance, the proportion of the variance attributed to overall model fit (ε) and the random intercept term (η), parameter estimates (β) and associated standard errors (SE) in Table 4.

RESULTS

There was substantial variation in growth rates, body size, and energy allocation among the study sites (Table 3). Accounting for site and time effects, we found that individual growth rates were negatively related to mass (n = 446, Table 4). The random intercept model was the best approximating model (w_i = 0.54; Table 2, class 1a), and the random intercept and slope model was the second best (w_i = 0.46), both showing a negative relationship between mass and growth rates (Table 4). Further, the fraction of consumed energy allocated towards somatic growth was also negatively related to fish mass, with the random intercept and slope model being the best in the candidate set (Table 2, class 1b).

Among the models relating individual growth rate to density, discharge, flow velocity, and maintenance metabolic cost (as incurred by the temperature and the mass of the fish), the random intercept and slope model of metabolic cost was the single best approximating model (Table 2, class 2, w_i = 1.00), showing a negative relationship between growth rate and metabolic cost (Table 4). Most of the variance (93 %) was caused by the random intercept. The models relating individual growth to density, discharge, and flow velocity received no relative support.

Because metabolic cost was such an important factor governing growth in our study system, we further analyzed how it related to temperature and fish mass. Holding temperature constant at 12.5 ^{o} C, the relationship between maintenance metabolic cost and the corresponding absolute ration showed that the consumption rates decreased with fish mass, from 242 $Jg^{-1}d^{-1}$ for 2.5 g fish to 155 $Jg^{-1}d^{-1}$ for 85 g fish (Figure 2). However, the associated ration sizes increased five-fold over the same size interval, from 606 J to 3090 J, respectively. Holding mass constant, the energetic demand for maintenance metabolism increases nonlinearly up to ca 15 ^{o}C, and then tapers off for the size range considered (Figure 3).

The energetic demands incurred by site-specific temperature were overall the highest from mid June to mid September (Figure 4). The largest difference in temperature between the coolest and warmest site was seen in late July, but due to the nonlinear relationship between temperature and maintenance metabolism, the difference in energetic demand was greater later in the season. For example, metabolic costs were 177 J in the coolest reach and 207 J in the warmest reach on July 25th, whereas during cold conditions on November 6th the values were 72 J and 137 J, respectively.

Taken together, this suggests that larger fish could not consume enough energy past keeping up with their maintenance metabolism, and that temperature appeared to be a more important factor in determining individual growth than were density, flow, and discharge.

DISCUSSION

We found that growth rates and energy allocation were negatively related to body mass, and that maintenance metabolic cost was the strongest predictor of the variation in growth rates. The bioenergetics model showed that mass-specific metabolic costs decreased with mass, but the absolute energetic demands increased over the same size range. Further, temperature has a multiplicative effect on metabolism, rising nonlinearly to approximately 15 ^{o}C. Taken together our results suggest that the effect of food limitation increased with fish size, primarily due to temperature-induced metabolic cost.

Identifying the drivers of variation in individual growth performance has been a key focus area for research on stream-rearing juvenile salmonids. For individuals that experience the same environment, studies have documented individual growth variation resulting from time of emergence and size-at-age (Chandler & Bjornn 1988), behavior (Abbott et al. 1985, Vøllestad & Quinn 2003, Einum et al. 2012), ontogenetic stage (Metcalfe 1998), and more recently, individual differences in physiology (Reid et al. 2011, 2012). Standard metabolic rate can vary considerably among individuals in a population and relate to dominance through the aggressive behavior of acquiring access to food and shelter (Biro & Stamps 2010, Reid et al. 2011). However, dominance is not beneficial unless the food resources are ample and predictable, which is generally not the case in natural streams (Abbott & Dill 1989, Reid et al. 2012). Further, in structurally complex environments such as natural streams, the dominant individuals are less likely to monopolize feeding stations (Martin-Smith & Armstrong 2002, Vøllestad & Quinn 2003, Höjesjö et al. 2004, Reid et al. 2012).

Our results show that, in habitats that approach and temporarily exceed the thermal tolerance for coolwater species such as steelhead, temperature and associated metabolic costs can be an important bottleneck to individual growth. Although mass-specific metabolic cost decreases with fish mass, the ration necessary to maintain body mass increases substantially. Further, the fraction of the total consumption allocated to growth was negatively related to mass. This strongly suggests that the possible advantages of large body size in acquiring resources are offset by the associated metabolic costs. Such energetic bottlenecks have previously been shown to limit both individual growth and population densities of *O. mykiss* in warm, food-limited streams (Railsback & Rose 1999, Boughton et al. 2007, McCarthy et al. 2009, Hartson & Kennedy 2014). For example, McCarthy et al. (2009) found that juvenile steelhead growth in California streams was limited by elevated temperatures and feeding rates. In a study that investigated the relationship between temperature and food, Boughton et al. (2007) found that food supplementation greatly increased average growth rates, but also inflated the variation among individuals at high temperatures. An earlier study in Lapwai Creek reported on interacting effects of density and body size that resulted in decreased apparent survival among the largest individuals, most significantly during periods and at locations where densities were highest (Hartson & Kennedy 2014).

When we considered biotic and abiotic factors that have the potential to affect growth rates, but that varied among the study sites, we found maintenance metabolic cost (as driven by temperature) to be a better approximating model of the variation in growth rates than were density, discharge, and flow velocity. Other studies that have investigated differential habitat use with contrasting temperature regimes have found strong effects of temperatures when they approach tolerance levels. When comparing growth and energetics across two Lake Michigan tributaries that differed in temperatures by less than 3 ^{o}C, Godby et al. (2007) found that steelhead in the warmer tributary had to feed 84 % more to achieve the same growth rates as in the cooler tributary. Hayes et al. (2008) found overall low summer growth rates in a California watershed, but faster growth was achieved by individuals rearing in a warm, but productive estuarine lagoon. Finally, during very warm, low-flow conditions, Nielsen et al. (1994) found that juvenile steelhead sought refugia in thermally stratified pools. These results underscore the importance of temperature on growth.

One potential reason that we found energetic cost as induced by high temperatures to be more important than the other factors is that the study was conducted under low-flow conditions. Consequently, the parameter range of the factors examined in this study reflected this. Other factors, such as seasonal floods, cold winter temperatures, and stochastic events clearly pose important constraints on survival and growth during the juvenile stage (Jensen & Johnsen 1999, Quinn 2005); however, they were of overall lesser importance in this study.

A major strength of our approach was that we could account for thermal and allometric effects in the bioenergetics model when comparing energetic constraints across sites (Hewett & Kraft 1993). With an overall warming trend in streams in the Columbia River basin due to climate change (Barnett et al. 2004) there is an increased need to understand the relationships between habitat, growth opportunities and life-history expression (McCarthy et al. 2009, Hegg et al. 2013). Clearly, a number of factors in addition to temperature are projected to change and must be taken into consideration when predicting range changes and population viability (Isaak et al. 2010, Wenger et al. 2011); however, this study has documented a potentially important mechanism operant during summer low-flow conditions.

Key drivers of growth variation result from a complex interplay between habitat configuration, food availability and -predictability, and population density through which individual physiological characteristics are mediated (Reid et al. 2011, 2012). These conditions vary, and their relative importance is context dependent (Elliott 1994, Gibson 2002, Höjesjö et al. 2004, Quinn 2005, Hartson & Kennedy 2014). In our study system the effects of temperature had the greatest effect on subyearling growth rates, indicating that the metabolic costs of larger relative body mass outweigh the possible competitive advantage of acquiring resources. We conclude that high water temperatures pose energetic bottlenecks and can be a potentially strong mechanism limiting growth in juvenile salmonids in summer (Railsback & Rose 1999, Boughton et al. 2007). This relationship has some potentially important consequences for population regulation. As individuals grow and their absolute energetic demands increase, the temperature-induced metabolic costs also increase. By such, the temperature in concert with density-dependent competition can create energetic bottlenecks and contribute to population regulation (Lobón-Cerviá 2007, McCarthy et al. 2009). With stream temperatures projected to increase in the Columbia River basin with climate change (Barnett et al. 2004), such bottlenecks can become increasingly important as ecological and evolutionary drivers (Harvey et al. 2006, Crozier et al. 2008, Kovach et al. 2012, Hegg et al. 2013).

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FIGURES AND TABLES

Figure 2.1

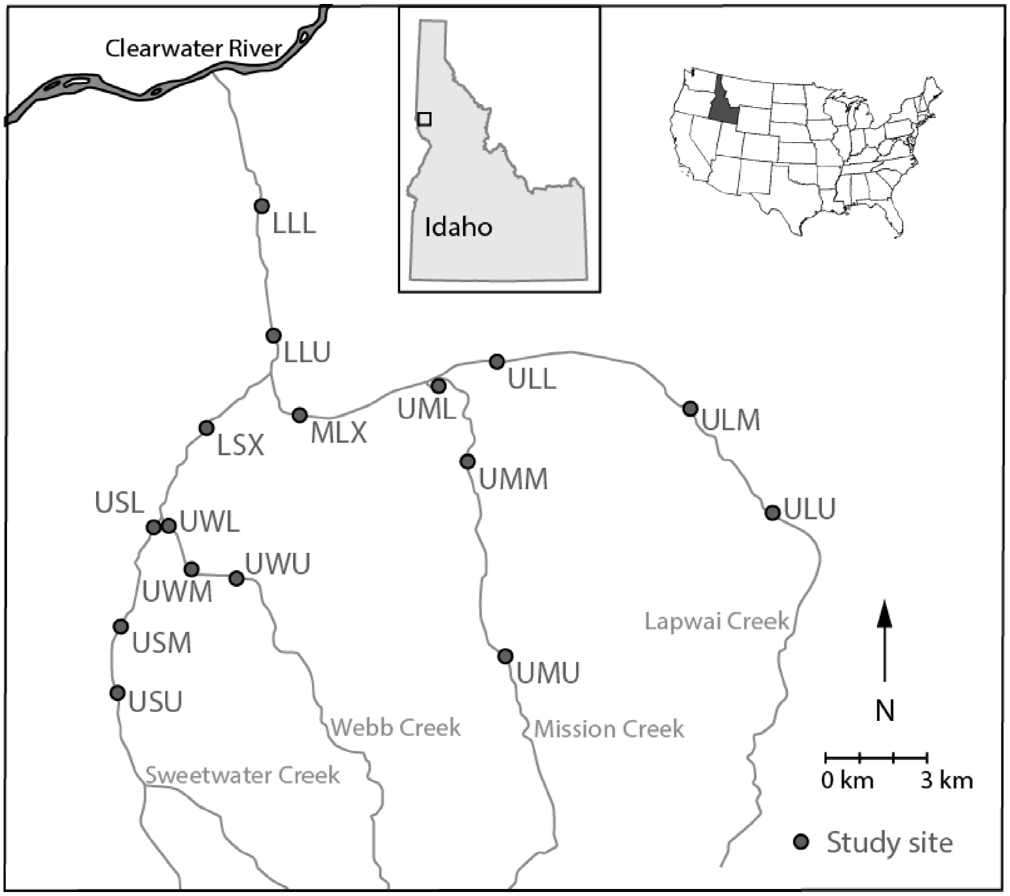

Figure 2.1. The map shows the four major streams in the Lapwai watershed and its location in North-Central Idaho (insert). The sites are coded with the first letter referring to stream segment (upper, middle, or lower), the second to stream (Sweetwater, Webb, Mission, or Lapwai), and the third to site position in that stream (upper, middle, or lower). For example, site ULU reads Upper Lapwai Upper. The Clearwater River is a tributary to the Columbia River.

Table 2.1

Table 2.1. Characteristics of the study reaches during July and September, 2010, showing the average monthly temperature, the highest daily average temperature, the number of days with daily averages exceeding 20 °C, the discharge, and the density of subyearling steelhead. The velocity distribution, measured once during the sampling season, is shown on the right. Standard deviations are shown in parentheses for the appropriate variables, except for density, for which the standard error is given.

	July					*September*					
Site	*Temp. (° C)*	*Max. (° C)*	*Days > 20 ° C*	*Discharge (ls^{-1})*	*Density (no. 100 m^{-2})*	*Temp. (° C)*	*Max. (° C)*	*Days > 20 ° C*	*Discharge (ls^{-1})*	*Density (no. 100 m^{-2})*	*Velocity (ms^{-1})*
LLL	18.8 (1.5)	21.1	6	246	8.34 (2.6)	15.6 (1.1)	17.9	0	127	4.31 (0.66)	0.34 (0.25)
LLU	18.5 (1.5)	20.6	5	207	23.4 (3.1)	15.2 (1.2)	17.5	0	122	18.9 (1.1)	0.31 (0.20)
LSX	17.2 (1.5)	19.5	0	212	2.57 (0.13)	14.4 (1.3)	16.7	0	158	2.42 (0.14)	0.42 (0.23)
MLX	18.4 (1.5)	20.9	5	19	27.4 (3.3)	15.9 (0.86)	17.6	0	19	34.1 (1.1)	0.24 (0.20)
ULL	16.4 (1.1)	18.4	0	33	14.3 (0.63)	14.8 (1.1)	17.1	0	11	20.1 (0.60)	0.14 (0.15)
ULM	17.1 (1.4)	19.5	0	41	7.74 (0.25)	14.6 (0.94)	16.5	0	19	5.38 (0.16)	0.16 (0.13)
ULU	15.8 (0.96)	17.3	0	43	2.96 (0.12)	14.1 (0.56)	15.3	0	33	7.71 (0.21)	0.19 (0.16)
UML	19.2 (1.8)	21.9	10	9	5.06 (0.27)	15.7 (1.3)	18.0	0	10	5.29 (0.19)	0.084 (0.087)
UMM	18.5 (1.8)	21.2	7	28	12.5 (0.62)	14.9 (1.3)	17.2	0	17	10.0 (0.14)	0.13 (0.10)
UMU	16.2 (1.7)	18.8	0	30	9.28 (0.97)	13.0 (1.3)	15.2	0	20	9.49 (0.20)	0.15 (0.14)
USL	16.3 (1.4)	18.3	0	168	0.645 (0.098)	14.0 (1.3)	16.3	0	131	1.65 (0.21)	0.41 (0.28)
USM	15.3 (1.3)	17.3	0	185	1.8 (0.52)	13.4 (1.2)	15.6	0	120	1.26 (0.014)	0.29 (0.27)
USU	14.8 (1.2)	16.9	0	172	2.55 (0.19)	13.2 (1.2)	15.2	0	220	4.02 (0.87)	0.46 (0.30)
UWL	18.2 (1.5)	20.3	3	14	7.53 (0.19)	14.1 (1.3)	16.5	0	44	7.84 (0.42)	0.11 (0.11)
UWM	17.5 (1.5)	19.5	0	17	14.9 (1.3)	13.5 (1.3)	15.8	0	54	14.7 (0.29)	0.14 (0.13)
UWU	17.0 (1.5)	18.9	0	22	14.3 (0.34)	13.0 (1.3)	15.3	0	52	20.03 (0.34)	0.16 (0.15)

Table 2.2

Table 2.2. Model selection results for the candidate models of n = 446 growth histories of subyearling steelhead, *O. mykiss*. Shown are the model structures, the grouping factors, random effects, number of parameters, and the AIC score. The models are grouped by comparison class and the Akaike weights (w_i's) reflect this classification.

Class	*Fixed effects structure*	*Grouping*	*Random effects*	*K*	AIC_i	w_i
1a	Growth = $\beta_0 + \beta_1$ mass	time*space	intercept + slope	5	454.0	0.46
		time*space	intercept	4	453.7	0.54
		time*space	slope	4	469.5	0.00
1b	Fraction = $\beta_0 + \beta_1$ mass	time*space	intercept + slope	5	-589.0	0.92
		time*space	intercept	4	-584.1	0.08
		time*space	slope	4	-577.6	0.00
2	Growth = $\beta_0 + \beta_1$ density	time*space	intercept + slope	5	*did not converge*	
		time*space	intercept	4	465.6	0.00
		time*space	slope	4	480.2	0.00
	Growth = $\beta_0 + \beta_1$ discharge	time*space	intercept + slope	5	*did not converge*	
		time*space	intercept	4	453.6	0.00
		time*space	slope	4	490.3	0.00
	Growth = $\beta_0 + \beta_1$ flow velocity	space	intercept + slope	5	*did not converge*	
		space	intercept	4	500.6	0.00
		space	slope	4	498.0	0.00
	Growth = $\beta_0 + \beta_1$ metabolic cost	time*space	intercept + slope	5	396.5	1.00
		time*space	intercept	4	444.0	0.00
		time*space	slope	4	431.9	0.00

Table 2.3

Table 2.3. The table shows the average and standard deviation in parentheses of the growth rates, mass, metabolic cost, and energy allocation for *n* recaptured individuals in each site during the month of September, 2010. Sites USL, USM, and USU (shaded) had low numbers of recaptured fish (< 5) and were not included in the models listed in Table 2.

Site	*n*	*Growth (% per day)*	*Mass (g)*	*Metabolic cost (J/g/d)*	*Fraction*
LLL	5	1.24 (0.18)	11.5 (3.5)	140 (5)	0.49 (0.035)
LLU	20	1.08 (0.26)	7.7 (3.5)	160 (15)	0.43 (0.072)
LSX	7	1.30 (0.29)	5.0 (1.8)	119 (33)	0.57 (0.11)
MLX	46	1.12 (0.45)	9.0 (3.6)	153 (23)	0.45 (0.12)
ULL	33	0.60 (0.34)	5.6 (2.0)	175 (21)	0.28 (0.14)
ULM	8	0.50 (0.19)	4.7 (1.2)	156 (54)	0.30 (0.16)
ULU	18	0.90 (0.31)	5.0 (1.5)	169 (18)	0.38 (0.09)
UML	9	0.97 (0.21)	7.2 (2.6)	137 (31)	0.46 (0.10)
UMM	12	1.47 (0.55)	5.6 (1.4)	125 (19)	0.57 (0.074)
UMU	14	0.66 (0.20)	3.9 (0.73)	155 (17)	0.32 (0.073)
USL	2	0.16 (0.45)	4.2 (0.21)	133 (54)	0.51 (0.21)
USM	3	1.07 (0.29)	6.2 (1.2)	145 (12)	0.44 (0.089)
USU	1	1.11	2.9	165	0.43
UWL	6	0.66 (0.29)	3.4 (0.75)	130 (29)	0.32 (0.14)
UWM	15	1.17 (0.28)	5.7 (1.6)	141 (17)	0.49 (0.072)
UWU	21	0.67 (0.28)	3.8 (0.83)	172 (16)	0.31 (0.11)

Table 2.4

Table 2.4. Parameter estimates for the best approximating models for the comparisons made in Table 2. Abbreviations in the header are comparison class (Cls.) and variance (Var.). Abbreviations in the table are intercept (i) and slope (s) for the random term. The fixed effects parameter β_0 refers to the intercept and β_1 refers to the slope of the linear mixed effects model.

Cls.	*Model*	*γ*	*ε*	*Var.*	*% ε*	*% η*	*β_0 (SE)*	*β_1 (SE)*
1a	Growth = mass	i, s	0.131	0.242	54	45	1.04 (0.0848)	-0.0239 (0.0115)
	Growth = mass	i	0.135	0.241	56	44	1.04 (0.0737)	-0.0236 (0.00635)
1b	Fraction = mass	i, s	0.0125	0.0220	57	42	0.420 (0.0261)	-0.00543 (0.00402)
2	Growth = metab. cost	i, s	0.108	1.59	7	93	1.57 (0.261)	-0.00435 (0.00182)

Figure 2.2

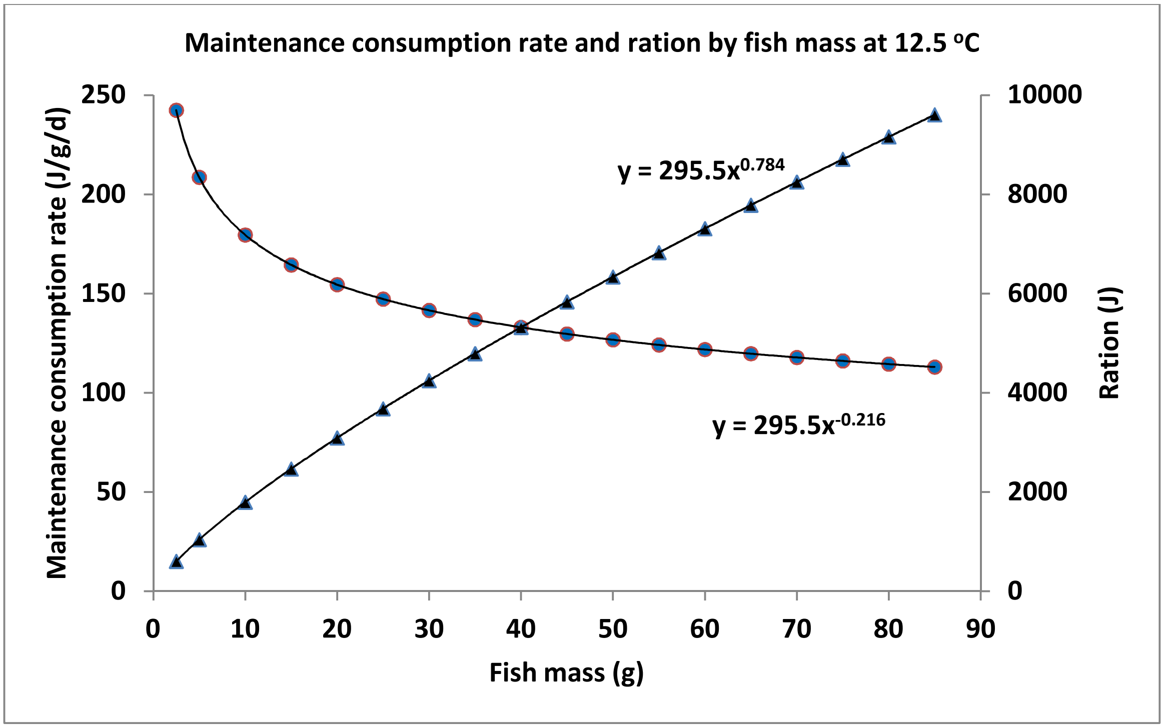

Figure 2.2. Calculated consumption rates to cover maintenance metabolic cost (*circles*, $Jg^{-1}d^{-1}$) and associated daily ration size (*triangles*, J) as functions of fish mass (range 2.5 to 85 g) at 12.5 °C. The relationship was generated by the bioenergetics model parameterized by values in Appendix 2.

Figure 2.3

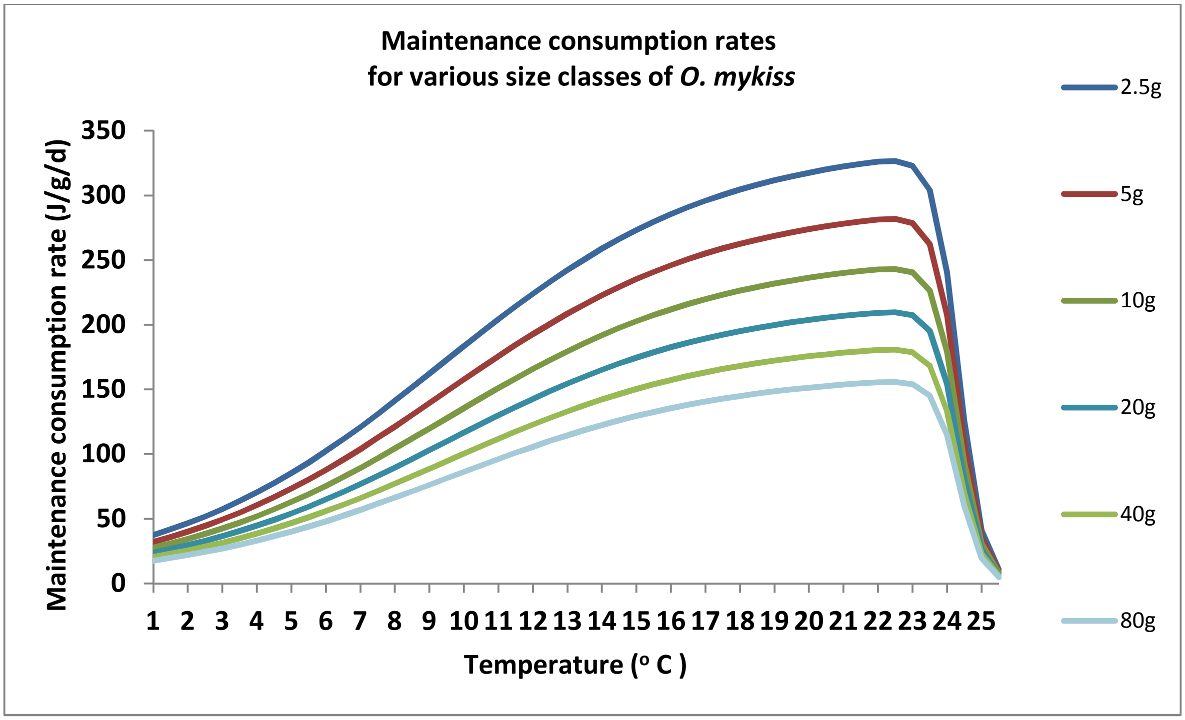

Figure 2.3. Calculated energetic demand for maintenance metabolic cost ($Jg^{-1}d^{-1}$) as a function of temperature for a size range of juvenile steelhead, *O. mykiss*.

Figure 2.4

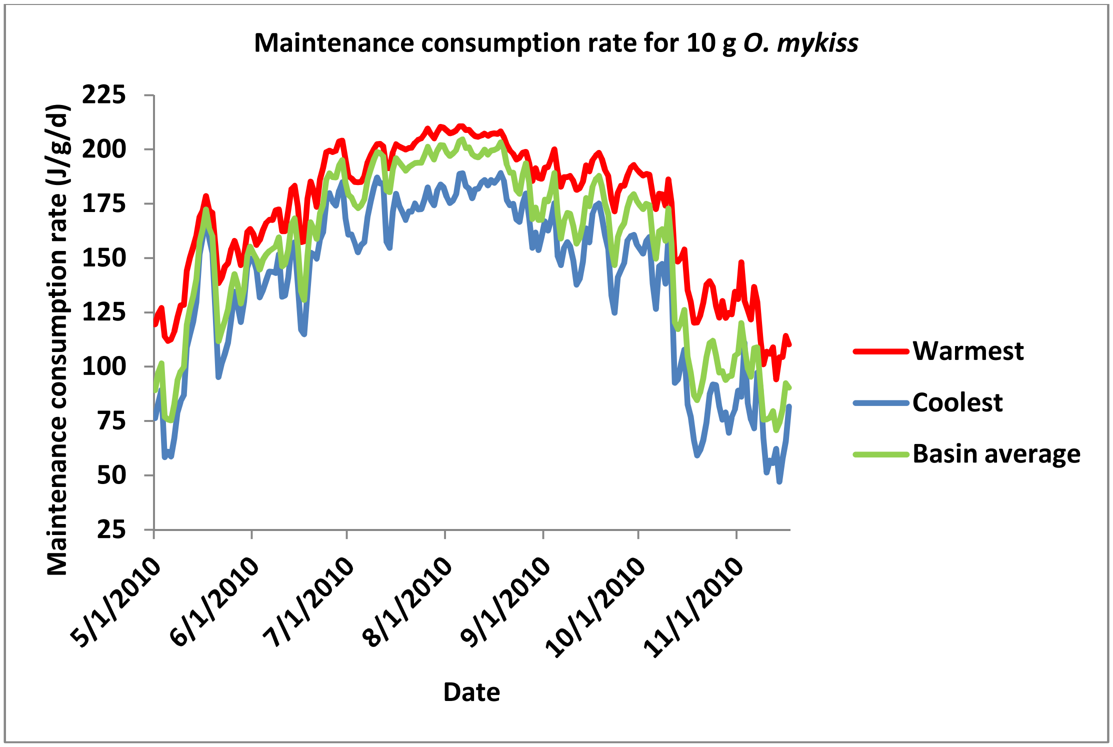

Figure 2.4. Calculated maintenance metabolic costs ($Jg^{-1}d^{-1}$) for juvenile steelhead, *O. mykiss*, in the warmest and coolest sites and the basin average, holding mass constant at 10 g.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Energy density (ED, J/g wet weight) values by taxonomic groups used in the bioenergetic model. The values for energy density and wet to dry ratio were obtained from the cited references either directly, averaged over the widest range of published values for the taxonomic group (a), or borrowed from the closest possible taxonomic level (b).

Appendix S2. Model-specified equations, variables, and associated parameters used in the bioenergetics modeling of subyearling steelhead.

Appendices are provided at the end of the dissertation as Appendix 1 and Appendix 2.

CHAPTER 3: METABOLIC CONSTRAINTS AND PHYSICAL HABITAT CHARACTERISTICS EXPLAIN THE SPATIAL VARIATION IN THE STRENGTH OF SELF-THINNING IN A STREAM SALMONID

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Keywords: AIC, bioenergetics, density dependence, Idaho, *Oncorhynchus mykiss*, physical habitat, self-thinning, steelhead

SUMMARY

1. Self-thinning patterns are frequently used to describe density dependence in populations on time scales shorter than the organism's life span, and have been used to infer carrying capacity of the environment. Among mobile animals, this concept has been used to document density dependence in stream salmonids. Self-thinning has been attributed to competition over food or space, but exact mechanisms have been difficult to determine.

2. Across a streamscape, the carrying capacity, growth conditions, and initial cohort sizes vary, which would influence the onset and strength of the thinning curves. However, despite much effort in

describing habitat relationships in stream fishes, few studies have explicitly tested how the physical environment affects the slope of the thinning curves.

3. Here we investigate the prevalence and strength of self-thinning in juvenile stages of a threatened population of steelhead (*Oncorhynchus mykiss*) in Idaho, USA. We further investigate the roles of physical habitat and metabolic constraints operant during the summer growing season in determining the intensity of self-thinning across discrete sampling reaches in the watershed.

4. We found that self-thinning patterns were statistically significant in only three out of 32 possible trajectories, and the slopes were shallower than predicted by the territory space-, consumption-, and metabolism hypotheses; however, most cohorts exhibited a negative relationship between mass and density. Certain abiotic factors could explain a relatively large portion of the variation in the strength of the self-thinning slopes. For subyearling steelhead, the slopes were negatively related to metabolic cost in the warmest months, explaining 44 % to 46 % of the variation, respectively. Physical habitat variables were more important in describing the thinning slopes of yearling steelhead. The variation in thinning slope was best explained by substrate size (w_i = 0.86, r^2 = 70 %), corresponding to stronger thinning occurring in the uppermost study reaches.

5. Our results show that self-thinning will occur under certain conditions, but that the phenomenon is not necessarily widespread or consistent across a heterogeneous watershed. Our results further indicate that temperature is important for population dynamics, because it can impose energetic bottlenecks on entire cohorts of juvenile salmonids.

INTRODUCTION

One of the primary interests in ecology is identifying the patterns and processes that govern population growth. Population size and growth rate can be *limited* by factors such as weather that act independently of population size, and *regulated* by density dependent factors, when the per capita growth rate of the population depends on its own density (Sinclair & Pech 1996, Sibly & Hone 2002). Which of the two processes has a stronger effect on populations has been heavily debated (Nicholson 1933, Andrewartha and Birch 1954), but there is general consensus that most populations are governed by a combination, rather than one or the other (Leirs *et al.* 1997, Karels & Boonstra 2000). Their relative importance varies by population, depending upon abiotic conditions, community organisation, and the population's size and trajectory (Begon, Harper & Townsend 1996, Einum 2005).

Detecting density dependence in populations over time intervals shorter than a single generation length has received much attention in agronomy and applied ecology (Westoby 1984). One particularly interesting pattern was formalised by researchers observing how tree mortality was proportional to the average mass of trees in the stand, as the stand was growing (pattern known as *self-thinning*; Yoda *et al*. 1963). Animal populations also thin over time, but there is rarely a factor that governs mobile animal taxa like the shared need for light among plants (Begon, Firbank & Wall 1986, Begon *et al*. 1996). Among mobile animals, the self-thinning framework has been invoked to describe numerical changes in stream salmonids as cohorts are maturing (e.g. Elliott 1993, Dunham & Vinyard 1997, Rincón & Lobón-Cerviá 2002, Keeley 2003). A relatively confined range, high reproductive capacity, and limited dispersal during summer have made salmonids a tractable system for the study of this phenomenon. The processes creating self-thinning patterns have been attributed to competition over food and space. The mass-density relationships follow power functions due to nonlinear energy conversion with size (Bohlin *et al*. 1994, Steingrimsson & Grant 1999), and behavioural mechanisms regulating territory size (Grant, Noakes & Jonas 1989, Grant & Kramer 1990) (see Keeley 2003 for a review of these hypotheses).

Although the territory size hypothesis has been implicitly tested in many studies, habitat factors have seldom been explicitly considered in studies on self-thinning, with a few notable exceptions (Steingrimsson & Grant 1999, Lobón-Cerviá 2008). As Lobón-Cerviá (2008) noted, most studies have assumed no effect from habitat factors related to growth and density on the self-thinning patterns in salmonids (e.g. Elliott 1993, Grant & Imre 2005, Imre, Grant & Cunjak 2005), which is very unlikely in streams with seasonal flooding and drought. Further, habitat quality, thermal regime, proximity to spawning grounds, and productivity can vary greatly within a watershed, all affecting initial densities, survival, and growth opportunities for juvenile salmonids (Gibson 2002, Ebersole *et al*. 2006). This variation could therefore manifest in varying degrees of thinning throughout the stream network as cohorts experience different conditions depending on their location.

Here, we test the hypothesis that cohorts of juvenile steelhead will thin according to predicable relationships (Grant & Kramer 1990, Steingrimsson & Grant 1999, Bohlin *et al*. 1994) across a watershed in Idaho, USA, designated as critical habitat for a population of steelhead that is listed as threatened under the Endangered Species Act. Following Steingrimsson & Grant (1999) and Lobón-Cerviá (2008) we sought to adduce the drivers of self-thinning, and specifically which environmental factors influence cohort trajectories. We first analyse the spatial and temporal conditions under which self-thinning patterns emerge, and secondly assess the extent to which the variation in thinning slopes can be attributed to physical habitat conditions and bioenergetic constraints. Because initial densities might vary throughout the watershed and the carrying capacity likely varies across time and space, we expect that the slopes of the thinning curves will overall be shallower than predicted by the food and space hypotheses.

METHODS

Study area and population

The Lapwai watershed is situated in North-Central Idaho, and drains an area of 694 km^2. There are four major tributaries in the watershed that together form the 4th order Lapwai Creek, which empties into the Clearwater River, 237 m.a.s.l. (Fig. 1). The streams drain the north slopes of Craig Mountain (1530 m.a.s.l.) and carve steep canyons through the landscape. The predominant geology in the watershed is Columbia River basalt, with a band of Idaho Batholith in the upper, high elevation portion. Mean annual precipitation is 490 mm, with larger amounts falling at higher elevations. The plateau above the escarpment is overlain with loess, and the predominant land use is dry land grain agriculture, which covers 34% of the watershed. Coniferous forests cover 29%, primarily at higher elevations above the prairie, and grasslands dominate the steep canyon sides and valley floors (Homer et al. 2007). Mean annual precipitation is 490 mm, with higher amounts falling at higher elevations, primarily from October through May.

Snake River steelhead and salmon (*Oncorhynchus* sp.) have declined in numbers since the 1870s due to hydropower development, overharvest, ocean conditions, and habitat degradation (Chapman 1986, NRC 1996). Although habitat quality in the Clearwater River Lower Mainstem has been significantly affected by land use alterations, particularly in low elevation arable areas, records suggest that streams in the Lapwai Creek watershed produced significant numbers of anadromous fish in the past (Johnson & Stangl 2000, NMFS 2006). Other fish species include, in order of abundance, longnose dace (*Rhinichtys cataractae*), sculpin (*Cottus* spp.), bridgelip sucker

(*Catostomus columbianus*), redside shiner (*Richardsonius balteatus*), northern pikeminnow (*Ptychocheilus oregonensis*), and chiselmouth (*Acrocheilus alutaceus*). In recent years juvenile coho salmon (*Oncorhynchus kisutch*) have been stocked as part of a supplementation program in lower reaches of the system, but are generally not sympatric in space or time with steelhead. No hatchery supplementation exists for steelhead in the watershed.

Study design

We sought to identify drivers of density dependence in a system that is characterised by high spatial and temporal variation in habitat conditions. We therefore assigned three study reaches on each of the tributaries, one below the confluence of each pair, and two study reaches on the mainstem, totalling 16 sites (Fig. 1). Site selection was conducted using a hierarchical stratified random approach (Frissell *et al*. 1986). We stratified based on several criteria with the intention to capture a gradient of physiographic (topography, geology, and land cover) and land use conditions within and across the four streams in the Lapwai watershed. At the largest spatial level, a general area (typically one stream-kilometre in length) was identified on the map informed by *O. mykiss* occurrence (Chandler & Parot 2003), distance to other study reaches, tributary inputs, and known spring inputs. Within these sections we further narrowed the search by means of dividing the general area into as many representative 100 m reaches as possible, informed by land use, land cover, channel constraints such as levees and channelization, and land ownership. Final selection was done randomly prior to the first visit in the field in 2010, and the sites were kept throughout the study. We visited each of the 16 sites 5 times between June and November of both 2010 and 2011. From this we could measure the size distribution of cohorts and estimate population size, as well as quantify the physical habitat characteristics and thermal regime.

Sampling methods and material

Steelhead data

Field data were collected between mid June and early November in 2010 and 2011. We began fish sampling when the flows were low enough to permit efficient electrofishing. We set block nets to ensure a closed population, and conducted three-pass depletion electrofishing using a Smith-Root LR-24 backpack electroshocker (Smith-Root Inc., Vancouver, WA). To reduce the stress of capture and handling on fish, sampling was conducted during early morning hours when the water temperatures did not exceed 18 °C. We set the voltage, frequency, and duty cycle within 20% of their mean values of 350 V, 30 Hz, and 15%, respectively. Juvenile steelhead were held in buckets filled with aerated stream water at ambient stream temperatures. Prior to any handling we anesthetised the fish with tricaine methanesulfonate (MS-222). We measured fork length in millimetres and weight to the nearest decigram. Prior to release, fish were first allowed to recover in buckets with aerated water, and were then moved to a live-well placed in the stream channel outside the sampling reach. We mimicked the stream environment inside the live well by providing rocks and vegetative cover. Upon completion of sampling, we removed the block nets and released fish back to the study reach. Densities were calculated using Carle & Strub's (1978) weighted maximum likelihood estimator of *K*-pass removal data (Fig. 2). Due to the small size and low discharge of these streams we obtained very high capture probabilities (season averages ± SD were 0.63 ± 0.14 in 2010 and 0.62 ± 0.13 in 2011, respectively) and consequently narrow confidence intervals around our population estimates. All fish sampling and -handling procedures were permitted as part of the Section 7 consultation for the Lewiston Orchards Biological Opinion (NMFS 2006), Idaho Department of Fish and Game, and the University of Idaho Institutional Animal Care and Use Committee.

Habitat data

To quantify habitat variables in the study reaches, we established transects perpendicular to the channel at 5 m intervals with the first transect 2.5 m above the lower end of the reach. The channel was first characterised into predominant geomorphic unit at each transect (riffle, run, pool, or glide), and percentages of each were calculated to express the channel's composition. The transects were then split into 5 sections of equal width. At each point we measured the velocity (*m/s*; Marsh McBirney, Loveland, CO), depth (*cm*), and the longest axis of a randomly selected piece of substrate (*mm*). The approach yielded approximately 100 point measurements of each of the physical variables, from which we calculated the average values (Table 1). We also calculated the percentage of the reach being composed of shallow and slow flowing water (< 6 cm deep with flow velocity < 0.15 m/s), noted *combination* in the tables), as these features are important for subyearling steelhead (Bjornn & Reiser 1991).

Temperature data

HOBO TidbiT v2 temperature loggers (Onset Computer Corporation, Pocasset, MA) installed at each site recorded water temperatures (^{o}C) every 30 minutes throughout the duration of the study. Daily averages of temperature were used in the bioenergetic modelling.

Bioenergetics data

We used Fish Bioenergetics 3.0 ("Wisconsin model"; Hanson *et al*. 1997) to calculate bioenergetic constraints on steelhead. The model was specified with Thornton & Lessem's (1979) consumption equation, Kitchell, Stewart & Weininger's (1977) respiration equation, Elliott's (1976) waste losses equation, and predator energy density equation number 2 in the package (Hanson *et al*. 1997) with a predator energy density of *5763* J/g wet weight (Glova & McInerney 1977). The model was parameterised with field data on temperature from both 2010 and 2011, and diet data from 431 steelhead over the 2010 season which averaged 4324 J/g wet weight (Myrvold & Kennedy, *in press*). To calculate the ration necessary to maintain body mass for a given period of time under a given temperature regime, we controlled for allometric effects by keeping body mass constant at the start value over that time period (Hewett & Kraft 1993). We chose to use a 5 g individual for the simulation because it is the average weight of subyearlings in the first months of summer, and we expressed the metabolic cost as the average daily rate over each month from June to October. By holding mass constant we could compare the maintenance metabolic costs across sites, which were entirely thermally driven patterns. We report metabolic rates as mass-specific rates of consumption (*J/g fish/day*). Data from June 2011 were limited to the period of June 14 to 30, because the temperature loggers in several sites were washed out by a flood.

Analyses

Thinning curves

We estimated the thinning slopes for each site by using the average mass and density of each cohort for each visit to each site. The data were natural log-transformed to linearise the function. The self-thinning relationship is then given as

$$\mathbf{ln}(mass) = a\,\mathbf{ln}(density) + b,$$

where the regression coefficient *a* refers to the slope of the thinning curve, and *b* is the intercept in the linear relationship (Yoda *et al*. 1963). Note that *a* is the same as the exponent in a power function, which is frequently used in self-thinning analyses. Deviation of *a* from zero in a negative direction (under the hypothesis of H_0: $a = 0$) was tested via simple linear regression, and the steepness of the slope is referred to as the *strength* of self-thinning in this paper.

The analyses were conducted within sites over time, and across sites within time points. In the former, we followed the average mass of individuals over the cohort trajectory. We plotted the mass-density combinations to obtain the slope of each cohort. In the latter, we used the mass-density combinations in each site for each monthly visit to analyse the time period when thinning was the strongest, expressed as the magnitude of the slope coefficient *a*. Because the regressions were all first order linear models, we used the simple coefficient of determination (r^2) as our model selection criterion. For all the tables we use the abbreviations *subyr* for subyearling and *yr* for yearling fish.

Habitat and bioenergetic constraints

We regressed the slopes of the thinning curves against site-specific habitat and bioenergetic characteristics using multiple linear regression models as specified in Table 3 and 5, respectively. The model structures were built *a priori* to evaluate hypotheses about abiotic determinants of *O. mykiss* abundance, and then confronted with the thinning slope data. One site, LLU, was omitted for yearling steelhead due to small sample size (n=5 visits). We separated the classes of models into two main analyses; habitat and bioenergetics.

We used an information-theoretic criterion to assess the relative plausibility of the candidate models (Akaike 1973, Burnham & Anderson 2002). Information-theoretic data analysis is based on Kullback-Leibler information, which is the information lost when statistical models are used to approximate full truth (Kullback & Leibler 1951). Akaike's information criterion (AIC) is given as

$$AIC = -2\ln\left(\ell\left(\hat{\theta}\middle|data\right)\right) + 2K,$$

where $\ln\left(\ell(\hat{\theta}|data)\right)$ is the value of the maximised log-likelihood over the unknown parameters given the data and the model, and *K* is the number of estimable parameters in that approximating model. We used the small-sample adjusted criterion (*AICc*; Hurvich & Tsai 1989). AICc is given as

$$AICc = AIC + \frac{2K(K+1)}{n-K-1}$$

AICc exhibits the same qualities as the ordinary criterion and the notations are therefore used interchangeably. The models *i* were ranked using the simple AIC differences, Δ_i, given as $\Delta_i = AIC_i - AIC_{min}$. The model for which AIC is minimal is selected as best for the given data. To make interpretation and inference easier, we normalised the likelihood functions of the models so that they sum to 1. The probability of model *i* being the K-L best model in the set is called the Akaike weight (*w*,) and is given as

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_i\right)}$$

We report model selection results with tables showing the number of estimable parameters (*K*), the residual sum of squares (*RSS*), the model selection criterion (*AICc*), the simple differences (Δ_i), and the Akaike weights (w_i) for the models in the candidate set. Interpretation and inference is based chiefly on the Akaike weights. We only provided parameter estimates for those models in each set which obtained substantial relative support (i.e. $w_{max}/w_i < 2$). For these models we presented the estimated standard error of the model (*SE*, the square root of the estimated variance), the parameter estimates (*β*-coefficients) and their associated standard errors (*SE*), and the multiple coefficient of determination (R^2). In order to compare the effects of habitat versus bioenergetic constraints, we compared the model fit for the best approximating models of each category. All analyses were conducted using PROC REG in SAS v. 9.2 (SAS Institute Inc., Cary, NC).

RESULTS

Prevalence and strength of self-thinning curves

For the subyearling cohort, only two of 16 sites (LLU and UMU) exhibited statistically significant self-thinning relationships, and for yearling fish only one site (ULU) showed significant thinning (Table 2). These significant curves had strong absolute support (r^2 from 0.52 – 0.81).

Despite within-site trends only occasionally having a significant slope, there were periods of time when many sites underwent thinning. The steepest drops in densities throughout the watershed occurred in mid summer when streams reached baseflow conditions. We found the most significant thinning to occur among subyearlings in July and August 2011 (Table 3), reflecting higher initial densities in 2011 compared to 2010. For yearlings, the most pronounced thinning happened in June, July, and August (Table 3), with the strongest effects in the month of July in both years (r^2 = 0.55).

Habitat and bioenergetic effects

For habitat factors, the percentage of slow flowing and shallow habitat was the best approximating model of subyearling slope (w_i=0.53), showing a negative, but weak (R^2 = 0.15) relationship. Among yearling steelhead, the single best approximating model was a negative relationship with substrate size (w_i = 0.86, r^2 = 0.70). These conditions collectively correspond to the uppermost study sites on each tributary, characterised by high gradients, confined morphology, and boulder and large cobble dominated substrate. Model selection results are summarised in Table 4, with parameter estimates for the best approximating models in Table 5.

For bioenergetic constraints, July and August 2010 metabolic costs were the best approximating model for subyearling slope (w_i = 0.37, R^2 = 0.46), showing a negative relationship with July metabolic cost and a positive relationship with August metabolic cost. There was no clear best model for yearlings, although June 2010 metabolic costs received the best support (w_i = 0.18, r^2 = 0.14). Model selection results are summarised in Table 6, with parameter estimates for the best approximating models in Table 7.

Comparing habitat- and bioenergetic effects on the self thinning slopes, our data showed that bioenergetic constraints during the warmest summer months were more important for subyearlings (Δ_i = 3.699), and habitat factors explained the variation in slopes better for yearlings (Δ_i = 15.51).

DISCUSSION

We found that self-thinning was evident in only three out of 32 possible trajectories, and the slopes were shallower than predicted by the territory space- (0.86; Grant & Kramer 1990), consumption- (0.73; Steingrimsson & Grant 1999), and metabolism- (0.87; Bohlin *et al*. 1994) hypotheses. The trajectories in most cases were nonsignificant, meaning that the slopes were statistically indistinguishable from zero; however, for most of them the trend was a negative relationship between mass and density. The second main finding showed that specific abiotic factors explain a relatively large portion of the variation in the strength of the self-thinning. For subyearling steelhead, the slopes were negatively related to metabolic cost in July and August, i.e. the warmest months, explaining 44 % to 46 % of the variation in the thinning slopes, respectively. For yearlings, physical habitat variables were more important in predicting the slopes, with substrate size being the single best approximating model, explaining 70 % of the variation.

Identifying the factors by which a population is limited is an important step in any wildlife management, particularly in threatened populations where mitigation and restoration efforts are undertaken (Sibly & Hone 2002, Armstrong 2005). Self-thinning can be used to diagnose density dependence in a population on time spans shorter than its life cycle, and estimate carrying capacity for the given size distribution (Westoby 1981). However, the exact mechanisms causing these patterns are impossible to identify in observational studies (Dunham & Vinyard 1997), and difficult even in experimental studies (Keeley 2003). Several studies have sought to unravel the underlying mechanism causing self-thinning patterns in stream salmonids. Two major hypotheses exist to explain how and why population density scales with average body mass. The food hypothesis focuses on the allometries of metabolism (Bohlin *et al*. 1994) or food consumption (Steingrimsson & Grant 1999). The space hypothesis concerns the territorial nature of stream salmonids in that the area of their territories increases with fish mass (Grant & Kramer 1990), analogous to shading in plants (Lonsdale & Watkinson 1983). Although several studies have observed the thinning pattern (e.g. Elliott 1993, Rincón & Lobón-Cerviá 2002), few studies have actually tested these hypotheses. Keeley (2003) tested the predictions from the food and space hypotheses in an experimental cohort of juvenile steelhead, and found stronger support for the food consumption hypothesis, which predicts a thinning slope of 0.73. However, the confidence intervals overlapped the values predicted from metabolic rate and territory size, and it consequently was impossible to reject those hypotheses. The similarity in theoretical predictions thus makes them difficult to distinguish (Dunham & Vinyard 1997), even with well designed experiments (Keeley 2003).

Our results were in many ways similar to those of Dunham & Vinyard (1997), who studied multiple salmonid species across multiple rivers in the intermountain Western United States, environments similar to Lapwai Creek. They found that several populations did not show significant thinning, probably owing to environmental variation and species-specific traits. Although the study was unable to identify the exact mechanisms underlying the thinning lines, Dunham & Vinyard (1997) contend the thinning lines reflected real, density dependent processes.

Growth opportunities and densities of salmonids can vary spatially across a river network (Gibson 2002, Ebersole *et al*. 2006). Hence, it is likely that the thinning slopes can vary accordingly. Multiple studies have shown how environmental conditions can determine population size by limiting survival or recruitment (Hayes, Ferreri & Taylor 1996, Armstrong 2005, Einum & Nislow 2005). However, we are only aware of two other studies that have linked variation in the strength of density dependence to these habitat characteristics (Steingrimsson & Grant 1999, Lobón-Cerviá 2008). Because we analysed cohorts from 16 discrete sites, we found a gradient of self-thinning slopes. Our thinning slopes were invariably shallower than what theory predicts, suggesting that both cohorts were below carrying capacity throughout the study area (Westoby 1981, Lobón-Cerviá 2008).

There are four potential reasons to why the cohorts were below carrying capacity. First, the populations might be limited by recruitment, and the cohorts do not saturate the habitat until reaching a larger body size, with the result that the thinning slopes were shallower due to delayed onset of density dependence (Rincón & Lobón-Cerviá 2002, Lobón-Cerviá 2008). Secondly, *O. mykiss* is a facultative anadromous species, meaning that individuals exhibit flexibility in their behavioural decisions to remain in freshwater as resident rainbow trout or become anadromous steelhead. Juveniles make this choice based on their growth trajectory and environmental cues (Metcalfe 1998, Satterthwaite *et al*. 2009), and densities may reflect different, localised emigration decisions. The habitat- and bioenergetics analyses further supported this spatial and temporal variability in that populations experiencing energetically stressful conditions and those inhabiting headwater sites (coarser substrate) exhibited steeper thinning curves. Thirdly, stochastic, density-independent events can limit population size and obscure both density dependent process as well as habitat relationships (Jensen & Johnsen 1999, Begon *et al*. 1996). We did not have the level of resolution in our data to formally analyse the effects of flooding events, but we suspect the flashy runoff regime of Lapwai

Creek to have large effects on physical habitat configuration, mortality, and displacement of juvenile steelhead. Lastly, we studied sites, not cohorts. Juvenile salmonids change habitat preferences throughout ontogeny, so if some sites have stage specific limitations, it would be reflected in the densities (Armstrong 2005, Einum, Sundt-Hansen & Nislow 2006), and hence in the site-specific thinning curves.

The reason we saw a gradient in the strength of density dependence is likely due to variation in the environmental conditions across the 16 sites. For example, stream temperatures in lower elevation drainages of the Snake River Basin can reach or even exceed the thermal tolerance of salmonids during summer baseflow conditions. Earlier work in the same watershed has shown that steelhead growth rates were largely limited by metabolic costs imposed by water temperatures in mid summer, and food limitation in fall (Myrvold & Kennedy, *in press*). This supports the view that high temperatures, coupled with food limitation, can pose energetic bottlenecks on individuals as well as cohorts.

In conclusion, our results show that self-thinning can occur under certain conditions, but that the process is not ubiquitous across a heterogeneous watershed. There are multiple potential causes for this lack of universal thinning patterns, but we identified bioenergetic constraints and habitat factors as potential drivers. Our results suggest that temperature is important for population dynamics in that it can pose energetic bottlenecks on entire cohorts of subyearling salmonids.

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FIGURES AND TABLES

Figure 3.1

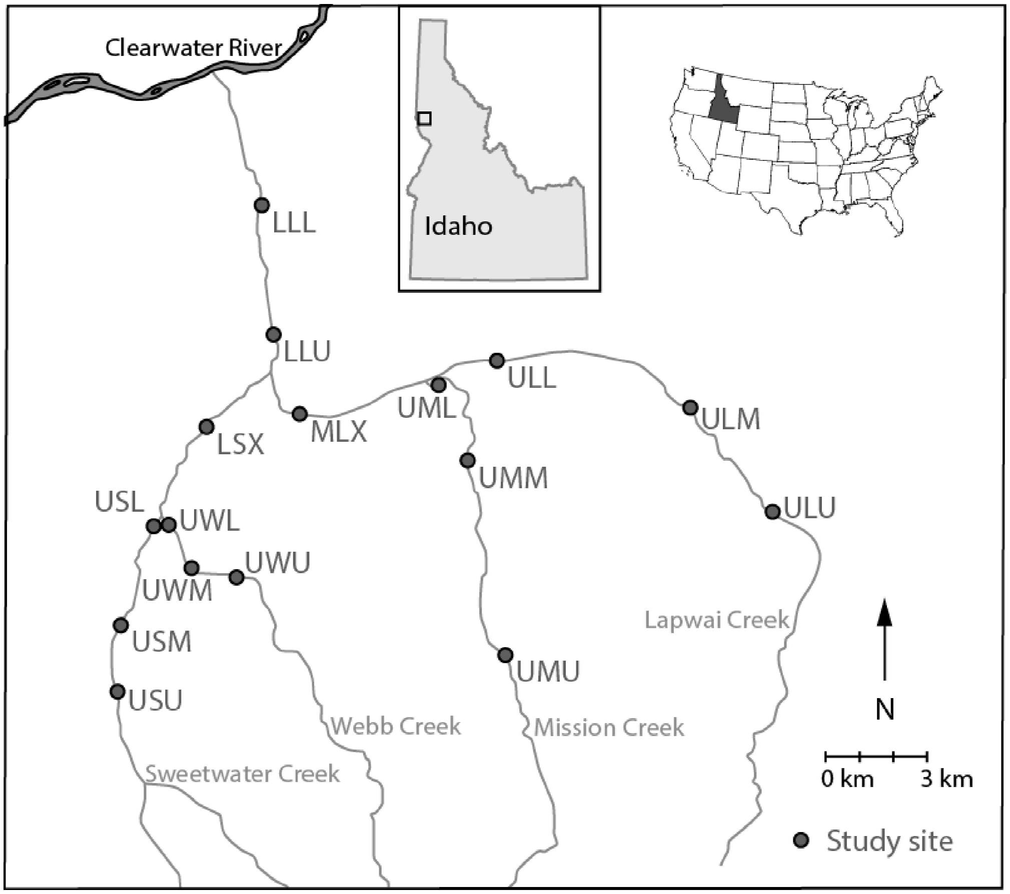

Figure 3.1. The map shows the four major streams of the Lapwai watershed and its location in North-Central Idaho, United States (insert).

Figure 3.2

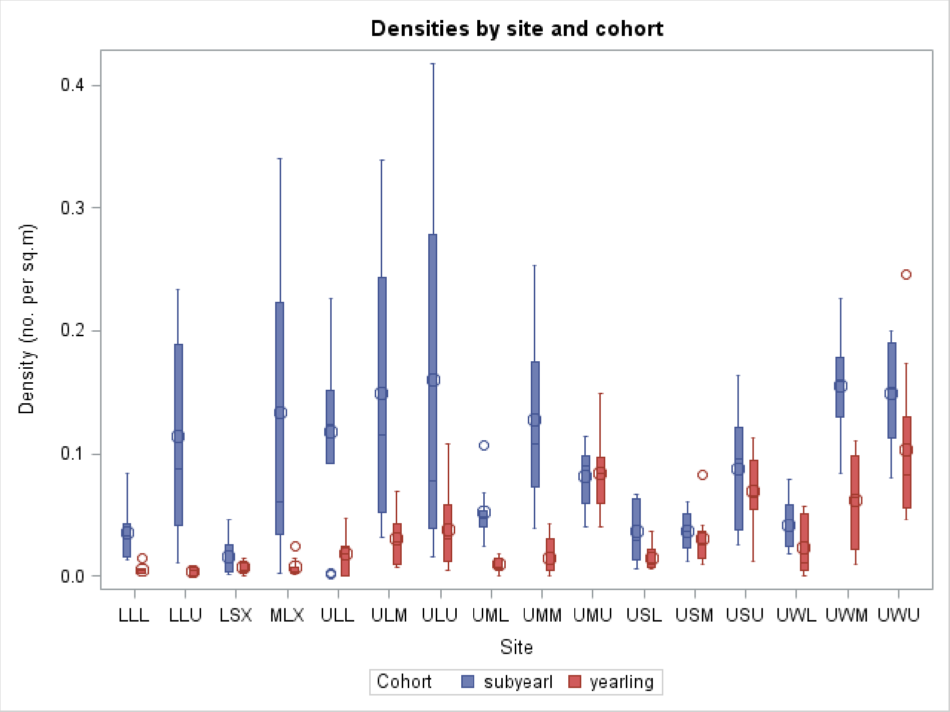

Figure 3.2. Density distribution (no. per m^2) of subyearling and yearling steelhead between 2010 and 2011 in the Lapwai watershed, Idaho.

Table 3.1

Table 3.1. Characteristics of the 16 study sites, showing the self-thinning slope for each cohort, the elevation and width, and the average channel covariates and their standard deviations used in the modelling.

Site	*Slope subyr.*	*Slope yr.*	*Elevation (m)*	*Width (m)*	*% Riffle*	*% Run*	*% Pool*	*% Glide*	*Depth (cm)*	*Velocity (m/s)*	*Substrate (mm)*	*% Combination*
LLL	-0.100	-0.070	280	5.1 (2.2)	14	57	14	7	22 (12)	0.34 (0.25)	129 (61)	50
LLU	-0.452	N/A	324	5.4 (1.5)	18	24	6	47	21 (11)	0.31 (0.20)	113 (47)	20
LSX	-0.024	0.020	390	4.8 (1.2)	40	35	20	0	20 (15)	0.42 (0.23)	108 (70)	2
MLX	0.193	0.029	357	3.7 (1.0)	50	20	25	0	17 (12)	0.24 (0.20)	105 (73)	5
ULL	0.204	-0.140	449	4.8 (1.9)	47	6	12	35	13 (8)	0.14 (0.15)	128 (98)	31
ULM	-0.034	-0.177	585	4.0 (0.8)	41	24	12	18	10 (8)	0.16 (0.13)	141 (77)	41
ULU	0.319	-0.273	693	3.8 (1.2)	35	40	10	10	12 (8)	0.19 (0.16)	213 (186)	21
UML	-0.019	-0.015	411	2.7 (1.2)	15	15	15	55	9 (5)	0.08 (0.09)	119 (66)	36
UMM	0.279	0.011	472	4.1 (1.2)	95	0	5	0	7 (4)	0.13 (0.10)	124 (96)	48
UMU	-0.384	-0.175	629	3.6 (1.0)	32	21	32	16	11 (5)	0.15 (0.14)	238 (226)	17
USL	0.398	-0.113	448	3.0 (1.3)	0	55	15	25	23 (13)	0.41 (0.28)	137 (180)	2
USM	0.505	0.125	531	4.0 (2.2)	0	30	35	30	31 (16)	0.29 (0.27)	86 (56)	1
USU	0.506	-0.039	575	3.1 (0.7)	15	65	15	0	19 (9)	0.46 (0.30)	107 (73)	1
UWL	-0.482	0.099	438	2.5 (0.8)	23	31	31	15	12 (12)	0.11 (0.11)	85 (48)	83
UWM	-0.975	0.028	490	2.8 (1.0)	63	11	21	5	11 (9)	0.14 (0.13)	103 (58)	22
UWU	0.187	-0.205	525	2.4 (0.7)	47	5	26	21	11 (9)	0.16 (0.15)	159 (98)	26

Table 3.2

Table 3.2. Statistically significant thinning functions by cohort and site where the model structure was ln(mass) =a*ln(density) + b. Reported are the site and cohort, the sample size (n visits), the slope of the linear function (a), the intercept (b), the standard errors of a and b (SE), the P-value of the regression equation (P), and the coefficient of determination (r^2).

Site	Cohort	n	a	SE	b	SE	P	r^2
LLU	subyr	7	-.452	.0972	1.24	.263	.0060	.81
UMU	subyr	8	-.384	.152	.382	.393	.040	.52
ULU	yr	10	-.273	.0782	2.57	.296	.0080	.60

Table 3.3

Table 3.3. The effects of time on cohort thinning. The model structure was ln(mass) =a*ln(density) + b. See Table 1 for statistics. Asterisk* denotes significance at $\alpha=0.05$ level.

Year	Visit	Cohort	n	a	SE	b	SE	P	r^2
2010	June	subyr	no data						
	July	subyr	16	0.162	0.133	1.62	0.386	0.245	0.095
	August	subyr	16	0.0195	0.115	1.70	0.319	0.867	0.0021
	September	subyr	16	-0.173	0.127	1.51	0.370	0.193	0.12
	October	subyr	15	0.249	0.204	2.88	0.580	0.244	0.10
	June	yr	13	-0.229	0.114	2.61	0.431	0.0700	0.27
	July	yr	13	-0.344	0.0942	2.51	0.343	0.00380*	0.55
	August	yr	15	-0.198	0.0754	2.75	0.344	0.0210*	0.35
	September	yr	14	-0.088	0.0859	3.31	0.361	0.326	0.081
	October	yr	15	-0.232	0.105	2.89	0.441	0.0460*	0.27
2011	June	subyr	no data						
	July	subyr	15	-0.251	0.110	0.824	0.296	0.0390*	0.29
	August	subyr	16	-0.226	0.0871	1.28	0.252	0.0210*	0.32
	September	subyr	15	-0.171	0.0940	1.59	0.271	0.0910	0.20
	October	subyr	15	-0.207	0.0950	1.62	0.303	0.0490*	0.27
	June	yr	15	-0.200	0.0611	3.01	0.220	0.00600*	0.45
	July	yr	14	-0.193	0.0500	3.06	0.199	0.00230*	0.55
	August	yr	15	-0.116	0.0897	3.48	0.384	0.219	0.11
	September	yr	14	-0.028	0.0670	3.81	0.295	0.686	0.014
	October	yr	15	-0.148	0.126	3.41	0.513	0.260	0.096

Table 3.4

Table 3.4. Model selection results for the habitat-slope analyses for the subyearling and yearling cohorts.

Cohort	Model	K	RSS	AICc	Δ_i	w_i
Subyr	substrate	3	2.505	-23.6671	2.53	0.15
	riffle + depth	4	2.243	-21.7973	4.40	0.06
	pool + depth	4	2.140	-22.5491	3.65	0.09
	combination	3	2.139	-26.1961	0	0.53
	velocity + run	4	2.164	-22.3710	3.83	0.08
	velocity + substrate	4	2.129	-22.6314	3.56	0.09
	global	9	1.932	12.1739	38.4	0.00
Yr	substrate	3	0.0582	-77.0905	0	0.86
	riffle + depth	4	0.155	-58.5809	18.5	0.00
	pool + depth	4	0.153	-58.8010	18.3	0.00
	combination	3	0.190	-59.3188	17.8	0.00
	velocity + run	4	0.183	-56.1308	21.0	0.00
	velocity + substrate	4	0.0576	-73.4409	3.65	0.14
	global	9	0.0346	-39.0961	38.0	0.00

Table 3.5

Table 3.5. Characteristics of the best approximating models of the habitat-slope analyses for both subyearling and yearling steelhead.

Cohort	Model structure	SE	β_0 (SE)	β_1 (SE)	R^2
subyr	$\beta_0 + \beta_1$ combination	0.391	0.184 (0.150)	-0.694 (0.447)	0.15
yr	$\beta_0 + \beta_1$ substrate	0.0669	0.239 (0.0575)	-0.00226 (0.000420)	0.70

Table 3.6

Table 3.6. Model selection results for the bioenergetics-slope analyses for the subyearling and yearling cohorts.

Cohort	Model	K	RSS	AICc	Δ_i	w_i
subyr	June 2010	3	2.473	-23.8768	6.02	0.02
	July 2010	3	1.893	-28.1506	1.74	0.15
	August 2010	3	2.253	-25.3619	4.53	0.04
	September 2010	3	2.470	-23.8945	6.00	0.02
	October 2010	3	2.496	-23.7284	6.17	0.02
	June 2011	3	2.464	-23.9349	5.96	0.02
	July 2011	3	2.328	-24.8382	5.06	0.03
	August 2011	3	2.293	-25.0854	4.81	0.03
	September 2011	3	2.456	-23.9847	5.91	0.02
	October 2011	3	2.506	-23.6654	6.23	0.02
	July 2010 + July 2011	4	1.408	-29.2480	0.65	0.27
	July 2010 + Aug 2010	4	1.352	-29.8950	0	0.37
	July 2011 + Aug 2011	4	2.209	-22.0404	7.85	0.01
	Global	14	0.685	391.588	421	0.00
yr	June 2010	3	0.164	-61.5853	0	0.18
	July 2010	3	0.177	-60.4366	1.15	0.10
	August 2010	3	0.180	-60.1263	1.46	0.09
	September 2010	3	0.182	-60.0227	1.56	0.08
	October 2010	3	0.189	-59.3983	2.19	0.06
	June 2011	3	0.182	-59.9807	1.60	0.08
	July 2011	3	0.181	-60.0378	1.55	0.08
	August 2011	3	0.186	-59.6687	1.92	0.07
	September 2011	3	0.189	-59.4248	2.16	0.06
	October 2011	3	0.191	-59.2818	2.30	0.06
	July 2010 + July 2011	4	0.176	-56.6749	4.91	0.02
	July 2010 + Aug 2010	4	0.176	-56.6912	4.89	0.02
	July 2011 + Aug 2011	4	0.140	-60.1625	1.42	0.09
	Global	13	0.0488	300.070	362	0.00

Table 3.7

Table 3.7. Characteristics of the best approximating models of the bioenergetics-slope analyses by cohort.

Cohort	Model structure	SE	β_0 (SE)	β_1 (SE)	β_2 (SE)	R^2
Subyr	$\beta_0 + \beta_1$ July2010	0.368	3.68 (1.73)	-0.0166 (0.0078)		0.25
	$\beta_0 + \beta_1$ July2010 + β_2 July2011	0.329	4.00 (1.55)	-0.0489 (0.0170)	0.0318 (0.0150)	0.44
	$\beta_0 + \beta_1$ July2010 + β_2 August2010	0.323	2.20 (1.65)	-0.0622 (0.0212)	0.0517 (0.0227)	0.46
Yr	$\beta_0 + \beta_1$ June2010	0.112	-0.702 (0.434)	0.00341 (0.00230)		0.14
	$\beta_0 + \beta_1$ July2010	0.117	-0.645 (0.564)	0.00266 (0.00256)		0.08
	$\beta_0 + \beta_1$ August2010	0.118	-0.604 (0.612)	0.00243 (0.00274)		0.06
	$\beta_0 + \beta_1$ September2010	0.118	-0.440 (0.457)	0.00192 (0.00229)		0.05
	$\beta_0 + \beta_1$ June2011	0.118	-0.404 (0.426)	0.00182 (0.00224)		0.05
	$\beta_0 + \beta_1$ July2011	0.118	-0.470 (0.488)	0.00192 (0.00227)		0.05
	$\beta_0 + \beta_1$ August2011	0.120	-0.356 (0.483)	0.00133 (0.00217)		0.03
	$\beta_0 + \beta_1$ July2011 + β_2 August2011	0.108	-0.575 (0.449)	0.0335 (0.0168)	-0.0301 (0.0158)	0.27

CHAPTER 4: AGE-SPECIFIC DENSITY DEPENDENCE AND ITS IMPACT ON INDIVIDUAL GROWTH RATES FOR A STREAM SALMONID

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ABSTRACT

Density dependence is manifested in population vital rates and can regulate population size directly through mortality or indirectly via altered birth rates. In organisms with flexible and indeterminate growth, density dependence can be a fundamental mechanism of population regulation due to its control over individual survival, fecundity, and life history expression. Recent work suggests that individual growth rates can be depressed even at low population densities in stream salmonids, which warrants examination in populations previously assumed to be below carrying capacity. We used linear mixed effect models and data from spatially extensive and temporally intensive monitoring of a threatened population of steelhead (*Oncorhynchus mykiss*) to investigate the effects of cohort and population densities on individual growth rates (n = 1229 subyearlings and 983 yearlings) in a tributary watershed to the Clearwater River in Idaho, USA. We found that growth rates in both age classes were negatively related to the total population densities, but that growth rates in one age class were inconsistently affected by the densities of the other age class. Whereas subyearling growth rates were negatively related to yearling densities, the opposite situation was not the case. The best approximating models for both subyearling and yearling steelhead also included individual mass and average mass in each cohort. Because of substantial spatial and temporal variation in densities, more of the overall variance in the models was induced by this clustering ($60\% < \eta < 85\%$) than by the fixed effects model structure. Our results demonstrate that density dependence can pose constraints on individual growth rates at low densities (< 1 fish m^{-2}), and underscore the importance of considering age classes separately when studying density dependence in age-structured populations.

INTRODUCTION

Identifying the patterns and processes of population growth is one of the primary interests in ecology (Turchin 1995). The distribution and abundance of organisms depends on a combination of abiotic and biotic factors (Karels and Boonstra 2000), but *regulation* only occurs when the population growth rate depends on its own density (Turchin 1995, Sinclair and Pech 1996, Sibly and Hone 2002). In many applications it is necessary to decompose the effects of density on the population growth rate into its constituents, primarily death and birth rates (Hixon et al. 2002). Whereas mortality and reproduction *directly* affect the numbers of individuals, other responses such as density-dependent changes in individual growth rate or movement, are *indirect*, and must lead to changes in mortality rate or reproductive success if they are to affect population size (Rose et al. 2001).

Detecting density-dependence in a population over shorter time intervals than their lifespan is however a difficult subject (Walters and Post 1993, Rose et al. 2001), but has received much attention in agronomy, forestry, and other applications where there is an optimal density-yield relationship for a given size structure (Westoby 1984). In mobile organisms, the best studied systems are longer-lived species with determinate growth and low fecundity (e.g. Clutton-Brock and Sheldon 2010). Although less studied, recent work in populations of stream salmonids suggests that population density acts primarily on movement and mortality at high densities, whereas the effects on individual growth are stronger at lower densities (Elliott 1994, Grant and Imre 2005, Einum et al. 2006, Lobón-Cerviá 2007).

Density-dependent growth is a fundamental mechanism of population regulation in organisms with flexible and indeterminate growth (Sogard 1997, Rose et al. 2001, Einum et al. 2006). Jenkins et al. (1999) found stronger negative effects of density on brown trout mass at densities < 1 fish m^{-2}, and that subyearling growth was more affected than that of yearling fish. Further, in a meta-analysis of 19 stream salmonid populations, Grant and Imre (2005) found significant decreases in growth rates with increasing densities in 15 populations, with most of the decrease occurring at densities < 1 fish m^{-2}. The ramifications can have profound consequences for fitness (Sogard 1997). For instance, studies have found that survival increases with smolt size in steelhead (Ward and Slaney 1988), coho (Quinn and Peterson 1996), and resident rainbow trout (Meyer and Griffith 1997).

Density dependence is often neglected in studies of small or threatened and endangered populations because it is often assumed to be of lesser importance than stochastic, density-independent factors limiting population size (Achord et al. 2003, Lobón-Cerviá 2007). However, with the potentially strong influence of density on individual growth rates, and subsequent consequences for life history expression and fitness, it is important to consider these effects at the individual level. Here we study the effects of population density on individual growth rates in juvenile cohorts of steelhead (*Oncorhynchus mykiss*) in a population listed as threatened under the Endangered Species Act (NMFS 2006). Previous research on regulation in this population showed little evidence of density dependent mortality (Myrvold and Kennedy in press). Due to differing ecology and habitat use among cohorts (Bjornn and Reiser 1991, Rosenfeld and Boss 2001), we hypothesize that individual growth rates in both subyearling and yearling steelhead are negatively related to the density of their cohort (Imre et al. 2005), and subyearlings being more negatively affected by yearlings than *vice versa* (Kaspersson and Höjesjö 2009).

MATERIAL AND METHODS

Study area and population

The Lapwai watershed is situated in North-Central Idaho and drains an area of 694 km^2 (Figure 1). The four main tributaries drain the north slopes of Craig Mountain (1530 m) through steep canyons before emptying into the Clearwater River (237 m). The predominant geology in the watershed is Columbia River basalt, with a band of Idaho Batholith in the upper, high elevation portion. The plateau above the escarpment is overlain with loess, and the predominant land use is dry land grain crops, which covers 34% of the entire watershed. Coniferous forests cover 29%, primarily at higher elevations above the prairie, and grasslands dominate the steep canyon sides and valley floors

(Homer et al. 2007). Mean annual precipitation is 490 mm, with higher amounts falling at higher elevations, primarily from October through May. The watershed is designated as critical habitat for wild Snake River steelhead (NMFS 2006) and there is no hatchery supplementation. Other fish species include, in order of abundance, longnose dace (*Rhinichtys cataractae*), sculpin (*Cottus* spp.), bridgelip sucker (*Catostomus columbianus*), redside shiner (*Richardsonius balteatus*), northern pikeminnow (*Ptychocheilus oregonensis*), and chiselmouth (*Acrocheilus alutaceus*). In recent years juvenile coho salmon (*Oncorhynchus kisutch*) have been stocked as part of a supplementation program in lower reaches of the system, but are generally not sympatric in space or time with steelhead.

We defined the study sites using a hierarchical stratified random approach (Frissell et al. 1986) to capture a gradient of physiographic (topography, geology, and land cover) and land use conditions within and across the four streams in the Lapwai watershed. At the largest spatial level, a general area (typically one stream-kilometer in length) was identified informed by *O. mykiss* occurrence (Chandler & Parot 2003), distance to other study reaches, tributary inputs, and known spring inputs. Within these sections we further narrowed the search by means of dividing the general area into as many representative 100 m reaches as possible, informed by land use, land cover, and channel constraints such as levees and channelization. We randomly chose one of these reaches and kept it as a study site for the duration of the study.

Steelhead sampling methods and data

Field data were collected over five visits each year from 2010 to 2012. We began fish sampling when the flows were low enough to permit efficient electrofishing. We set block nets to ensure a closed population, and conducted three-pass depletion electrofishing using a Smith-Root LR-24 backpack electroshocker (Smith-Root Inc., Vancouver, WA). To reduce the stress of capture and handling on fish, we conducted the sampling during early morning hours when the water temperatures did not exceed 18 ^{o}C. We set the voltage, frequency, and duty cycle within 20% of their mean values of 350 V, 30 Hz, and 15%, respectively. We held the juvenile steelhead in buckets filled with aerated stream water at ambient stream temperatures. Prior to any handling we anesthetized the fish with tricaine methanesulfonate (MS-222). We measured fork length in millimeters and weight to the nearest decigram. Steelhead were scanned for PIT tags using a FS-2001F-ISO reader (Destron Fearing, St.

Paul, MN) and data on the individuals were recorded in program P3 (PIT-Tag Information System for the Columbia Basin). For untagged individuals 65 mm and larger we inserted 134.2 kHz PIT tags (Biomark Inc., Boise, ID) into the ventral body cavity posterior to the tip of the pectoral fin. Prior to release, fish were first allowed to recover in buckets with aerated water, and were then moved to a live-well placed in the stream channel outside the sampling reach. Upon completion of sampling, we removed the block nets and released fish back to the study reach. Seven sites were only sampled in 2010 and 2011, the rest were sampled in all three years (Figure 1).

We calculated densities using Carle and Strub's (1978) weighted maximum likelihood estimator of *K*-pass removal data. Due to the small size and low discharge of these streams we obtained very high capture probabilities (season averages ± SD were 0.63 ± 0.14 in 2010, 0.62 ± 0.13 in 2011, and 0.64 ± 0.13 in 2012) and consequently narrow confidence intervals around our population estimates. Growth rates from recaptured individuals were calculated as percent change in body mass per day between capture events.

Candidate models

We build model structures *a priori* to test hypotheses of density dependence within and between age classes. We used three types of density measurements (all expressed as no. per m^{-2}) as predictor variables for each of these responses, namely total density, cohort density, and density of the other cohort (i.e. yearling density for subyearlings, and *vice versa*). Further, we added the covariates individual mass (*g*) and average cohort mass (*g*) to these three base models (Table 1), as these are proven important in the literature (Fausch 1984, Bjornn and Reiser 1991, Elliott 1984, Imre et al. 2005, Kaspersson and Höjesjö 2009). For each cohort, we compared model fit separately between models using total density and cohort density as their base model structures (models a-f) and between the models using the other cohort density (models g-i) due to varying sample sizes. The fixed effects variables set up the overall model structure of density effects on growth, whereas the random effects allowed for site-level variation in the relationship. To account for varying conditions across time and space, all models were specified with a random slope and intercept term (by specifying the grouping factor year x visit x site). The random slope variable was the same as the fixed effects density variable. We truncated the dataset to only include visits with 4 or more recapture events.

Statistical analyses

Due to the clustered design and repeated measures we had to account for non-independence in the data to avoid pseudoreplication (Hurlbert 1984, Pinheiro and Bates 2000). The non-independence is induced by correlation in the grouping factor *site*. We used linear mixed effects models to model the effects of population density on individual growth rates. The linear mixed model is a generalization of the standard linear model by including a random effect term, which permits the data to exhibit correlation and nonconstant variability. In matrix notation it can be represented as

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}\gamma + \varepsilon,$$

where $\boldsymbol{y}$ denotes the vector of the observed values, $\mathbf{X}$ is the known fixed effects design matrix, β is the unknown fixed effects parameter vector, $\mathbf{Z}$ is the known design matrix for random effects, γ is a vector of the unknown random-effects parameters, and ε is an unknown random error vector whose elements are not required to be independent and homogenous (Pinheiro and Bates 2000). We used SAS v.9.2 Proc MIXED (SAS Institute, Cary, N.C.) specified with the Kenward and Roger (1997) approximation of denominator degrees of freedom in the model, and maximum likelihood as the estimator. The null model likelihood ratio test was highly significant for all models ($P < 0.001$) and we hence specified an unstructured covariance structure (Littell et al. 2006).

We used an information-theoretic criterion to assess the relative plausibility of these candidate models (Akaike 1973, Burnham and Anderson 2002). Information-theoretic data analysis is based on Kullback-Leibler information, which is the information lost when statistical models are used to approximate full truth. Akaike's information criterion (AIC) is given as

$$AIC = -2\ln\left(\ell\left(\hat{\theta}\middle|data\right)\right) + 2K,$$

where $\ln\left(\ell\left(\hat{\theta}\middle|data\right)\right)$ is the value of the maximized log-likelihood over the unknown parameters, given the data and the model, and K is the number of estimable parameters in that model. The model with the lowest AIC value is the best approximating model of the data. The models i were ranked using the simple AIC differences, Δ_i, given as $\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{\min}$. To make interpretation and inference easier, we normalized the likelihood functions of the models so that they sum to 1. The probability of model i being the best approximating model in the set is called the Akaike weight (w_i), and is given as

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R} \exp\left(-\frac{1}{2}\Delta_i\right)}$$

Within each cohort we provided parameter estimates for models with strong relative support (i.e. $w_{max}/w_i < 2$) for models a-f and g-i, respectively.

RESULTS

Densities of both subyearling and yearling age classes varied considerably between and within study sites (Figure 2). The densities of subyearlings were always higher than those of yearling fish, but their combined numbers were always less than one individual m^{-2}. Within each site there was considerable variation over time, represented by the error bars. Individual growth rates were on average higher for subyearling steelhead (Figure 3), with considerable variation within and among sites.

In order assess the effects of cohort density on individual growth rates we had to account for the variation in densities over time. Comparing models *a-f* for the effects of density on subyearling growth rates, the subyearling model containing total density, individual mass, and average cohort mass received the most relative support (Table 2; model c, $w_i = 0.47$), as did the model containing total density and individual mass (model b, $w_i = 0.36$). Among the models relating subyearling growth to the density of yearling steelhead (h-i), the model containing yearling density and individual mass received the most relative support (model h, $w_i = 0.72$). In all cases the relationships between individual growth rate and densities were negative (Table 4).

The same three model structures proved to be the best approximating models of the effects of density on yearling growth rates (Table 3). The best approximating model (Table 3; model b, $w_i = 0.52$) was marginally better than the second best model (model c, $w_i = 0.39$), both relating individual yearling growth rates to the total density of steelhead. The best approximating model of the models relating yearling growth rates to subyearling densities (model h, $w_i = 0.88$) showed a positive relationship with subyearling density (Table 4).

Most of the overall variation in the density-growth models was induced by the site-level random effect slope ($60\ \% < \eta < 85\ \%$ in all the AIC-best models, with the exception of yearling model h). This results from the large variation in densities across both space and time.

DISCUSSION

Our results support the prediction that individual growth rates were negatively affected by the population density even at the relatively low population densities in our study system. Further, our results showed that growth rates in the younger age class were negatively related to densities of older fish, but not *vice versa*. Because we accounted for spatial and temporal correlation in the modeling we feel confident that the patterns reflect true density dependent processes.

Density dependent growth occurs when individual feeding rates are depressed due to the presence of conspecifics (Rose et al. 2001). In stream salmonids, results from previous studies (Grant and Imre 2005, Einum et al. 2006) suggest that population density primarily affects individual *dispersal* at high densities, whereas it is manifest in *growth rates* at lower (< 1 fish m^{-2}) densities, i.e. growth rates are negatively related to density up to approximately 1 fish m^{-2}, after which increased dispersal is the main population vital rate that changes. Jenkins et al. (1999) combined a multiscale field study with experimental manipulations, and found that density negatively affected individual growth rates more strongly at densities < 1 fish m^{-2}, and that the negative changes in subyearling growth rates were larger than in yearling fish. Grant and Imre (2005) conducted a meta-analysis of 19 populations of stream-dwelling salmonids to explore whether growth rates are depressed at such lower population densities. In the majority of these populations, density dependence manifested itself in depressed growth rates, with the strongest reduction in growth rates occurring at densities < 1 fish m^{-2}. Taken together, the present study as well as previous studies demonstrate that population densities can influence individual performance even at low densities.

The role of individual performance on population dynamics is receiving increased attention as a driver of ecological and evolutionary processes (DeRoos et al. 2003, DeAngelis and Mooij 2005). Because growth rates are largely indeterminate in fishes, density-dependent changes in growth rate are indirect and must ultimately lead to changes in mortality rate or reproductive success if they are to affect population size (Rose et al. 2001). Density-dependent growth can result in decreased survival *via* prolonged stage duration, which can increase predation risk and size-dependent mortality (Werner and Gilliam 1984), and reproductive success through altered fecundity, egg quality, and spawning location (Einum and Fleming 1999, Morita and Takashima 1998, Rose et al. 2001). Although anadromous salmonids depend on more than juvenile rearing habitat to complete a generation, rapid growth and large body size has been shown to confer fitness advantages through increased survival (Ward and Slaney 1988, Ward et al. 1989, Kahler et al. 2001). The relatively poorer survival of smaller smolts could be offset by a larger outmigrating cohort and increased feeding opportunities in the ocean (closing the size gap between large and small smolts), however, such compensation might not apply where migration corridors are largely altered such as the Columbia River (Quinn 2005).

The primary mechanism for density-dependent growth is competition, and in territorial stream salmonids the primary resources are access to space (interference competition, Grant and Kramer 1990) and food (exploitative competition, Bohlin et al. 1994). Competition imposes a net negative effect on individual performance, and is usually asymmetric, i.e. it affects some individuals more than others (Jenkins 1969, Keeley 2001). Our results were similar to Kaspersson and Höjesjö (2009), who found that the presence of yearling fish led to a reduction in subyearling growth rate, but not *vice versa*. Within age classes, we found that growth rates were negatively related to mass, which is contrary to many previous studies which have found larger individuals to be superior competitors (e.g. Holtby et al. 1990). Although our data were of high resolution, we could not attribute our findings to any one or any portion of either of the above mechanisms (Ward et al. 2007). However, the abiotic environment can mediate biotic responses (DeAngelis and Mooij 2005). Previous work in the watershed found that bioenergetic constraints due to temperature and food limitation increased with fish size (Myrvold and Kennedy *in press*), which provides a potentially strong mechanism limiting individual growth.

Effective management of imperiled biota requires a comprehensive examination of factors influencing population vital rates (Hixon et al. 2002, Sibly and Hone 2002). Because the consequences of density dependence are easier detected at high densities, many studies have focused on its effect on mortality and emigration. One partially neglected effect is that density dependence can affect vital rates also in small populations (Achord et al. 2003). In stream salmonids, several studies have shown that intraspecific competition can have important consequences for individual growth even at low densities (Jenkins et al. 1999, Grant and Imre 2005, Imre et al. 2005, Lobón-Cerviá 2007). Because individual growth is particularly important for individual fitness in organisms with flexible and indeterminate growth such as stream salmonids (Sogard 1997, Rose et al. 2001), density dependence at low densities can have important consequences for population regulation (Jenkins et al. 1999, Einum et al. 2006).

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FIGURES AND TABLES

Figure 4.1

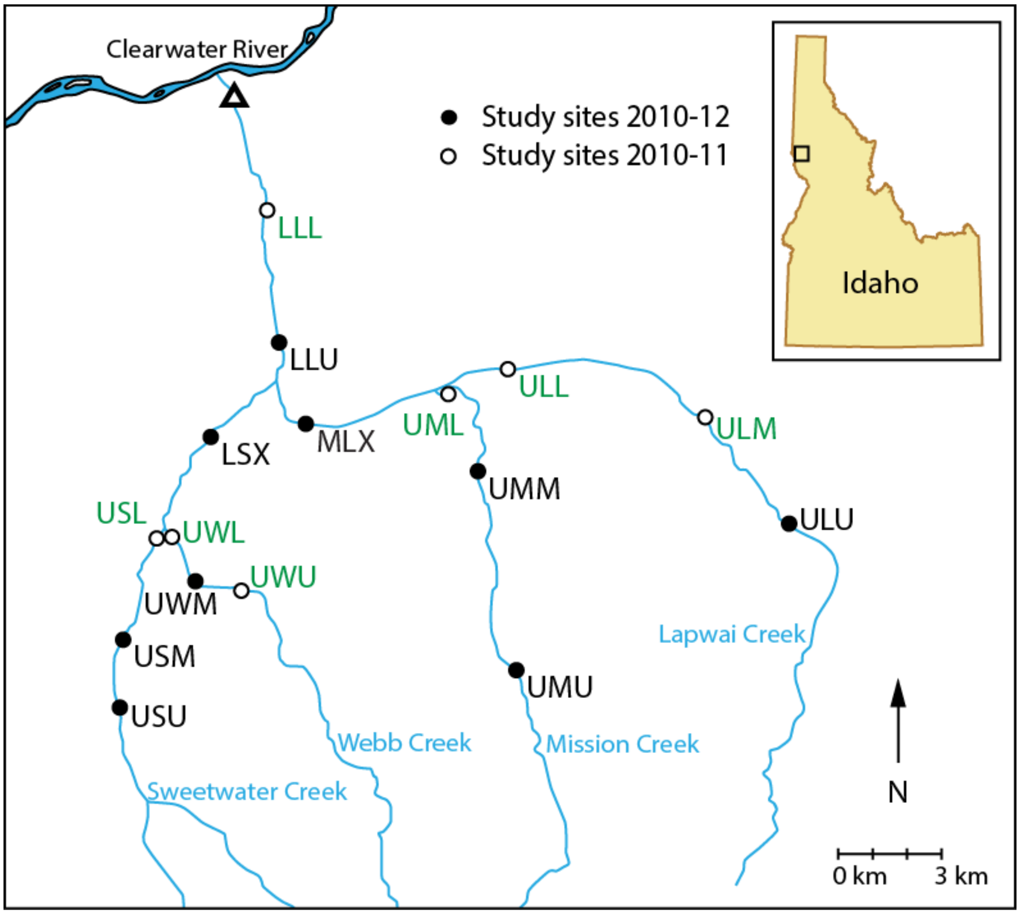

Figure 4.1. The map shows the four major streams of the Lapwai watershed and its location in North-Central Idaho, United States (insert). All 16 study sites were sampled in 2010 and 2011, whereas seven of these (open circles) were discontinued in 2012.

Figure 4.2

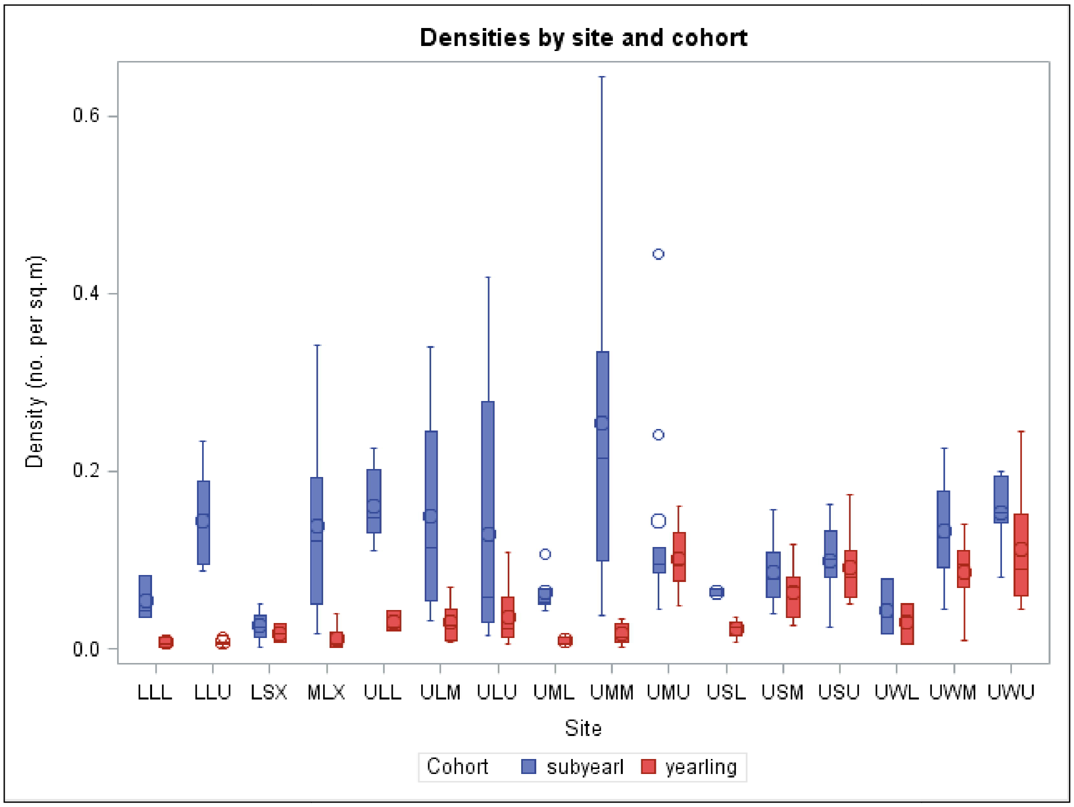

Figure 4.2. Densities (m^{-2}) of subyearling (blue bars) and yearling (red bars) steelhead estimated (Carle and Strub 1978) for the study sites in the Lapwai Creek watershed between 2010 and 2012.

Figure 4.3

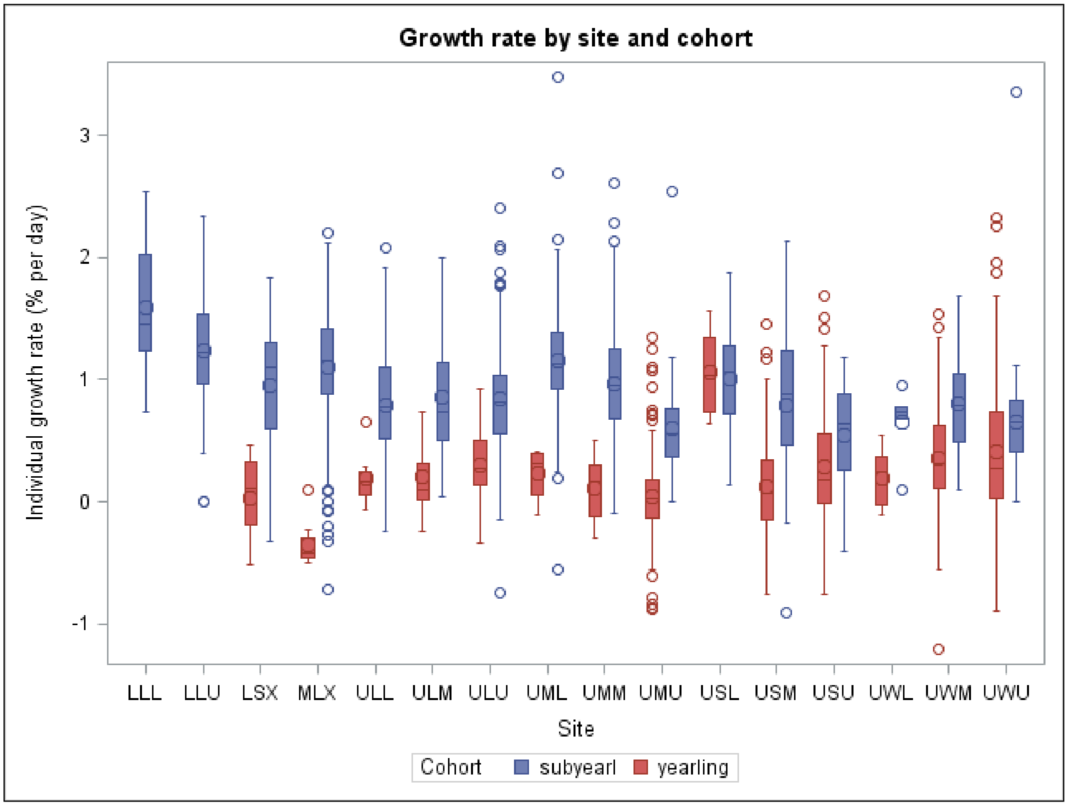

Figure 4.3. Growth rates (% change in body mass day^{-1}) of individually tagged subyearling (blue bars, n = 1229) and yearling (red bars, n = 983) steelhead in the Lapwai Creek watershed between 2010 and 2012. The growth histories are grouped by study site, and the variation within each site reflects individual variation.

Table 4.1

Table 4.1. Candidate model structures considered for the study of density-dependent growth in juvenile steelhead. The two cohorts subyearling and yearling were analyzed separately.

ID	Model rationale	Fixed effects
a	Test how the total density of steelhead influences the growth rate in individual fish when controlling for site and time effects	Total density
b	In addition to a), test how the individual's mass influences its growth rate	Total density, mass
c	In addition to b), test the effects of cohort average body size on individual growth rates	Total density, mass, average cohort mass
d	Test how cohort density influences the growth rate in individual fish when controlling for site and time effects	Cohort density
e	In addition to d), test how the individual's mass influences its growth rate	Cohort density, mass
f	In addition to e), test the effects of cohort average body size on individual growth rates	Cohort density, mass, average cohort mass
g	Test how the density of the other cohort influences the growth rate in individual fish when controlling for site, year, and time effects	Other cohort density
h	In addition to g), test how the individual's mass influences its growth rate	Other cohort density, mass
i	In addition to h), test the effects of cohort average body size on individual growth rates	Other cohort density, mass, average cohort mass

Table 4.2

Table 4.2. Model selection results for subyearling steelhead for models a-f and g-I, showing the model structure, sample size (n individuals), number of estimable parameters (K), the likelihood of the model (ℓ(i|x)), the AIC value, the simple AIC differences (Δ_i), and the Akaike weight (w_i).

ID	Fixed effects	n	K	ℓ(i|x)	AIC	Δ_i	w_i
a	β_1 total density	1229	4	0.00	1310.6	15.1	0.00
b	β_1 total density, β_2 mass	1229	5	0.78	1296	0.5	0.36
c	β_1 total density, β_2 mass, β_3 average cohort mass	1229	6	1.00	1295.5	0	0.47
d	β_1 cohort density	1229	4	0.00	1313.7	18.2	0.00
e	β_1 cohort density, β_2 mass	1229	5	0.14	1299.5	4	0.06
f	β_1 cohort density, β_2 mass, β_3 average cohort mass	1229	6	0.23	1298.4	2.9	0.11
g	β_1 yearling density	1134	4	0.00	1279.2	118.9	0.00
h	β_1 yearling density, β_2 mass	1134	5	1.00	1160.3	0	0.72
i	β_1 yearling density, β_2 mass, β_3 average cohort mass	1134	6	0.39	1162.2	1.9	0.28

Table 4.3

Table 4.3. Model selection results for yearling steelhead for models a-f and g-i. See Table 2 for description of statistics.

ID	Fixed effects	n	K	ℓ(i|x)	AIC	Δ_i	w_i
a	β_1 total density	983	4	0.00	762.1	51.3	0.00
b	β_1 total density, β_2 mass	983	5	1.00	710.8	0	0.52
c	β_1 total density, β_2 mass, β_3 average cohort mass	983	6	0.74	711.4	0.6	0.39
d	β_1 cohort density	983	4	0.00	767.1	56.3	0.00
e	β_1 cohort density, β_2 mass	983	5	0.12	715.1	4.3	0.06
f	β_1 cohort density, β_2 mass, β_3 average cohort mass	983	6	0.06	716.5	5.7	0.03
g	β_1 subyearling density	661	4	0.00	454.2	35	0.00
h	β_1 subyearling density, β_2 mass	661	5	1.00	419.2	0	0.88
i	β_1 subyearling density, β_2 mass, β_3 average cohort mass	661	6	0.14	423.1	3.9	0.12

Table 4.4

Table 4.4. Parameter estimates for the best approximating models for both subyearling and yearling steelhead. The table shows the model residual error (ε), the sum of variance for fixed and random effects (Var.), the proportion that variance which is caused by the model structure (% ε) and the random effects slope (% η), respectively, and the parameter estimates (β) with associated standard errors (SE) of the fixed effects variables.

Chrt.	ID	ε	Var.	% ε	% η	β_0 (SE)	β_1 (SE)	β_2 (SE)	β_3 (SE)
Sub.	b	0.140	2.84	5	60	1.11 (.0990)	-0.587 (.385)	-0.0197 (.00480)	
	c	0.140	3.07	5	60	0.871 (.173)	-0.314 (.00491)	-0.0213 (.00491)	0.0338 (.0214)
	h	0.137	20.0	1	88	1.14 (.0764)	-3.71 (.923)	-0.0234 (.00512)	
Yr.	b	0.102	4.43	2	85	0.399 (.0720)	-0.347 (.449)	-0.00398 (.00054)	
	c	0.102	4.60	2	85	0.312 (.104)	-0.324 (.447)	-0.00413 (.00055)	0.00268 (.00232)
	h	0.092	0.429	21	0	0.273 (.0542)	0.470 (.549)	-0.00351 (.0006)	

CHAPTER 5: A COMBINATION OF WATERSHED CHARACTERISTICS AND IN-STREAM HABITAT FACTORS EXPLAIN THE SPATIAL VARIATION IN DENSITIES OF JUVENILE STEELHEAD

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ABSTRACT

Habitat characteristics can affect the abundance and distribution of species, and are frequently used to predict the standing crop of stream fishes for purposes of understanding their ecology and better direct management. However, the scale of the investigation and the resolution of the data can hence largely affect the results of such an analysis. Using mixed-effects models we coupled metrics of watershed level topography, geology, land cover, and land use with in-stream habitat variables to model the densities of cohorts of juvenile steelhead, *Oncorhynchus mykiss*, in a tributary watershed to the Clearwater River, Idaho. When comparing all models, models that combined watershed-scale topography and instream-scale variables pertaining to flow (velocity and discharge) performed better in describing densities of subyearling steelhead and total densities, whereas the instream-scale model flow velocity was the single best approximating model (w_2 = 0.97) of yearling densities. A quadratic model of flow velocity was either the single best or among the best approximating instream-scale models for both subyearling and yearling steelhead, depicting a downward concave relationship in both cases. Effective management and conservation of stream ecosystems would

benefit from a quantitative means to relate instream processes to watershed-level characteristics due to the nested hierarchy of physical processes. We believe our approach is useful for identifying the physical factors that partly determine the variation in stream salmonid densities, but caution against assuming causation and stress that correlative studies should be interpreted in concert with detailed knowledge about life history variation in the study system.

INTRODUCTION

Identifying the principal determinants of population abundance is one of the main questions in ecology, and also one of the most widely disputed (Nicholson 1933, Andrewartha and Birch 1954). The discussion has centered on the question of whether and how populations are regulated at their upper limits by factors that slow down the intrinsic rate of increase (Begon et al. 1996, Hixon et al. 2002). While it is clear that density dependent processes are necessary to *regulate* a population (Murdoch 1994, Turchin 1995), their importance in *determining* abundance is much more contingent on the species' life history characteristics and the environment it inhabits, in which factors that act independent of population density can strongly limit its size. Abundance is hence determined by the combined effect of all factors and processes that act on the population, dependent or independent of its density (Begon et al. 1996, Sinclair et al. 2005).

Highly fecund organisms such as anadromous stream salmonids are a particularly suitable study system to test the role of environmental constraints on population size. Their high fecundity, being realized by productive feeding opportunities in the ocean, has the potential to saturate the stream environment with offspring (Bjornn and Reiser 1991). Further, juveniles have highly stage-structured habitat requirements depending on age (Bjornn and Reiser 1991, Rosenfeld and Boss 2001), and their life history causes some fraction of the population to outmigrate prior to the recruitment of a new cohort. Density cannot be used as a single metric of habitat quality (VanHorne 1983, Gaillard et al. 2010), however, if patterns of spatial density differences are consistently associated with a range of certain habitat factors, it suggests these factors are important (Pess et al. 2002, Fausch 2010).

The basic premise when studying habitat relationships is that certain habitat features produce some response in an organismal metric, such as fish density, because they confer some fitness advantage (MacArthur and Pianka 1966, Rosenzweig 1981, Gaillard et al. 2010). Because of their effects on growth, survival and reproduction, much effort has been devoted to understanding the mechanisms through which environmental conditions affect stream salmonids (Bjornn and Reiser 1991). This has primarily been conducted at the scale of microhabitats (0.1 m) to stream segments (100 m; Frissell et al. 1986), and the most important variables include depth, cover, flow velocity, and substrate (Everest and Chapman 1972, Heggenes 1988, Beecher et al. 1993, Chun et al. 2011). Large-scale physical factors and land use practices control the distribution of these site-specific stream habitat characteristics (Frissell et al. 1986, Richards et al. 1996, Wiley et al. 1997, Johnson et al. 2000, Allan 2004), and the nesting in this hierarchy can be utilized for understanding distribution patterns on broader spatial scales (Wiens 1989, 2002). For example, watershed geology can influence salmonid rearing habitat potential by constraining the morphological characteristics of stream reaches resulting in spatial variation in habitat productivity beyond what could be predicted by channel-level metrics alone (Burnett 2001, Hicks and Hall 2003, Coulombe-Pontbriand and Lapointe 2004, Montgomery 2004).

In this study we couple metrics of watershed level topography, geology, land cover, and land use with in-stream habitat variables to model the densities of juvenile steelhead, *Oncorhynchus mykiss*, in a tributary watershed to the Clearwater River, Idaho. We develop mixed effects models based on habitat factors deemed important for stream salmonids in the literature and confront them with steelhead density data from a spatially extensive and temporally intensive monitoring approach. While acknowledging that habitat factors alone cannot explain all the variation in abundances, we were driven by identifying which factors are more important in predicting the standing crop of rearing juveniles at the scale of the watershed, the instream channel, and a combination of the two. We expect the cohort densities to be determined by different factors pertinent to both habitat preferences and ontogenetic changes.

MATERIAL AND METHODS

Study area and population

The four main streams in the Lapwai watershed (694 km^2) drain the north slopes of Craig Mountain (1530 m), carve steep canyons through the landscape, and empty into the Clearwater River (237 m) (Fig. 1). The predominant geology in the watershed is Columbia River basalt, with a band of Idaho

Batholith in the upper, high elevation portion. The plateau above the escarpment is overlain with loess, and the predominant land use is dry land grain agriculture, which covers 34% of the watershed. Coniferous forests cover 29%, primarily at higher elevations above the prairie, and grasslands dominate the steep canyon sides and valley floors. Mean annual precipitation is 490 mm, with larger amounts falling at higher elevations. Five percent of the watershed area is classified as urban, i.e. developed for housing and infrastructure (Homer et al. 2007). Flood control levees and infrastructure have channelized the mainstem reaches (Richardson and Rasmussen 2007) and prevent connectivity with the floodplain (Williams 2011).

Other fish species include, in order of abundance, longnose dace (*Rhinichtys cataractae*), sculpin (*Cottus* spp.), bridgelip sucker (*Catostomus columbianus*), redside shiner (*Richardsonius balteatus*), northern pikeminnow (*Ptychocheilus oregonensis*), and chiselmouth (*Acrocheilus alutaceus*). In recent years juvenile coho salmon (*Oncorhynchus kisutch*) have been stocked as part of a supplementation program in lower reaches of the system, but are generally not sympatric in space or time with steelhead. No hatchery supplementation exists for steelhead in the watershed.

We defined the study sites using a hierarchical stratified random approach (Frissell et al. 1986) to capture a gradient of physiographic (topography, geology, and land cover) and land use conditions within and across the four streams in the Lapwai watershed. At the largest spatial level, a general area (typically one stream-kilometer in length) was identified informed by *O. mykiss* occurrence (Chandler & Parot 2003), distance to other study reaches, tributary inputs, and known spring inputs. Within these sections we further narrowed the search by means of dividing the general area into as many representative 100 m reaches as possible, informed by land use, land cover, and channel constraints such as levees and channelization.

Sampling methods and material

Steelhead densities

Field data were collected in 2010, 2011, and 2012. We set block nets to ensure a closed population, and conducted three-pass depletion electrofishing using a Smith-Root LR-24 backpack electroshocker (Smith-Root Inc., Vancouver, WA). To reduce the stress of capture and handling on fish, we conducted the sampling during early morning hours when the water temperatures did not exceed 18

^{o} C. We set the voltage, frequency, and duty cycle within 20% of their mean values of 350 V, 30 Hz, and 15 %, respectively. We held the juvenile steelhead in buckets filled with aerated stream water at ambient stream temperatures. Prior to any handling we anesthetized the fish with tricaine methanesulfonate (MS-222). Prior to release, fish were first allowed to recover in buckets with aerated water, and were then moved to a live-well placed in the stream channel outside the sampling reach. Upon completion of sampling, we removed the block nets and released fish back to the study reach. Densities were calculated using Carle and Strub's (1978) weighted maximum likelihood estimator of *K*-pass removal data. Due to the small size of these streams we obtained very high capture probabilities (season averages ± SD were 0.63 ± 0.14 in 2010, 0.62 ± 0.13 in 2011, and 0.64 ± 0.13 in 2012) and consequently narrow confidence intervals around our population estimates. Sixteen sites were sampled in the first two years, with a third year of sampling in nine sites. We expressed the population densities as the estimated number of fish per 100 m^2, which was the response variable in this study. In instances when subyearlings were not efficiently recruited to our sampling gear (lengths < 40 mm), typically at the first visit per year, we discarded the estimates from the analysis. The sample sizes were 198 for both cohorts, 198 for yearlings, and 175 for subyearlings.

Temperature, discharge, and instream habitat data

We had HOBO TidbiT v2 temperature loggers (Onset Computer Corporation, Pocasset, MA) installed at each site recording water temperatures (^{o}C) every 30 minutes. We used daily averages of temperature as the basis in the modelling.

We calculated discharge (m^3s^{-1}) at each visit by taking approximately 15 stream depth and velocity readings spaced evenly along an established transect that had near laminar flow across the entire width according to standard practices (Fisher et al. 2012). The velocity reading at each point was obtained as an average of multiple readings at 60 % of the depth using a Marsh McBirney Flo-Mate Velocity Meter (Hach Company, Loveland, CO).

We quantified the instream habitat once per year in August. We established transects perpendicular on the channel spaced 5 meter apart throughout the entire electrofishing reach. At each transect we measured wetted channel width, and counted the number of large woody debris pieces (LWD; dead wood > 100 mm diameter and 1.00 m long) in the channel. The transects were then split into 5 sections of equal width. At each point we measured the flow velocity, depth, substrate (longest axis), and visually estimated whether there was > 33 % overhanging cover with live vegetation less than

2.00 m above the water surface and/or undercut banks, above the section. The approach yielded approximately 100 point measurements of each of the physical variables as well as their location.

From these measurements we derived the variables used in the modeling of juvenile *O. mykiss* densities. Because steelhead utilize different habitat features throughout their juvenile stages, we categorized these habitat variables as considering 1) *all* point measurements in the reach, or 2) *margin* measurements only (i.e. the two measurements per transect closest to either bank). Unless otherwise indicated, the variables are derived from all point measurements. Most variables are self explanatory and have units given in Table 1. *Slow* refers to < 0.15 m/s; *shallow* refers to < 6 cm; *slow&shallow* refers to sections which include those two characteristics simultaneously; *weeklytemperature* refers to the average temperature on the 7 days prior to sampling; and *slowest* refers to the average of the slowest section of each transect.

Watershed topography, geology, land cover and land use data

Watershed data were computed in the application StreamStats (USGS 2012). StreamStats delineates drainages above specified points (here, study sites) based on a 30 m DEM, calculates slopes and elevation profiles within this polygon, and overlays the polygon on spatial datasets on land cover, land use, and geology (Vogelmann et al. 2001, Hortness 2006, Homer et al. 2007). Watershed variables were expressed as percentage cover of the drainage above a site, with the exception of area (km^2) and mean elevation of the drainage (m).

The data were collected on a time interval that reflects their rate of change as well as their relative difference among the study sites. The watershed-level data were assumed constant over the course of the study. The channel hydraulic, cover, and complexity variables were collected once per year as these change primarily during bankfull flood events after snowmelt in the spring, prior to fish sampling. Lastly, discharge and temperature vary on a daily or even hourly basis, and were hence collected during each visit (discharge) or continually (temperature).

Candidate models

We build model structures *a priori* to test hypotheses of the relationships between habitat factors and *O. mykiss* densities. We based our variable selection and model specification on published literature in steelhead and other stream salmonids (reviewed by Fausch et al. 1988, Bjornn and

Reiser 1991, Quinn 2005). Due to the differing ecology between subyearling and overyearling fish (Bjornn and Reiser 1991, Rosenfeld and Boss 2001), we modeled the cohorts separately. In addition, we modeled the total density (i.e. the sum of the two cohorts), which was natural log-transformed to ensure convergence in the algorithm.

The models were built to represent three levels of potential influence. At the smallest spatial extent, models include variables pertaining to channel hydraulics (depth, velocity, substrate), cover and complexity (undercut banks, overhanging vegetation, woody debris), temperature, and discharge. At the largest spatial extent, we build models to describe the topography, geology, land cover, and land use in the drainages above each site. To link the watershed-scale variables with the mechanistic properties of the instream-scale variables, we coupled the two levels in the third category of models (denoted *combination*; Table 1).

To avoid multicollinearity we first assessed the correlation among the variables in each model by looking at the covariance matrix with $r = 0.7$ as the cutoff. Two models had strong collinearity among the predictor variables and were eliminated from further analyses (not included in Table 1).

Statistical analyses

Due to the clustered design and repeated measures we had to account for non-independence in the data to avoid pseudoreplication (Hurlbert 1984, Pinheiro and Bates 2000). The non-independence is induced by correlation in the grouping factor *site*. The mixed effect model permits the data to exhibit correlation and non-constant variability, and consists of both fixed and random effects (Littell et al. 2006). The fixed effects variables set up the overall model structure of habitat and density relationships, whereas the random effects allow for site-level variation in the relationship (as sites have differing carrying capacity and hence support different densities). In matrix notation it can be represented as

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}\gamma + \varepsilon,$$

where $\boldsymbol{y}$ denotes the vector of the observed values, $\mathbf{X}$ is the known fixed effects design matrix, β is the unknown fixed effects parameter vector, $\mathbf{Z}$ is the known design matrix for random effects, γ is a vector of the unknown random-effects parameters, and ε is an unknown random error vector whose elements are not required to be independent and homogenous (Pinheiro and Bates 2000). We used

SAS v.9.2 Proc MIXED (SAS Institute, Cary, N.C.) specified with sampling site as the grouping factor for the random intercept; the Kenward and Roger (1997) approximation of denominator degrees of freedom in the model, and restricted maximum likelihood as the estimator. The null model likelihood ratio test was highly significant for all models ($P < 0.001$) and we hence specified an unstructured covariance structure (SAS Institute 2008).

We used an information-theoretic criterion to assess the relative plausibility of these candidate models (Akaike 1973, Burnham and Anderson 2002). Information-theoretic data analysis is based on Kullback-Leibler information, which is the information lost when statistical models are used to approximate full truth (Kullback and Leibler 1951). Akaike's information criterion (AIC) is given as

$$AIC = -2\ln\left(\ell\left(\hat{\theta}\middle|data\right)\right) + 2K,$$

where $\ln\left(\ell\left(\hat{\theta}\middle|data\right)\right)$ is the value of the maximized log-likelihood over the unknown parameters, given the data and the model, and K is the number of estimable parameters in that model. The model with the lowest AIC value is the best approximating model of the data. The models i were ranked using the simple AIC differences, Δ_i, given as $\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{min}$. To make interpretation and inference easier, we normalized the likelihood functions of the models so that they sum to 1. The probability of model i being the best approximating model in the set is called the Akaike weight (w_i), and is given as

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_i\right)}$$

We performed four comparisons for each cohort category, which pertain to the three levels of models (instream, watershed, and combination), as well as all models compared simultaneously. The rank of the various models depends on the comparison made, and these are displayed with their Akaike weights in Table 2. Within each cohort we provided parameter estimates for models with strong relative support (i.e. $w_{max}/w_i < 2$). For these models we present the estimated total variance, the proportion of the variance attributed to overall model fit (ε) and random effects (η), parameter estimates (β) and associated standard errors (SE) in Table 3.

RESULTS

Densities of the two age classes of juvenile steelhead varied considerably both among study sites and within study sites as represented by the vertical spread (Figure 2). In order to study which environmental factors that could explain this variation in density while accounting for the variation within sites, we modeled these hypothesized relationships at three spatial scales. Model likelihood results by cohort are given in Table 1, whereas model selection results are given in Table 2 in relation to the comparison made.

Instream-scale models

Among instream habitat models, densities of juvenile steelhead were better explained by variables pertaining to the entire stream width than by variables describing the stream margin habitat. Model 2, a quadratic model of flow velocity, was either the single best or among the best approximating instream-scale models for both subyearlings and yearlings (Table 2), depicting a downward concave relationship in both cases (Table 3). Model 25, an additive linear relationship with discharge and temperature, received substantial support for both total and subyearling densities, with a positive dependence on temperature and a negative dependence on discharge. The total density of juvenile steelhead was negatively related to stream discharge (model 19).

Watershed-scale models

Among the watershed models, subyearling densities were best explained by the model that depicted incised canyons (model 29, positive relationship with the proportions of volcanic rock and slopes greater than 50 %), whereas yearling densities were best explained by the mean elevation of the drainage (model 32, positive relationship). The variation in total density was better explained by model 27 (% volcanic rock, positive relationship) and model 35 (% developed land). Taken together, these models show that steelhead densities were higher at study sites higher up in the watershed, and that topographic and geological variables were generally better predictors than land cover and land use variables.

Combination models

Among models that combine watershed-scale and instream variables, model 43 was among the best approximating models for all three cohort categories, whereas model 42 was among the top two models for both total and subyearling densities. Models 42 and 43 relate drainage topography with discharge and flow velocity, and the relationship was negative with discharge and positive with flow velocity for subyearling and total densities. For yearlings, the relationship with discharge in model 43 was positive. Further, for yearling steelhead, densities were positively related to the proportion of forest cover in the drainage and the proportion of the stream covered by overhanging vegetation (model 45).

All spatial scales compared

When comparing all models, models that combined watershed-scale and instream-scale variables (42 and 43) performed better in describing densities of subyearling steelhead, whereas the instream-scale model flow velocity was the single best approximating model ($w_2 = 0.97$) of yearling densities (Table 2). These two models, together with the instream model 25 (temperature and discharge), also were the best approximating models of total density. The total variance of the models was generally split similarly between the fixed effects residual term and the random error term, with the least variation induced by site-level grouping in subyearling models (average 18 %) and the most in yearlings (average 47 %). This spatial variation in densities suggests that yearlings to a greater extent than subyearlings are patchily distributed across the watershed.

DISCUSSION

We found that the variation in densities of subyearling steelhead were best explained by a combination of watershed-level and instream-level habitat variables, and that they showed an overall sensitivity to stream discharge. Yearlings were overall best explained by the instream-level variable flow velocity, whereas drainage elevation, forest cover, and overhanging cover were most influential at the watershed-level. The total density of juvenile steelhead (subyearlings and yearlings combined) was negatively related to discharge at all levels of models, showed a positive relation to steep topography, and was negatively related to the amount of developed land (urban and infrastructure) in the above watershed.

An extensive body of literature exists to relate habitat factors to preference, densities, biomass, and distribution of stream salmonids (e.g. Fausch 1984, Fausch et al. 1988, Bjornn and Reiser 1991, Heggenes et al. 1999, Railsback and Harvey 2002). Determining which factors are causative and which are merely correlative is not a straight-forward undertaking because it is inherently ridden by the influence of study design and the spatial scale of the investigation (Feist et al. 2003), covarying biotic factors (Reeves et al. 1987, Abbott and Dill 1989, Tinus and Reeves 2001), and the size and composition of the study population (Heggenes et al. 1999, Lóbón-Cerviá 2005). However, certain variables are more mechanistic by nature, and parameter ranges have been described for most species of stream salmonids (e.g. Elliott 1994). Among these mechanistic variables, the importance of flow velocity, substrate size and depth have been pointed out by several studies (e.g. Everest and Chapman 1972, Heggenes 1988, Beecher et al. 1993, Chun et al. 2011).

Among instream variables, we found a parabolic model of average flow velocity more important in predicting yearling steelhead densities, in which a range of velocities was associated with higher densities. At the individual level, drift-feeding stream fishes are confronted with an energy expenditure-intake tradeoff in which both prey delivery rates and energy costs acquiring those resources increase with flow velocity (Fausch 1984, Hughes and Dill 1990). Scaling up to the level of stream reaches, a higher proportion of suitable microhabitats would confer a higher standing stock of individuals (Fausch et al. 1988). Subyearlings were similarly related to flow velocity, in addition to temperature and discharge. In early ontogeny, temperature has been shown to relate positively to individual growth and performance in salmonids (Elliott 1994, Lóbón-Cerviá and Mortensen 2005). Discharge can negatively affect subyearlings through displacement, cost of swimming, and sub-optimal temperatures for growth (Jensen and Johnsen 1999, Lóbón-Cerviá and Mortensen 2005). Other studies have found that subyearling steelhead tend to utilize stream margins early in summer, likely to avoid such high discharges, and then switch to riffle habitat when their swimming capabilities improve and food requirements increase (Everest and Chapman 1972, Fausch 1984). However, we found no such direct evidence in the models we tested.

At the drainage level, yearling densities were positively related to drainage elevation and the models that combine forest cover, overhanging vegetation, and discharge. These are characteristics of the study sites situated higher in the Lapwai watershed, where densities were consistently higher over the three years of study. Subyearling densities were positively related to the percentages of surficial volcanic rock and slopes greater than 50%, which corresponds to sites situated in canyons below the escarpment, but above the confluences of the tributaries. Temperatures were slightly higher in these sites, and the higher potential for lateral movement in the streams could dissipate high discharge events could likely explain the higher densities of subyearlings in these sites.

Studies that have examined the relationships between watershed characteristics and salmonid abundance have reported on a range of geological, topographic, and land cover factors (Burnett 2001, Pess et al. 2002, Thompson and Lee 2002, Feist et al. 2003, Coulombe-Pontbriand and Lapointe 2004, Reaney et al. 2011, Steel et al. 2012). Because mechanisms are not explicitly tested, and studies are conducted over large spatial extents, but in oftentimes very different ecosystems, the studies have reported a variety of results (Durance et al. 2006, Fausch 2010, Reaney et al. 2011). A critical step is hence to couple these large-scale ecological filters with a fine-scale, mechanistic understanding of fish-habitat relationships and life history variation (Armstrong 2005). For example, the higher densities of yearlings in the upper reaches of the Lapwai watershed, and relatively large variation among sites overall, might actually not reflect habitat choice *per se*, but rather a lack of growth. Previous studies have found growth to be density dependent in the system (Myrvold and Kennedy *in prep*.), owing to food limitation rather than thermal stress in these uppermost study sites (Myrvold and Kennedy *accepted*). Collectively, these density-dependent and –independent processes could cause individuals to stay longer in the parr stage in the upper sites.

This spatial variation in the expression of life history trajectories results in challenges when predicting standing stock of stream salmonids (Armstrong 2005), and must be taken into account when interpreting the results. Although mechanisms of individual habitat choice are better understood at the scale of stream channels and microhabitats, it is critical to put them into the context of watershed conditions when scaling up to population-level response metrics due to resultant variation in stream productivity and population size and -composition (Burnett 2001, Hicks and Hall 2003, Coulombe-Pontbriand and Lapointe 2004, Montgomery 2004, Ebersole et al. 2006).

As with most broad-scale, correlation-based habitat studies (Johnson and Gage 1997, Steel et al. 2004), we caution against assuming causation in our findings. The basic premise in habitat selection is that organisms will select for certain characteristics of the microhabitat (i.e. more than at random), and that those features are capable of producing a response in some organismal metric such as density (Rosenzweig 1981, Gaillard et al. 2011, but see VanHorne 1983). Extending this to the stream-segment scale, the relative distribution of those habitat features would be capable of producing a similar variation in the organismal response at that spatial extent. Clearly, this is an oversimplification of reality, as it does not account for behavior, ontogenetic changes, density-dependent population regulation, interspecific interactions, or stochastic changes in the environment not represented by the data (Reeves et al. 1987, Höjesjö et al. 2004, Lóbón-Cerviá 2005). However, our study was designed to span gradients of physical habitat, biotic communities, and human impacts on the stream channels. Further, our monitoring lasted over three years, and the data were collected on a temporal resolution that reflected both the range and the rate of change in the variables. Hence, the study sites differed by means of these characteristics. Therefore, when patterns emerge from data that cover the range of the factors, there is good reason to believe the results are both sound and useful.

The imperilment of stream fishes on the northern hemisphere owes largely to habitat destruction, and this is particularly evident in anadromous salmonids in the Western United States (Nehlsen et al. 1991, NRC 1996). Although mechanisms and processes concerning limiting habitat factors are fairly well understood, these factors are not easily scaled up and incorporated into the level at which land use planning is conducted (Wiens et al. 1993). Although several conceptual models have been developed, effective management and conservation of stream ecosystems would benefit from a quantitative means to relate instream mechanisms to watershed-level characteristics due to the nested hierarchy of physical processes (Feist et al. 2003, Reaney et al. 2011). We believe our study approach is useful for furthering our understanding of the physical factors that partly determine the variation in stream salmonid densities.

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FIGURES AND TABLES

Figure 5.1

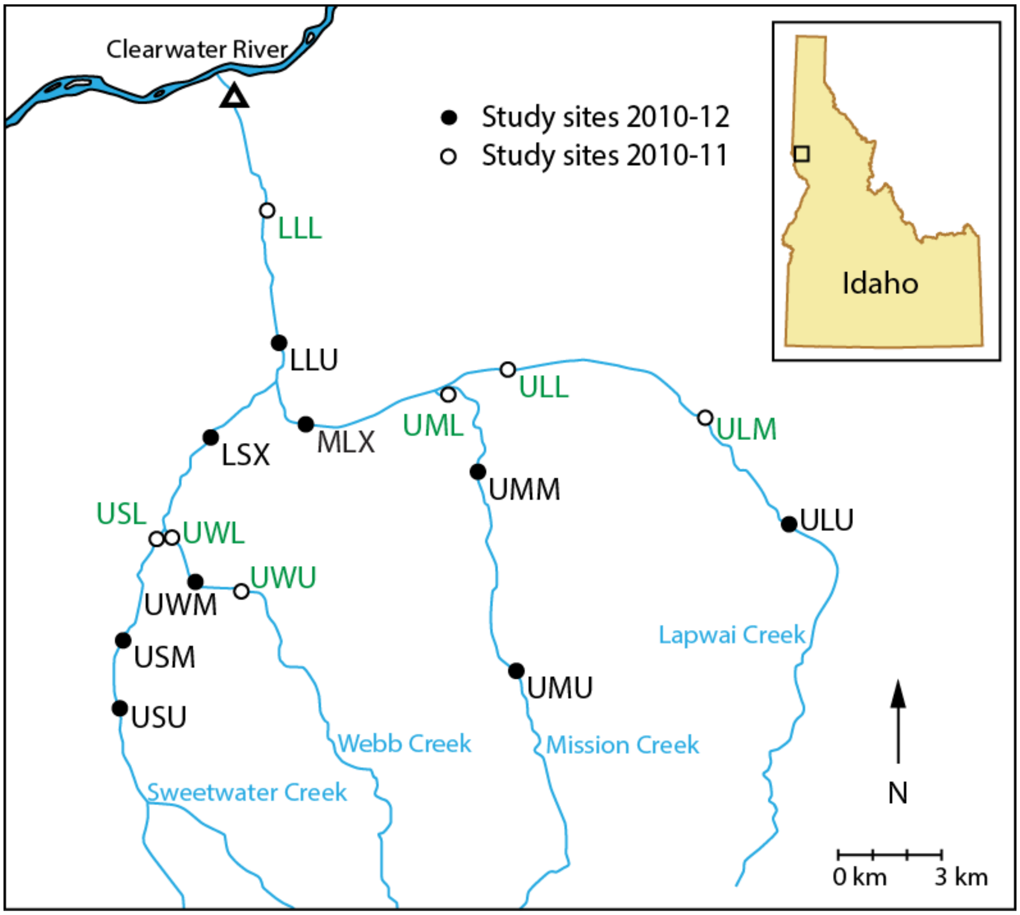

Figure 5.1. The map shows the four major streams of the Lapwai watershed and its location in North-Central Idaho, USA (insert). All 16 study sites were sampled in 2010 and 2011, whereas seven of these (open circles) were discontinued in 2012.

Figure 5.2

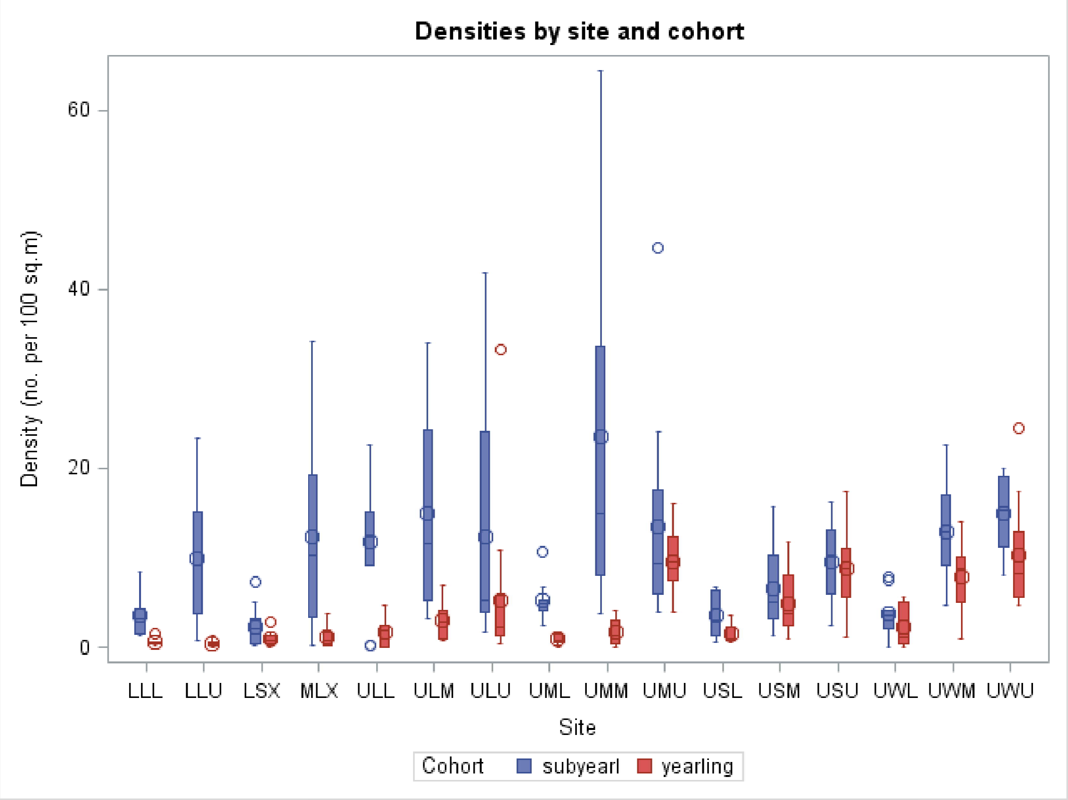

Figure 5.2. Densities (no. per 100 m^2) of subyearling (blue bars, n=175 estimates) and yearling (red bars, n=198 estimates) steelhead for each of the 16 study sites.

Table 5.1

Table 5.1. Candidate models confronted with the densities of subyearling, yearling, and both cohorts. Shown is the scale of the model, the model ID number, the structure with fixed-effect variables, the number of estimable parameters, and the AIC values for each cohort.

Model	Fixed effects	K	ln(both)	Subyr.	Yr.
INSTREAM					
1	β_1 Velocity(ms^{-1})	4	479.3	1286.6	1088.5
2	β_1 Velocity(ms^{-1}) β_2 velocity^2(ms^{-1})	5	458.6	1265.2	1068.1
3	β_1 Velocity(ms^{-1}) β_2 substrate(mm)	5	488.8	1291.9	1091.2
4	β_1 Velocity(ms^{-1}) β_2 substrate(mm) β_3 depth(cm)	6	489.1	1291.4	1091.6
5	β_1 Slowest(ms^{-1}) β_2 depth(cm)	5	474.0	1281.5	1092.1
6	β_1 Slow&shallow(%)	4	478.9	1286.9	1092.5
7	β_1 Depth(cm)	4	484.8	1295.3	1101.5
8	β_1 Depth(cm) β_2 depth^2(cm)	5	480.2	1287.0	1101.3
9	β_1 Depth(cm) β_2 overhanging(%)	5	483.5	1287.7	1082.6
10	β_1 Depth(cm) β_2 undercut(%)	5	483.2	1287.5	1096.9
11	β_1 Depth(cm) β_2 overhanging(%) β_3 LWD(m^{-1})	6	482.9	1282.2	1077.8
12	β_1 Substrate(mm)	4	490.8	1299.4	1104.1
13	β_1 Substrate(mm) β_2 LWD(m^{-1})	5	490.3	1293.9	1100.3
14	β_1 Marginvelocity(m/s) β_2 margindepth(cm)	5	479.8	1283.0	1091.1
15	β_1 Slowmargins(%)	4	481.7	1289.2	1090.5
16	β_1 Slow&shallow margins(%)	4	479.9	1289.0	1090.9
17	β_1 Overhangingmargins(%)	4	480.2	1288.8	1083.2
18	β_1 Slow&shallow(%) β_2 overhangingmargins(%)	5	479.2	1283.5	1077.0
19	β_1 Discharge(m^3s^{-1})	4	419.0	1270.3	1096.5
20	β_1 Discharge(m^3s^{-1}) β_2 depth(cm)	5	419.7	1270.9	1095.1
21	β_1 Discharge(m^3s^{-1}) β_2 substrate(mm) β_3 depth(cm)	6	424.1	1275.2	1094.1
22	β_1 Temperature(^oC)	4	483.5	1292.5	1104.7
23	β_1 Temperature(^oC) β_2 temperature^2(^oC)	5	486.6	1296.6	1110.8
24	β_1 Weeklytemperature(^oC)	4	482.5	1290.5	1104.5
25	β_1 Temperature(^oC) β_2 discharge(m^3s^{-1})	5	418.2	1266.3	1098.3
26	β_1 Temperature(^oC) β_2 slow&shallow(%)	5	480.9	1284.8	1094.0
WATERSHED					
27	β_1 Volcanic(%)	4	483.3	1291.2	1106.3
28	β_1 Unconsolidated(%)	4	485.4	1296.4	1104.6
29	β_1 Volcanic(%) β_2 slope50(%)	5	484.8	1288.7	1104.4
30	β_1 Area(km^2)	4	491.3	1301.3	1106.3
31	β_1 Area(km^2) β_2 meanslope(%)	5	493.1	1297.7	1107.3
32	β_1 Meanelevation(m)	4	485.2	1298.1	1096.6

33	β_1 Elevation(m) β_2 slope30(%)	5	490.8	1297.7	1102.0
34	β_1 Agricultural land(%)	4	488.3	1296.6	1103.4
35	β_1 Developed(%)	4	483.4	1292.0	1098.5
36	β_1 Forested(%)	4	487.4	1296.9	1100.3
37	β_1 Forested(%) β_2 unconsolidated(%)	5	492.5	1299.2	1103.8
COMBINATION WATERSHED AND INSTREAM VARIABLES					
38	β_1 Unconsolidated(%) β_2 substrate(mm)	5	494.9	1301.7	1106.0
39	β_1 Unconsolidated(%) β_2 slow&shallow(%) β_3 slowest(ms^{-1})	6	468.2	1271.1	1086.1
40	β_1 Area(km^2) β_2 discharge(m^3s^{-1})	5	427.3	1276.8	1088.2
41	β_1 Meanslope(%) β_2 discharge(m^3s^{-1})	5	422.7	1269.1	1097.1
42	β_1 Meanslope(%) β_2 discharge(m^3s^{-1}) β_3 velocity(ms^{-1})	6	417.7	1260.4	1081.8
43	β_1 Slope50(%) β_2 discharge(m^3s^{-1}) β_3 velocity(ms^{-1})	6	417.2	1261.0	1080.7
44	β_1 Meanelevation(m) β_2 temp(^oC)	5	486.9	1296.0	1098.3
45	β_1 Forested(%) β_2 overhanging(%)	5	486.0	1289.6	1080.3
46	β_1 Forested(%) β_2 LWD(m^{-1})	5	486.9	1291.3	1096.3

Table 5.2

Table 5.2. The best approximating models (model number) by cohort and their Akaike weights in parentheses for each level of comparison.

Comparison	ln(Both)	Subyearling	Yearling
Instream (1-26)	25 (.46)	2 (.58)	2 (.98)
	19 (.31)	25 (.34)	
Watershed (27-37)	27 (.29)	29 (.64)	32 (.58)
	35 (.28)		
Combination (38-46)	43 (.54)	42 (.57)	45 (.42)
	42 (.42)	43 (.42)	43 (.35)
All models (1-46)	43 (.31)	42 (.52)	2 (.97)
	42 (.24)	43 (.39)	
	25 (.19)		

Table 5.3

Table 5.3. Parameter estimates for the best approximating models of each cohort density. See text for information on the statistics and parameters.

Cohort	ID	ε	Var.	% ε	%	β_0 (SE)	β_1 (SE)	β_2 (SE)	β_3 (SE)
ln(Both)	19	.398	.700	59	41	2.68 (.152)	-3.82 (.451)		
	25	.382	.666	57	43	2.23 (.223)	.0324 (.0115)	-3.85 (.443)	
	27	.539	.838	64	36	-.00274 (.924)	.0273 (.0115)		
	35	.539	.973	55	45	2.29 (.578)	-.0316 (.135)		
	42	.391	.698	56	44	3.69 (.940)	-.0731 (.0505)	-3.90 (.454)	1.77 (1.00)
	43	.392	.730	53	47	1.48 (1.58)	.0933 (.163)	-3.89 (.456)	1.29 (.942)
Subyr.	2	80.7	97.3	83	17	-3.36 (5.97)	138 (47.5)	-287 (88.4)	
	25	75.1	91.2	82	18	8.58 (2.67)	.396 (.163)	-33.7 (7.34)	
	29	83.3	101	82	18	-9.95 (13.9)	.247 (.103)	.0512 (1.41)	
	42	76.5	93.8	82	18	25.2 (8.09)	-.780 (.475)	-33.2 (7.88)	17.1 (13.4)
	43	77.1	97.3	79	21	12.4 (14.2)	.00925 (1.43)	-33.1 (8.01)	6.30 (11.7)
Yearling	2	11.2	24.2	46	54	-6.36 (2.39)	75.4 (18.2)	-120 (35.6)	
	32	12.5	16.4	76	24	-31.7 (7.44)	.0317 (.00661)		
	43	11.5	28.9	40	60	-7.12 (11.0)	.661 (1.14)	3.49 (2.48)	16.2 (5.40)
	45	11.3	21.6	52	48	-6.41 (2.77)	.125 (.0552)	13.6 (3.36)	

CHAPTER 6: ESTIMATION OF SALMONID ABUNDANCE BASED ON SINGLE-PASS ELECTROFISHING IN SMALL STREAMS

Manuscript prepared for submission as management brief to *North American Journal of Fisheries Management*

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ABSTRACT

Electrofishing is one of the most widely used methods for sampling fish in small, wadeable streams, but mounting evidence of detrimental effects on fishes call for restriction in its use. Here we confront candidate models for abundance estimation based on single-pass electrofishing with a large monitoring dataset on federally listed steelhead *Oncorhynchus mykiss*. We found a strong linear relationship between the number of fish caught on the first pass and the corresponding three-pass depletion estimate of juvenile steelhead, expressed as *population estimate = 2.63 + 1.55*pass1* (r^2 = 0.94). Our second objective was to look at factors influencing the relationship between first pass and subsequent pass catch rates. There was no effect of previous handling. Among environmental covariates, the models that received the most relative support included temperature and discharge for subyearlings and both cohorts combined, whereas for yearlings the global model, including area and stream width, received the most support; however, inclusion of these covariates only slightly

improved fit (1 %) compared to the base models. By using these models to predict population size we could potentially reduce exposure time by two-thirds for approximately 35% of the population. We encourage other studies where such data exist to assess the feasibility of such an approach.

INTRODUCTION

In order to build our ecological understanding and inform management decisions, scientists must acquire reliable data on fish abundance and distributions. Electrofishing is one of the most common and effective capture methods for fish in wadeable streams and small lakes (Bohlin et al. 1989, Reynolds and Kolz 2012). Besides its effectiveness, the major appeal of the technique is that the gear is mobile, which allows scientists to relate individual fish to the specific habitats in which they are found in real-time, rather than relying on the passage through fixed structures for detection. This is particularly important when monitoring stream salmonids whose patchy distribution, territoriality, and habitat-specific requirements necessitate the practice of spatially extensive surveys. Despite efforts to reduce negative impacts (Reynolds and Kolz 2012), electrofishing is inevitably harmful to salmonids and other fishes (*see* Snyder 2004 for a review). Detrimental effects include direct and acute mortality, injuries to skeletal parts and hemorrhages, altered behavior, and disruption of feeding.

Although alternative methods exist for presence documentation and abundance estimation (Bozek and Rahel 1991, Thurow and Schill 1996, Mullner et al. 1998), capture and handling is necessary to obtain individual morphometric data and implant tags. When electrofishing is the only feasible method for capture, actions can be taken to reduce harm. Snyder (2003) reported that field intensity and exposure time are the primary factors affecting physiological stress and mortality. By reducing exposure time, we can reduce the overall likelihood of harm, as reducing field intensity would come at the expense of capture efficiency (Reynolds and Kolz 2012). Exposure time is primarily determined by the number of passes in a typical multiple depletion approach. Under similar conditions it can therefore be useful to analyze the relationships between the number of fish caught on the first pass and the corresponding depletion estimate when such data exist.

Kruse et al. (1998) established a regression approach to relate single-pass catch to multiple-pass population estimates for sparse populations of trout across 30 sites in Wyoming streams with little cover. They found strong relationships ($R^2 = 0.94$ for the base model), but cautioned that such relationships would have to be developed for each watershed rather than corroborating their model parameters. Identifying the factors that influence the strength of the relationship would help to identify when and where scaled-back approaches are feasible. Here, we extend the approach by utilizing a large monitoring dataset on federally listed steelhead *Oncorhynchus mykiss* in the Lapwai Creek watershed, Idaho to assess the extent to which a reduced effort can be used to index population size. Specifically, we test for avoidance due to previous handling, separate the steelhead by cohorts, and use model selection to identify which habitat factors were more influential in predicting the abundance of the cohorts.

METHODS

Study area and -population

The study was conducted in the Lapwai Creek watershed in North-Central Idaho. There are four major tributaries in the watershed that together form the 4th order Lapwai Creek, which drains an area of 694 km^2, and empties into the Clearwater River, 237 m.a.s.l. The streams drain the north slopes of Craig Mountain (1530 m.a.s.l.) and carve steep canyons through the landscape. The predominant geology in the watershed is Columbia River basalt, with a band of Idaho Batholith in the upper, high elevation portion. Mean annual precipitation is 490 mm, with larger amounts falling at higher elevations. The plateau above the escarpment is overlain with loess, and the predominant land use is dry land grain crops, which covers 34% of the watershed. Coniferous forests cover 29%, primarily at higher elevations above the prairie, and grasslands dominate the steep canyon sides and valley floors (Homer et al. 2007).

The Lapwai Creek population is part of the Snake River steelhead distinct population segment, which has declined in numbers since the 1870s due to hydropower development, overharvest, ocean conditions, and habitat degradation (Chapman 1986, NMFS 2005). Two of the streams in the Lapwai watershed have altered streamflow due to water diversions for irrigation purposes. Following the listing of Snake River steelhead in 1997, the main mitigation effort is a minimum flow requirement for the juvenile life stage (NMFS 2006). The data we use in this paper come from the consequent monitoring of 16 study sites; three study reaches on each of the tributaries, one below the confluence of each pair, and two study reaches on the mainstem. Site selection was done in a stratified random fashion (Frissell et al. 1986) based on several criteria, with the intention to capture a gradient of physiographic (topography, geology, and land cover) and land use conditions within and across the four streams. We scaled the number of sites back to nine in 2012 in a way that minimized the reduction in physiographic variation. No hatchery supplementation exists for steelhead in the watershed.

Field collection of fish and habitat data

Field data were collected once per month for five months from early summer to late fall in each of 2010, 2011, and 2012 when flows were close to or at baseflow, resulting in 198 electrofishing days. We set block nets to ensure a closed population (Carle and Strub 1978) and conducted three-pass depletion electrofishing (Reynolds and Kolz 2012) using a Smith-Root LR-24 backpack electroshocker (Smith-Root Inc., Vancouver, WA). To reduce the stress of capture and handling on fish, we conducted the sampling during early morning hours when the water temperatures did not exceed 18 ^{o}C. We set the voltage, frequency, and duty cycle within 20% of their mean values of 350 V, 30 Hz, and 15%, respectively. We held the juvenile steelhead in buckets filled with aerated stream water at ambient stream temperatures, separated by pass number. We anesthetized the fish with tricaine methanesulfonate (MS-222), and measured fork length in millimeter and weight to the nearest 0.1 g. Fish > 40 mm recruited to our gear and were consequently included in the population estimates. Abundances were calculated using Carle and Strub's (1978) weighted maximum likelihood estimator of *K*-pass removal data with a constant probability of capture between passes. Classification by cohort was done based on examination of body size histograms. The mean width of the streams was 4.2 m (SD, 1.3) and the mean discharge was 0.13 m^3s^{-1} (SD, 0.12). The size and accessibility of the study sites favored high capture probabilities (season averages ± SD were 0.63 ± 0.14 in 2010, 0.62 ± 0.13 in 2011, and 0.64 ± 0.13 in 2012). The electroshocker was always operated by the same individual for each effort, and the crew size was identical. All fish sampling and -handling procedures were permitted as part of the Section 7 consultation for the Lewiston Orchards Biological Opinion (NMFS 2006), Idaho Department of Fish and Game, and the University of Idaho Institutional Animal Care and Use Committee.

We quantified discharge at each visit based on 15 to 25 readings across the stream channel (Fisher et al. 2012) using a Flo-Mate Velocity Meter (Marsh McBirney Inc., Loveland, CO) at 60% of the depth. We removed large rocks to reduce turbulence. We had HOBO TidbiT v2 temperature loggers (Onset Computer Corporation, Pocasset, MA) installed at each site recording water temperatures (^{o}C) every 30 minutes. We used daily average of temperatures in the analyses.

We omitted two outliers in the yearling dataset and three outliers in the dataset for both cohorts combined. In the yearling data set, the first point (ULU 25.6.2012) was left out due to unusually high numbers. The second data point omitted (UWU 26.6.2011) had very poor depletion (capture probability of 0.18), owing to high discharge and turbidity on that visit. In the dataset with both cohorts combined, the aforementioned UWU data point was omitted, as were two datapoints from site ULM in 2011. At ULM the capture probabilities were low (0.38 and 0.21, respectively). The reason is that following a large flood event on April 1st 2011 the habitat configuration in this site changed substantially, leaving two deep pools and the rest a shallow riffle. Nearly all the fish in this site were caught in these two pools, and the patchy distribution caused unusually poor depletion.

Testing the effect of previous handling

The monitoring of the steelhead population in the Lapwai watershed involves tagging of individuals with 134.2 kHz Passive Integrated Transponders (PIT tags, Biomark Inc., Boise, ID). To test for potential behavioral changes due to previous handling we calculated capture probabilities based on previously tagged and untagged fish, respectively. We truncated the dataset to include those visits with more than 15 untagged and 15 previously tagged individuals (n = 27 visits). We calculated the capture probabilities for each group (Carle and Strub 1978) and compared the mean effects using a two-sample t-test.

Candidate models and analyses

We built a candidate set of linear multiple regression models that were confronted with the data for subyearlings, yearlings, and both cohorts combined. In addition to the first order base model, which had the number of fish caught on the first pass as the only predictor variable, the other models in the set included covariates that could influence capture probability, and in turn the population estimate (*see* Table 1 for model structures). Importantly, we focused on variables that can easily be collected in the field over the course of one pass.

We used an information-theoretic approach to assess the relative plausibility of the candidate models (Akaike 1973, Burnham and Anderson 2002). Information-theoretic data analysis is based on Kullback-Leibler information, which is the information lost when statistical models are used to approximate full truth (Kullback and Leibler 1951). Akaike's information criterion (AIC) is given as

$$AIC = -2\ln\left(\ell\left(\hat{\theta}\middle|data\right)\right) + 2K,$$

where $\ln\left(\ell\left(\hat{\theta}\middle|data\right)\right)$ is the value of the maximized log-likelihood over the unknown parameters, given the data and the model, and *K* is the number of estimable parameters in that model. Because our models were linear, we used least squares estimations, for which AIC is expressed as

$$AIC = nln(\hat{\sigma}) + 2K,$$

where *n* is the sample size, $\hat{\sigma}$ is the residual sum of squares (RSS) divided by *n*, and *K* is the number of estimable parameters, including the intercept and error variance. The model with the lowest AIC value is the best approximating model of the given data. The models *i* were ranked using the simple AIC differences, Δ_i, given as $\Delta_i = AIC_i - AIC_{min}$. To make interpretation and inference easier, we normalized the likelihood functions of the models so that they sum to 1. The probability of model *i* being the best approximating model in the set is called the Akaike weight (w_i), and is given as

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_i\right)}$$

Model selection results were reported as recommended by Anderson et al. (2001), with tables showing the number of estimable parameters (*K*), the residual sum of squares (*RSS*), the model selection criterion (*AIC*), the simple differences (Δ_i), the Akaike weights (w_i), and the evidence ratio (i.e. w_{max}/w_i). We only provided parameter estimates for the base model in each set and the AIC-best model for both cohorts. For these models we presented the estimated standard error of the model (*SE*, the square root of the estimated variance), the parameter estimates (*β*-coefficients) and their associated standard errors (*SE*), and the multiple coefficient of determination (R^2). All analyses were conducted using SAS v. 9.2 Proc REG (SAS Institute Inc., Cary, NC).

RESULTS

We found a very strong relationship between the number of steelhead caught on the first pass and the population estimates based on the corresponding three-pass depletion electrofishing effort (r^2 = 0.94, Figure 1). There was no effect of previous handling (P = 0.36, t = 0.93, df = 51). The capture probabilities of untagged (0.665) and previously PIT-tagged individuals (0.689) were within 3.5 % of each other. When including environmental factors that had the potential to affect capture efficiency we found that the best approximating models included positive relationships with temperature and discharge for both subyearlings ($w_i = 0.32$) and both cohorts combined ($w_i = 0.78$) (Tables 1 and 2). These models imply that the population estimate depends positively on temperature and discharge in addition to the first pass captures. For yearling steelhead, the global model (which contained all covariates) received the most absolute (R^2 = 0.936) and relative support (w_i = 0.69*)* among the candidate models. Within each cohort category, the coefficients of determination for all candidate models were within one percent of each other. The inclusion of environmental covariates in the best approximating models hence reduced the bias but did not contribute to substantially better fit. We hence provide parameter estimates for the base model for all three cohort categories, and the best approximating model for both cohorts combined.

DISCUSSION

Our results demonstrate that in small wadeable streams, we may use the modeled relationships to accurately index population size with a reduced effort. Although the best approximating models included first pass capture numbers, temperature, and discharge, the two environmental covariates did not substantially improve the absolute fit over the base models for subyearlings and both cohorts combined, and similarly, the addition of area and width for the yearling cohort did not greatly improve fit for that cohort. Hence, the basic relationship between the number of fish caught on the first pass could be used to predict the three-pass depletion estimate in the study system.

Our results were very similar to those of Kruse et al. (2008) by means of base model fit, but the slope of their regression model was shallower (i.e. the β_1 in the $abundance = \beta_0 + \beta_1 pass1 + error$ – relationship was smaller), owing to slightly higher capture probabilities. We extended on their approach by having a larger dataset and conducting simultaneous tests of candidate models. We think this approach could be a viable method for population estimation or -indexing when the capture probability is consistently high, and data are collected within the same watershed or under similar conditions. We point out that only three field personnel conducted the electrofishing over the three seasons considered in this study, which greatly reduces the potential for observer error. Snyder (2003) reported that field intensity and exposure time are the primary factors affecting physiological stress and mortality in fishes during electrofishing. Our approach reduces the overall exposure time by two-thirds. Approximately 65% of the population was affected by the first pass (i.e. $1/\beta_1$), but exposure time was reduced to one-third relative to a three-pass effort for the remaining 35% of the population. This is a substantial reduction in exposure when abundance can be calculated without appreciable loss of confidence.

A paradox in managing threatened and endangered species is that the lower the effective population size, the more documentation is needed on its status, and in most instances this requires capturing and handling individuals to obtain those data (Nielsen 1998). We think the approach presented in Kruse et al. (1998) and the present study could represent an important step towards minimizing the adverse effects of scientific sampling. While encouraging the development of techniques and models that reduce such negative effects, we agree with Kruse et al. (1998) and caution against borrowing of model parameters to other systems as site-specific environmental conditions are primary factors influencing capture probabilities.

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FIGURES AND TABLES

Figure 6.1

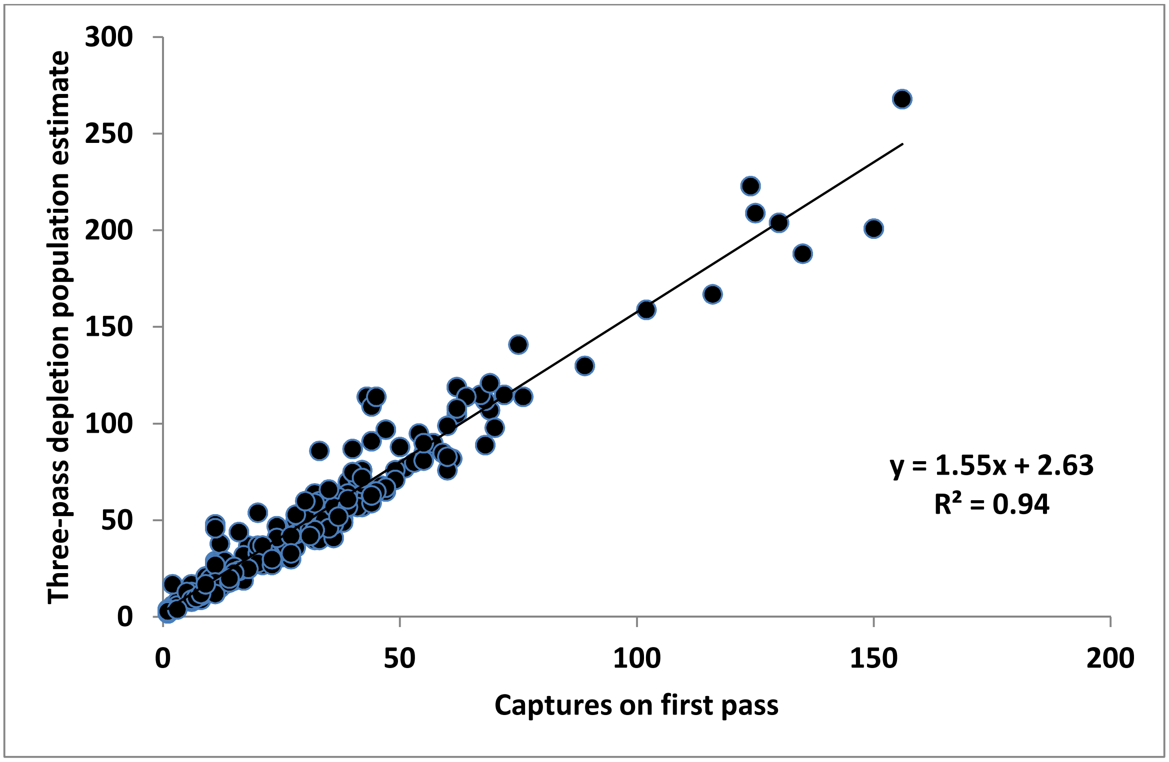

Figure 6.1. Relationship between the numbers of juvenile *O. mykiss* (subyearlings and yearlings combined, n = 195 estimates) caught on the first pass and the Carle and Strub (1978) weighted maximum likelihood population estimate of three-pass removal electrofishing.

Table 6.1

Table 6.1 Model selection results for the candidate models relating the number of *O. mykiss* caught on the first pass to the Carle and Strub (1978) weighted maximum likelihood population estimate for the subyearling (n=198) and yearling (n=196) cohorts as well as both cohorts combined (n = 195). Highlighted are the base model (light shading) and the AIC-best model (dark shading).

Cohort	Model	K	RSS	AIC	AIC – AIC$_{min}$	Δ_i	w_i	Evidence ratio	R^2
Subyearling	pass	3	22884	944.486	2.17	0.3379	0.108	2.96	0.937
	pass width	4	22554	943.609	1.29	0.5239	0.168	1.91	0.938
	pass width discharge	5	22547	945.546	3.23	0.1989	0.064	5.03	0.938
	pass discharge temp	5	22182	942.316	0	1	0.320	1	0.939
	pass discharge	4	22719	945.049	2.73	0.2550	0.082	3.92	0.937
	pass area	4	22607	944.072	1.76	0.4156	0.133	2.41	0.938
	pass area discharge	5	22592	945.939	3.62	0.1634	0.052	6.12	0.938
	global	7	22064	945.264	2.95	0.2290	0.073	4.37	0.939
Yearling	pass	3	3286	556.612	9.57	0.0083	0.006	120	0.930
	pass width	4	3278	558.137	11.1	0.0039	0.003	257	0.930
	pass width discharge	5	3121	550.461	3.42	0.1808	0.125	5.53	0.933
	pass discharge temp	5	3125	550.740	3.70	0.1572	0.109	6.36	0.933
	pass discharge	4	3207	553.803	6.76	0.0340	0.024	29.4	0.932
	pass area	4	3285	558.555	11.5	0.0032	0.002	317	0.930
	pass area discharge	5	3159	552.842	5.80	0.0550	0.038	18.2	0.933
	global	7	3005	547.040	0	1	0.693	1	0.936
Both cohorts	pass	3	22927	933.578	13.2	0.0013	0.001	746	0.941
	pass width	4	22844	934.871	14.5	0.0007	0.001	1424	0.941
	pass width discharge	5	22351	932.622	12.3	0.0022	0.002	462	0.943
	pass discharge temp	5	20988	920.349	0	1	0.788	1	0.946
	pass discharge	4	22380	930.867	10.5	0.0052	0.004	192	0.943

pass area	4	22809	934.574	14.2	0.0008	0.001	1227	0.941
pass area	5	22368	932.761	12.4	0.0020	0.002	496	0.943
discharge global	7	20851	923.073	2.72	0.2561	0.202	3.90	0.947

Table 6.2

Table 6.2. Model structures for the base models for each cohort category and the best approximating model for both cohorts. The models relate the number of *O. mykiss* caught on the first pass with the estimate from the three pass depletion electrofishing effort.

Cohort	*Model structure*	*SE*	*β_0 (SE)*	*β_1 (SE)*	*β_2 (SE)*	*β_3 (SE)*	*R^2*
Subyearling	$\beta_0 + \beta_1$pass1	10.81	1.78 (1.0)	1.61 (0.030)			0.937
Yearling	$\beta_0 + \beta_1$pass1	4.116	0.726 (0.40)	1.52 (0.030)			0.930
Both	1. $\beta_0 + \beta_1$pass1	10.90	2.67 (1.2)	1.55 (0.028)			0.941
	2. $\beta_0 + \beta_1$pass1 + β_2 discharge + β_3 temperature	10.48	-9.08 (3.0)	1.56 (0.030)	12.5 (7.0)	0.68 (0.19)	0.946

CHAPTER 7: PATTERNS AND PROCESSES OF SITE FIDELITY IN A STREAM SALMONID

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Keywords: Idaho, movement, non-migratory, *Oncorhynchus mykiss*, steelhead

ABSTRACT

1. Animal movement provides an important ecological link between individual behaviour and population vital rates and has important consequences for genetic variation and evolutionary potential.

2. Stream fishes were previously thought to display limited movement, with individuals being largely sedentary to the channel unit or reach scale as they are defending territories and feeding on continually renewing prey in the drift. However, recent studies have documented substantial non-migratory movement in several species of salmonids, although the processes remain largely untested.

3. To identify the processes causing these patterns of movement and site fidelity we coupled observational monitoring and experimental translocation of individually marked juvenile steelhead (*Oncorhynchus mykiss*) across discrete study sites in a heterogeneous watershed in Idaho, United States, each spanning 700 stream metres.

4. We documented an overall high proportion of mobile steelhead relative to the proportion exhibiting site fidelity (range 58 – 83 % between the seven study sites). Among the fish that were retained in the study system, most individuals exhibited site fidelity at the scale of 50 m. Channel configuration was overall a better predictor of site fidelity than were biotic factors and individuals characteristics. Yearling steelhead were more likely to remain in sections with higher amounts of pool habitats. For subyearling steelhead there was no single factor that explained site fidelity, which was reflected in their overall higher mobility (79 %). Growth rates were depressed among fish originally residing in sections that received increased densities following the translocation treatment.

5. Our results support the notion that movement is the rule rather than the exception in stream salmonids, and that local abiotic and biotic factors influence an individual's propensity to remain or move. These results further underscore the importance of continuous, barrier-free habitat.

INTRODUCTION

A population of mobile organisms is at any point in time made up by those individuals that were recruited on site and migrants that have moved there. The relative proportion of migrants and residents can vary widely across taxa, but studies have reported on relatively large contributions of migrants in populations of birds, mammals, and fishes (Greenwood et al. 1978, Gaines and McClenaghan 1980, Gowan and Fausch 1996, Rodriguez 2002). Movement hence provides an important ecological link between individual behavior and population vital rates (Begon et al. 1996, Turchin 1998, Fraser et al. 2001), and has important consequences for genetic variation and evolutionary potential (Hanski 1999, Morissey and Ferguson 2011).

Food, cover, and other resources that individuals select for are typically patchily distributed across the landscape and dynamic over time. Ideally, consumers should distribute themselves accordingly to maximise their net energy gain, which would require substantial movement if these resources are patchy. This idea was formalised by Fretwell and Lucas (1970) and Sutherland (1983) as the Ideal Free Distribution. The model functions under certain conditions at appropriate spatial scales, but has notable weaknesses (Tregenza 1995); however, the concept remains useful for thinking about the factors that contribute to both individual movement and aggregations of organisms in space and time.

Stream fishes were previously thought to display very limited movement, with individuals being largely sedentary to the channel unit or reach scale as they were defending territories and feeding on continually renewing prey in the drift (Gerking 1959). However, with increased focus on monitoring stream salmonids and with developments in fish tagging technology, recent studies have documented substantial non-migratory movement behavior in several species across a variety of stream ecosystems (Gowan et al. 1994, Kahler et al. 2001, Gowan and Fausch 2002, Morissey and Ferguson 2011).

Understanding the proximate factors for why fish move requires examining both individual characteristics and population demographic variables, as well as the habitat conditions they select for (Turchin 1998, Gilliam and Fraser 2001, Kahler et al. 2001, Morissey and Ferguson 2011). Habitat selection has been documented based on net energy intake in relation to flow and prey delivery rates (Fausch 1984, Hughes and Dill 1990), for habitat correlates based on aggregations (e.g. Bisson et al. 1988, Hicks and Hall 2003, Coulombe-Pointbriand and Lapointe 2004), for refugia (Nielsen et al. 1994), and for behavioural interactions (Tinus and Reeves 2001); whereas factors triggering movement and migration include ontogenetic shifts and energetic state (Metcalfe 1998, Forseth et al. 1999), competition (Keeley 2001, Einum et al. 2006), and environmental cues (Bjornn 1971, Elliott 1986, Kahler et al. 2001).

The literature suggests that fish start to move when flows increase in the fall (Bjornn 1971, Bjornn and Reiser 1991, McCormick et al. 1998, Gresswell and Hendricks 2007). However, stream discharge can be confounded by simultaneous changes in temperature, and fluctuate widely over the course of the summer without necessarily triggering movement (Bjornn and Reiser 1991). To test the extent to which movement occurs before the first flood, but during the time that the streams cool off in the fall, we monitored individually tagged juvenile steelhead (*Oncorhynchus mykiss*) across seven valley-segment scale reaches which spanned gradients of habitats, densities, and land use impacts. Our first objective is to identify proximate factors pertaining to individual characteristics, population densities, and habitat factors that can explain individual site fidelity. The second objective is to quantify movement on the short scale (50 m) among fish that did exhibit site fidelity, and to quantify the consequences of these choices on their growth rates. In an effort to separate out the effect of population density on individual growth performance we manipulated densities in certain sections of the study reaches.

METHODS

Study area and population

The Lapwai watershed is situated in North-Central Idaho and drains an area of 694 km^2 (Figure 1). The four main tributaries drain the north slopes of Craig Mountain (1530 m) through steep canyons before emptying into the Clearwater River (237 m). The predominant geology in the watershed is Columbia River basalt, with a band of Idaho Batholith in the upper, high elevation portion. The plateau above the escarpment is overlain with loess, and the predominant land use is dry land grain crops, which covers 34% of the entire watershed. Coniferous forests cover 29%, primarily at higher elevations above the prairie, and grasslands dominate the steep canyon sides and valley floors (Homer et al. 2007). Mean annual precipitation is 490 mm, with higher amounts falling at higher elevations, primarily from October through May. The watershed is designated as critical habitat for wild Snake River steelhead (NMFS 2006) and there is no hatchery supplementation. Other fish species include, in order of abundance, longnose dace (*Rhinichtys cataractae*), sculpin (*Cottus* spp.), bridgelip sucker (*Catostomus columbianus*), redside shiner (*Richardsonius balteatus*), northern pikeminnow (*Ptychocheilus oregonensis*), and chiselmouth (*Acrocheilus alutaceus*). In recent years juvenile coho salmon (*Oncorhynchus kisutch*) have been stocked as part of a supplementation program in lower reaches of the system, but are generally not sympatric in space or time with steelhead.

Study design

In order to understand the relative importance of the factors (individual characteristics, competition, habitat, and disturbance) that have the potential to influence individual movement decisions, we identified seven study sites in the watershed that spanned gradients of biotic and abiotic conditions (Figure 1). Each study site consisted of a ca 100 m monitoring reach, in which steelhead abundance and growth were monitored intensively, and adjacent sections extending 300 m in both the upstream and downstream directions (Figure 2). Each direction was broken into five discrete sections, labelled according to their distance from the study site: 0-50, 50-100, 100-150, 150-200, and 200-300 m.

In September and October 2012 we captured juvenile steelhead and quantified the physical habitat in the seven study sites, each totalling 700 stream meters. We kept track of the section where individuals were captured and tagged by noting the name of the section in their tagging file. Following handling as described in section 2.3.1, the fish we caught in September were released back into their respective sections, with one exception: we translocated all fish from downstream section ds100-200 to upstream section us100-200. These sections are henceforth referred to as removal (R) and addition (A) sections, respectively, whereas the remaining sections are referred to as control sections (0). We returned fish from us100-150 and us150-200 to their respective sections. Fish from ds100-150 and ds150-200 were recovered in the same bucket to ensure randomising individuals prior to translocation. 50 % of these individuals were then stocked into us100-150 and the rest were stocked into us150-200.

On the October visit the primary objective was to assess how fish responded to the removal (R) and addition (A) treatment by means of growth and movement. Consequently we did not tag new fish, but recorded morphometric and location data on all captured individuals. All fish were released back to the section where they were caught. We assumed that mortality was zero. Clearly this is an oversimplification (Hartson and Kennedy 2014); however, because of the short duration of the study and not enough capture periods to model survival, the potential bias of omitting survival is less than what the induced uncertainty of assigning correlates would be, making our assumption an acceptable trade-off.

The study was conducted prior to the elevated flow conditions that start in late fall (Figure 3), which are known to trigger migration in steelhead (Bjornn 1971, Bjornn and Reiser 1991). Movement is hence effectively attributed to non-migratory behaviour in this study. Densities in the control, removal, and addition sections both prior to and after the translocation are shown in Table 1, whereas the treatment sizes and their consequences on the translocated fish and fish originally residing in the addition sections are shown in Table 2.

Sampling methods and material

Fish data

We conducted three-pass depletion electrofishing in monitoring reaches and single-pass electrofishing in the rest using a Smith-Root LR-24 backpack electroshocker (Smith-Root Inc., Vancouver, WA) as described in Myrvold and Kennedy (*in review*). To reduce the stress of capture and handling on fish, we conducted the sampling when the water temperatures did not exceed 18 ^{o} C. We set the voltage, frequency, and duty cycle within 20% of their mean values of 350 V, 30 Hz, and 15%, respectively. We held the juvenile steelhead in buckets filled with aerated stream water at ambient stream temperatures. Prior to any handling we anesthetised the fish with tricaine methanesulfonate (MS-222). We measured fork length in millimetres and weight to the nearest decigram. Steelhead were scanned for PIT tags using a FS-2001F-ISO reader (Destron Fearing, St. Paul, MN) and data on the individuals were recorded in program P3 (PIT-Tag Information System for the Columbia Basin). We inserted 134.2 kHz PIT tags (Biomark Inc., Boise, ID) into the ventral body cavity posterior to the tip of the pectoral fin in individuals 65 mm and larger. Prior to release, fish were first allowed to recover in buckets with aerated water. Fish were then released back into the stream as specified in the study design. All fish sampling and handling procedures were permitted as part of the Section 7 consultation for the Lewiston Orchards Biological Opinion (NMFS 2006), and reviewed by the Idaho Department of Fish and Game and the University of Idaho Institutional Animal Care and Use Committee.

Growth rates for recaptured individuals were calculated and expressed as percent change in body mass per day between capture and recapture. The consistently high capture efficiencies from previous monitoring (2010-2012) in the system allowed us to develop a regression approach to estimating abundance based on single-pass electrofishing (Myrvold and Kennedy (*in review*). Single-pass electrofishing captures an estimated 65 (± 0.028) % of the abundance estimated from three-pass depletion electrofishing (based on Carle and Strub's [1978] weighted maximum likelihood estimator for k-pass removal data), and is deemed an appropriate method for calculating densities of stream salmonids in established study systems (Kruse et al. 1998).

Habitat data

For each section we conducted a rapid habitat assessment (Fisher et al. 2012). The section was categorised into channel geomorphic units (pool, glide, run, pocket, and run) based on the habitat prevailing features along the channel thalweg. We recorded the length of each unit (m), its maximum depth (cm), lengths of overhanging vegetation and undercut banks of the unit (m), and the number of large woody debris pieces (count). For standardisation among sections we calculated the following metrics to be used in the modelling: proportion of each channel geomorphic unit, proportion of each unit with overhanging vegetation or undercut banks, the number of large woody debris pieces per stream meter, the average depth of the section, and the average depth of the pools in the section. Characteristics are shown in Table 3.

Candidate models

To test hypotheses of factors that could influence an individual's choice to stay or leave the study system we developed a set of candidate models (Table 4). These models included covariates of individual characteristics, cohort and population densities both before and after the experimental translocation, the location of the fish in relation to the treatment, and physical habitat factors describing the channel geomorphology and overhanging cover. Because of differing ecology throughout ontogeny (Bjornn and Reiser 1991, Rosenfeld and Boss 2001) we modelled the cohorts separately. The variables included in the models were screened for collinearity with a correlation coefficient cut-off of 0.7.

Statistical analyses

The first objective was to identify potential determinants of site fidelity in individually tagged juvenile steelhead. Because the response variable was binary (stay or go), we modelled the odds of an individual remaining in the study reach in relation to these factors. Because of the clustered design of this study we had to account for the correlation among individuals residing in the same site and section to avoid pseudoreplication. We hence specified mixed effects logistic regression models with random intercepts to model the log-odds for individually tagged steelhead remaining in the study system. Model structures for fixed effects variables (other than the intercept) are shown in Table 4. The mixed effects logit model is given as

$$\ln\left[\frac{p_{ij}}{1-p_{ij}}\right] = \alpha_i + \beta x_{ij} \ ,$$

where α_i represents a random intercept for site *i* and is n(0, σ^2), x_{ij}'s represent variables for individual *j* in site and section *i*, and β's represent the fixed-effects parameter estimates. We used SAS v. 9.2. Proc GLIMMIX to specify random intercept models with clustering at the site and section level, a logit-link function and binary distribution for the response, and Gaussian quadrature maximum likelihood estimation (Allison 2012) to allow for comparison across models using information criteria. All models proved statistically significant (P<0.05) for the random intercept using the mixture likelihood ratio chi-square test (SAS Institute 2008).

We used an information-theoretic criterion to assess the relative plausibility of these candidate models (Akaike 1973, Burnham and Anderson 2002). Information-theoretic data analysis is based on Kullback-Leibler information, which is the information lost when statistical models are used to approximate full truth. Akaike's information criterion (AIC) is given as

$$AIC = -2\ln\left(\ell\left(\hat{\theta}\middle|data\right)\right) + 2K,$$

where $\ln\left(\ell\left(\hat{\theta}\middle|data\right)\right)$ is the value of the maximised log-likelihood over the unknown parameters, given the data and the model, and *K* is the number of estimable parameters in that model. The model with the lowest AIC value is the best approximating model of the data. The models *i* were ranked using the simple AIC differences, Δ_i, given as $\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{\min}$. To make interpretation and inference easier, we normalised the likelihood functions of the models so that they sum to 1. The probability of model *i* being the best approximating model in the set is called the Akaike weight (w_i), and is given as

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_i\right)}$$

Within each cohort we provided parameter estimates for models with strong relative support (i.e. $w_{max}/w_i < 2$).

The second objective was to look at the effect of the treatment on site fidelity and growth rates. This objective concerned only those fish that were encountered on both visits. To test for differences in site fidelity among the treatment sections we performed one-tailed t-tests with unequal variances. Site fidelity was expressed as the proportion of individuals remaining in a given section. Similarly, to look at the overall consequences of the movement and site fidelity choices on growth rates in relation to the density treatment, we performed one-tailed t-tests assuming unequal variances to test for differences in growth rates.

RESULTS

The overall retention of fish over the course of the experiment averaged 32 (SD ± 10) % for all sites combined, and varied from 17 % to 42 % across the seven sites (Table 5). Broken into cohorts, 125 (21.4 %) out of 583 individually tagged subyearling steelhead remained in the study reaches from September to October, and for the 868 yearling steelhead the number was 342 (39.4 %).

Determinants of site fidelity

For yearling steelhead, models depicting the proportion of pool habitat received the most support (52 % combined) (Table 6) in explaining their odds of staying in the study reach, showing a positive dependence on the amount of pool habitat and a negative relationship with the amount of glide habitat.

For subyearling steelhead, several models (models 9, 11, 14, and 19) received similar levels of support (51 % combined) (Table 6). Three of these models depicted habitat conditions whereas the fourth (model 9) depicted whether the fish was caught in an experimental removal reach (i.e. translocated). Subyearlings were more likely to remain in stream sections with higher proportions of pool and run habitat, and less likely to remain in sections with riffle habitat (Table 6).

Effects of density treatment and translocation on site fidelity

To test whether site fidelity varied among the treatment sections and the control sections we performed one-tailed t-tests with unequal variances. There was no statistically distinguishable difference between fish originally residing in added sections and those of control sections ($t = 0.206$, d.f. = 7, $P = 0.42$); no statistical difference between original fish in added sections and translocated fish ($t = 1.68$, d.f. = 9, $P = 0.06$); and statistical difference between translocated fish and fish in control sections ($t = 1.83$, d.f. = 9, $P = 0.01$). Due to small sample sizes at site LSX, each recaptured individual had great leverage on the summary statistics, and hence on the comparative analysis of site fidelity. Omitting site LSX from the analysis, there was a statistically significant difference between fish originally residing in added sections and translocated individuals ($t = 2.0$, d.f. = 8, $P = 0.04$).

Among recaptured fish in the control sections (n = 341), 293 (86 %) remained in their section, i.e. exhibited site fidelity (Figure 4). Twelve tagged individuals (3.5 %) moved into available habitat (removal sections, R) and 5 (1.5 %) moved into added sections (A), whereas 31 (9 %) moved to other control sections.

Among the fish that exhibited site fidelity (i.e. remained in their original sections, n = 391) there was no evidence of depressed growth rates for fish that were translocated (Table 7); in fact, they grew on average faster than fish originally residing in the sections with increased densities (means and variances of 0.45 % day $^{-1}$ (0.29) and 0.22 % day $^{-1}$ (0.02), respectively). Compared to individuals in control sections that exhibited site fidelity, fish originally residing in A sections achieved significantly lower growth ($t = -1.86$, d.f. = 8, $P = 0.05$), whereas growth rates in translocated individuals were statistically indistinguishable from those in control sections ($t = -0.067$, d.f. = 6, $P = 0.47$).

DISCUSSION

We found that overall retention rates ranged from 0.17 to 0.42 among the seven study sites; retention rates were greater among yearlings (0.39) than subyearlings (0.21); habitat factors were better predictors of retention than were biotic factors and individual characteristics; site fidelity among translocated individuals was lower than in control sites; and average growth rates for fish that remained in control sections were similar to those of translocated fish, and greater than those of fish originally residing in sections where density was experimentally increased.

Over the course of only 4 weeks we found the majority of the individuals (range 58-83 %) in the populations in our study area to move distances exceeding that of our study design, which was 700 stream meters. Studies on the site fidelity or retention of stream salmonids have reported varying degrees of movement. Whereas some have reported the majority of the population exhibiting strong site fidelity at the scale of meters (Steingrimsson and Grant 2003), others have found the majority of the individuals moving several channel units to kilometres (Gowan et al. 1994, Kahler et al. 2001, Morissey and Ferguson 2011). Individual decisions of site fidelity and non-migratory movement represent a behavioural response to external triggers such as dynamic abiotic and biotic conditions. Such factors vary across space and time within watersheds (Ebersole et al. 2006) and more so across larger geographical extents (Gibson 2002). We would therefore not expect similar levels of movement across systems that vary with respect to these conditions (Kahler et al. 2001). It is therefore not surprising that the range of reported values is large.

To understand the potential mechanisms that can influence individual choices of movement and site fidelity we examined hypotheses relating to individual characteristics, competition, habitat, and perturbation (Turchin 1998, Gilliam and Fraser 2001, Kahler et al. 2001, Morissey and Ferguson 2011). Among the fish that were retained in the study system, most individuals exhibited site fidelity at the scale of 50 m, which suggests they were selecting for certain habitat features. We found that the strongest predictors of retention, and thus individual site fidelity, were variables describing habitat features on the stream segment scale (i.e. composition of the segment into various proportions of channel geomorphic units). Juvenile steelhead and other stream salmonids show strong preferences for habitat characteristics that confer profitable conditions for feeding and sheltering (Heggenes 1988, Bjornn and Reiser 1991, Beecher et al. 1993, Chun et al. 2011). When water temperature decreases in the fall, steelhead tend to chose pool habitats and shift their behaviour from feeding and defending territories to sheltering (Bjornn and Reiser 1991). Our results could hence be influenced by fish that already had established this behaviour.

Because subyearlings were more mobile (overall retention rate was 21 %, as opposed to 39 % in yearlings) it is not surprising that many models received substantial relative support in approximating their site fidelity. Yearling steelhead showed nearly twice the site fidelity, and because little movement was documented among retained fish, it is hence evident that they were strongly associated with the amount of pool habitat (Heggenes 1988, Bjornn and Reiser 1991)

Biotic factors such as population density are previously shown to be important determinants of individual performance and migration rates, in which migration rates are thought to be a function of density due to competition (Keeley 2001, Einum et al. 2006, 2012). A potential reason that cohort density and total density were not among the best predictors of site fidelity in this study could be that our analysis compared all factors simultaneously, and that densities were not sufficiently high to affect migration rates. Density did, however, cause depressed growth rates among individuals in sections with artificially high densities (see below), which is in line with the recent research on the consequences of density dependence on individual performance (Jenkins et al. 1999, Einum et al. 2006).

Among fish that exhibited site fidelity, little movement on the 50 m scale was detected: 293 (86 %) out of 341 fish in control sites stayed put in their section even as habitat opened up in the removal sections and densities increased in addition sections, creating a potential for intrusion by excess individuals. Fish in control sections moved into the removal sections at a higher rate than to other control sections. Whereas 12 fish moved in to the removal sections, 31 moved into other control sections, which had approximately 5 times the area, hence yielding a 1.7 times higher rate. However, although the densities in the removal sections were lower in October after the density treatment, the same trend was evident in the control and addition sections. This suggests that the available habitat was occupied primarily by immigrants from outside the study area, more so than by fish in the control sections.

Site fidelity in relation to the treatment revealed lower site fidelity among translocated fish than among fish originally residing in the sections with increased densities and fish in control sites. We could, however, not determine whether this owed to the density treatment directly, or due to the fact that these individuals were removed from their home range. There was no evidence of depressed growth rates among these fish relative to residents of the addition sections and control sections, but fish originally residing in the addition sections, however, showed depressed growth rates relative to control sections. We therefore conclude that the density treatment was the cause of depressed growth rates in fish originally residing in the addition sections, and the cause of increased dispersal rates among translocated fish.

This study along with others (Gowan et al. 1994, Kahler et al. 2001) showed that mobility is the rule rather than the exception in stream salmonids, and that rates of site fidelity vary by a factor of 2.5

among stream reaches. Whether or not movement vs. site fidelity confers fitness advantages and hence contributes to population vital rates in anadromous populations depends on a multitude of other factors (Holtby et al. 1990, Quinn 2005); however, it underscores the importance of barrier-free corridors and continuous habitat (Deiner et al. 2007, Anderson et al. 2008). Our results also suggest that resident individuals suffer potentially detrimental fitness consequences of artificial stocking if such stocking increases densities to levels not supported by the environment.

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FIGURES AND TABLES

Figure 7.1

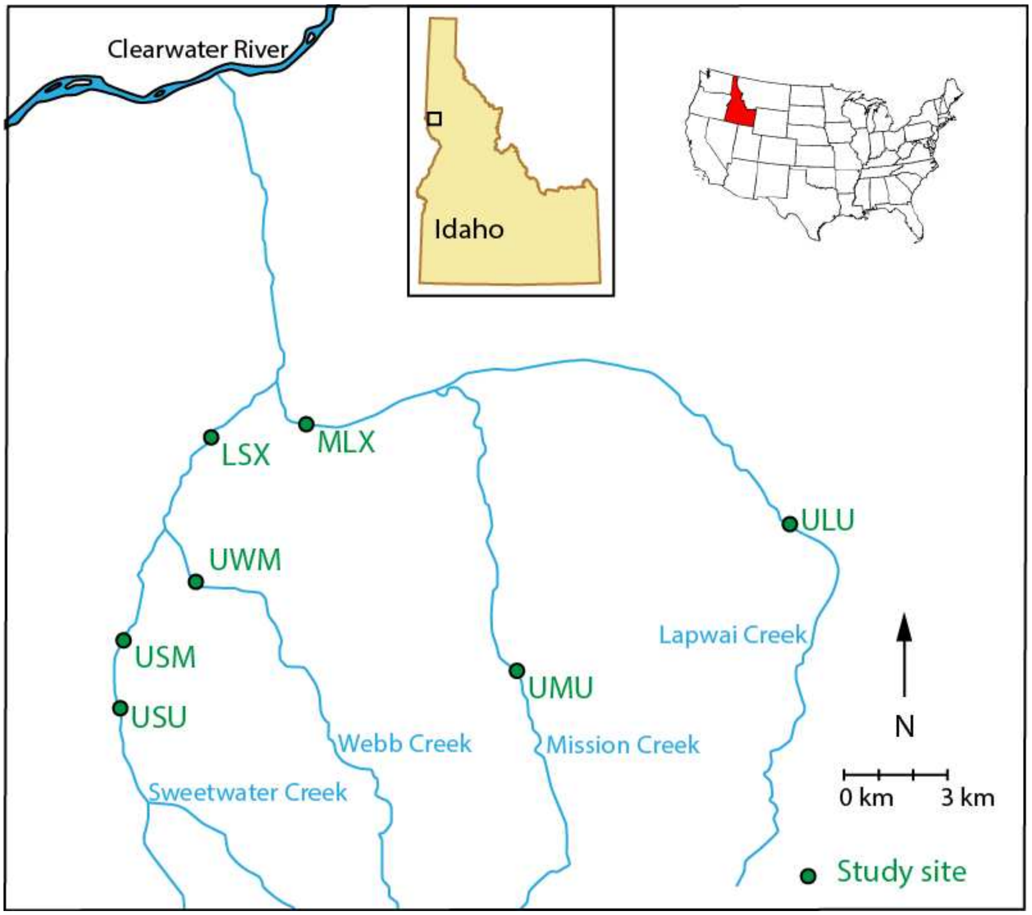

Figure 7.1. The map shows the four major streams in the Lapwai watershed and its location in North-Central Idaho, United States (insert). The Clearwater River is a tributary to the Columbia River.

Figure 7.2

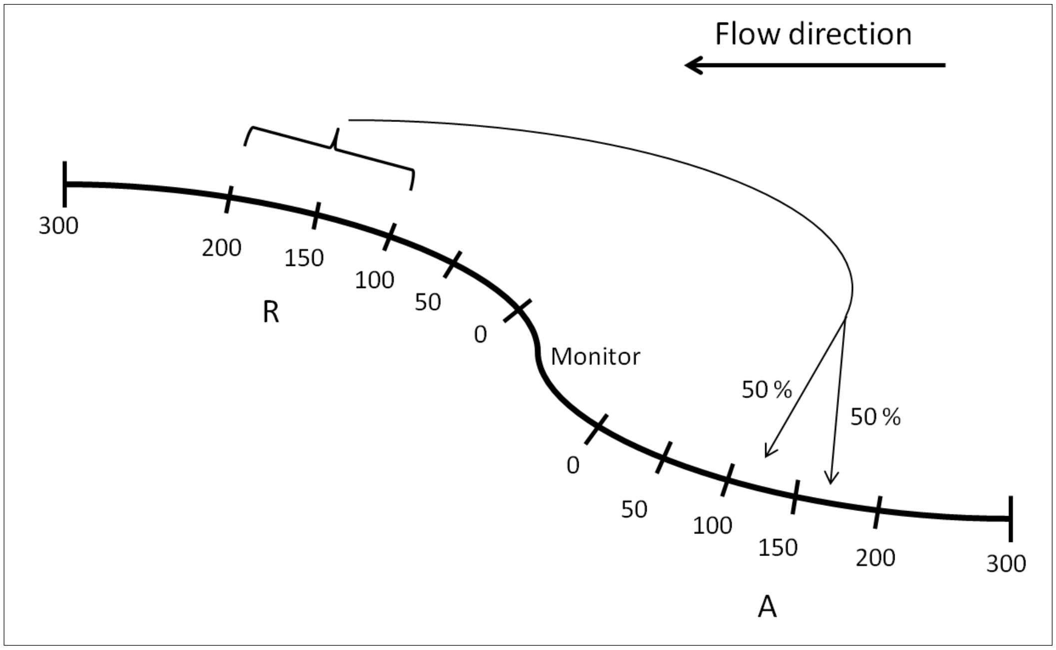

Figure 7.2. Experimental design for translocation of juvenile steelhead from two downstream sections to two upstream sections. Translocated fish were randomised and split evenly among the two upstream sections. “R” refers to removal sections, and “A” refers to addition sections.

Figure 7.3

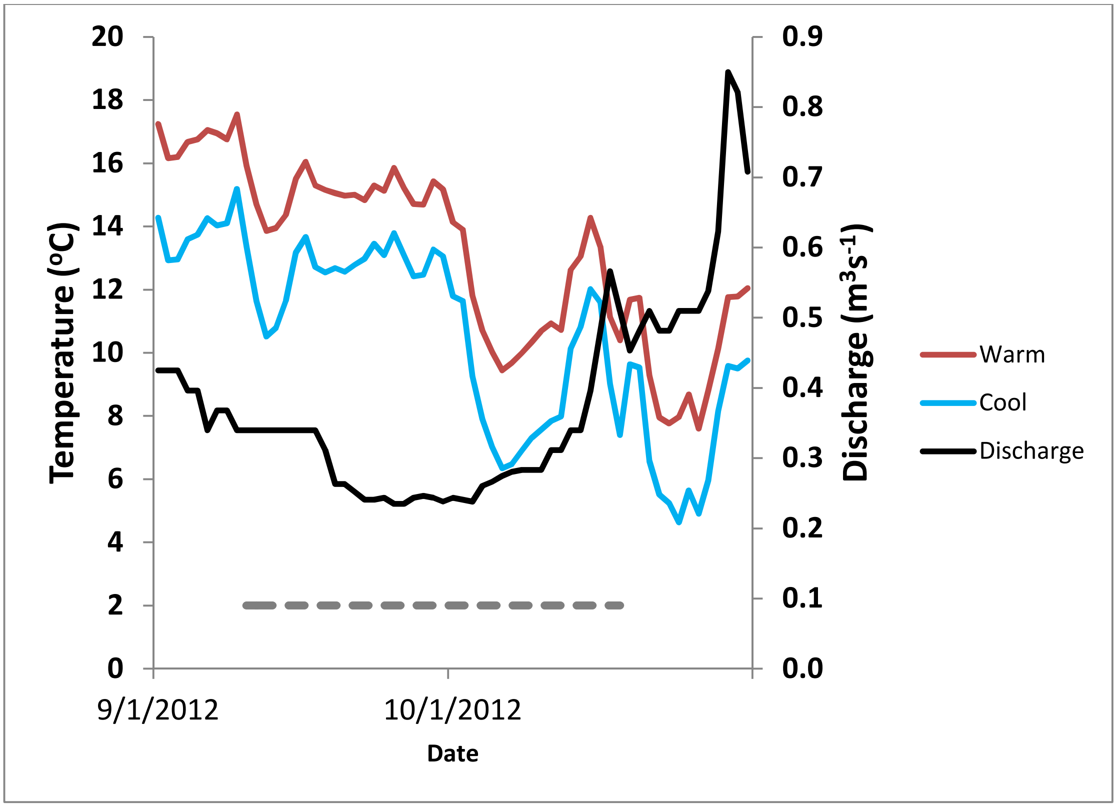

Figure 7.3. The study was undertaken before the increased flows in late fall as indicated by the dashed line. Discharge is projected on the right vertical axis (m^3s^{-1}) and temperatures from the warmest and coolest sites of the study are projected on the left vertical axis (^{o} C).

Table 7.1

Table 7.1. Predicted total densities of juvenile steelhead (no. 100 m^{-2}) and associated standard errors in parentheses by site and treatment categories for the seven study sites.

Site	Period	Control - 0 density (SE)	Removal - R density (SE)	Addition - A density (SE)
LSX	September	5.6 (0.2)	7.2 (0.02)	4.9 (0.5)
	October	5.1 (0.1)	5.9 (0.01)	4.2 (0.3)
MLX	September	7 (0.1)	3.9 (0.01)	7.0 (0.3)
	October	10 (0.1)	8.7 (0.02)	6.3 (0.4)
ULU	September	21 (0.2)	3.0 (0.007)	27 (0.3)
	October	18 (0.2)	1.6 (0.004)	36 (0.3)
UMU	September	40 (0.2)	37 (0.11)	45 (0.5)
	October	22 (0.1)	21 (0.06)	40 (0.5)
USM	September	27 (0.2)	20 (0.06)	45 (0.9)
	October	21 (0.2)	17 (0.05)	19 (0.4)
USU	September	20 (0.2)	19 (0.07)	35 (0.4)
	October	19 (0.2)	16 (0.05)	19 (0.4)
UWM	September	12 (0.1)	20 (0.05)	12 (0.3)
	October	25 (0.2)	25 (0.08)	18 (0.4)

Table 7.2

Table 7.2. Treatment size of the translocation of fish from removal sections to addition sections. The table shows the increase per 100 m^2, the new density in the addition sections (fish 100 m^{-2}), and the ratio between new and old density for both translocated fish and the fish originally residing in the addition sections.

Site	Treatment size (no.)	Density increase 100 m^{-2}	New density (100 m^{-2})	New:old for R fish	New:old for A fish
LSX	29	5.8	10	2.020	2.505
MLX	33	8.7	15	2.505	3.393
ULU	6	1.5	37	32.70	1.043
UMU	76	41.5	83	4.000	2.086
USM	57	16.5	35	2.276	1.993
USU	49	16.3	35	2.168	1.869
UWM	78	25.2	43	1.703	2.428

Table 7.3

Table 7.3. Physical habitat characteristics of the study reaches. Shown are the relative proportions of the channel geomorphic units (sum to 100 %), the percentages of undercut banks and overhanging vegetation (not mutually exclusive), the number of large woody debris pieces per 100 stream meters (count), the average pool depth (cm), and the average depth of the entire study reach. Standard deviations are shown in parentheses.

Site	% Pool	% Riffle	% Pocket	% Run	% Glide	% Undercut	% Overhanging	LWD 100 m^{-1}	Pool depth (cm)	Reach depth (cm)
LSX	22 (13)	62 (13)	2 (7)	9 (13)	4 (8)	35 (17)	48 (13)	20 (19)	59 (29)	37 (7)
MLX	24 (9)	31 (19)	0 -	27 (19)	18 (22)	9 (11)	46 (24)	6 (7)	54 (11)	36 (6)
ULU	31 (24)	28 (21)	5 (12)	22 (22)	14 (15)	6 (9)	39 (17)	4 (5)	41 (30)	30 (9)
UMU	19 (10)	23 (9)	41 (18)	15 (12)	2 (7)	5 (7)	26 (15)	11 (16)	40 (14)	31 (4)
USM	48 (14)	31 (12)	3 (6)	16 (13)	1 (4)	36 (17)	83 (13)	41 (33)	54 (8)	38 (4)
USU	22 (12)	44 (10)	11 (18)	23 (19)	0 -	20 (14)	76 (12)	28 (15)	40 (15)	31 (3)
UWM	19 (12)	49 (17)	14 (14)	16 (15)	3 (5)	15 (9)	46 (18)	17 (11)	47 (22)	31 (4)

Table 7.4

Table 7.4. Candidate models used to test hypotheses of determinants of site fidelity in 583 individually tagged subyearling steelhead and 868 yearlings. The data were modelled using mixed effects logistic regression models with the variables specified in each fixed-effects structure. Of these, 125 subyearlings and 342 yearlings remained in the study reaches. Also shown are the associated AIC values for each cohort.

Model	Model structure	K	AIC_i subyr	AIC_i yr
1	β_1 Initial mass	4	603.24	1159.64
2	β_1 Total density prior to translocation	4	603.17	1161.01
3	β_1 Yearling density prior to translocation	4	603.24	1160.09
4	β_1 Subyearling density prior to translocation	4	602.92	1160.76
5	β_1 Total density after translocation	4	602.14	1161.21
6	β_1 Total density after translocation + β_2 treatment size (#)	5	604.13	1162.8
7	β_1 Total density after translocation + β_2 treatment size (#m^{-2})	5	604.12	1162.93
8	β_1 Total density after translocation + β_2 treatment size (#m^{-2}) + β_3 interaction	6	605.85	1164.42
9	β_1 Not caught in removal section	4	601.19	1161.07
10	β_1 Not caught in addition section	4	603.24	1158.85
11	β_1 % pool	4	601.82	1157.39
12	β_1 % pool + β_2 pool depth + β_3 interaction	6	603.37	1155.26
13	β_1 % glide + β_2 % pool	5	603.48	1156.37
14	β_1 % riffle	4	600.9	1160.63
15	β_1 % riffle + β_2 section depth	5	602.87	1162.62
16	β_1 % riffle + β_2 overhanging + β_3 % overhanging(riffle)	6	602.81	1163.09
17	β_1 % pocket	4	602.69	1160.49
18	β_1 % pocket + β_2 % overhanging + β_3 % overhanging(pocket)	6	605.5	1163.54
19	β_1 % run	4	600.61	1160.9
20	β_1 % run + β_2 % overhanging(run)	5	602.47	1162.48
21	β_1 LWD m^{-2}	4	603.23	1160.9
22	β_1 LWD m^{-2} + β_2 % pool + β_3 section depth	6	605.42	1159.06

Table 7.5

Table 7.5. Distribution of all PIT-tagged individuals (left panel) and recaptured individuals (mid panel) by treatment category, and their site fidelity over the course of the study (right panel). *A* refers to sections to which fish were added, *R* to sections from which fish were removed, and *0* to control sections with no direct density treatment. The site fidelity panels display as proportions the overall retention of individuals in the study area and site fidelity in relation to treatment category.

	Distribution of all PIT tagged individuals				Distribution of recaptured individuals by treatment category				Site fidelity			
Site	Total	A	R	0	Total	A	R	0	overall retention	A to A, remain	R to A, stay	0 to 0, remain
LSX	86	9	14	63	15	0	1	14	0.17	0.00	0.00	0.19
USM	229	28	29	172	85	8	9	68	0.37	0.25	0.31	0.32
USU	212	23	23	166	88	14	9	65	0.42	0.61	0.17	0.32
UWM	310	32	45	233	65	4	11	50	0.21	0.13	0.04	0.18
MLX	159	12	17	130	40	2	4	34	0.25	0.17	0.18	0.22
ULU	250	80	2	168	105	45	0	60	0.42	0.49	0.00	0.33
UMU	205	29	20	156	69	13	6	50	0.34	0.34	0.20	0.30
Total	1451	213	150	1088	467	86	40	341				
Average (SD)									0.32 (0.10)	0.28 (0.21)	0.13 (0.12)	0.27 (0.07)

Table 7.6

Table 7.6. The table shows the models from Table 4 with the highest relative support based on Akaike's Information Criterion. Shown are the variance of the random intercept (α), the chi-square likelihood ratio test for the random intercept (H_0: $\alpha=0$), parameter estimates (β) and their associated P-values, and the Akaike weight (w_i) for the models. Standard errors are given in parentheses where appropriate.

Cohort	Model	α_i (SE)	$P>\chi$	β_0 (SE)	P	β_1 (SE)	P	β_2 (SE)	P	β_3 (SE)	P	w_i
Subyr.	9	0.46 (0.28)	0.002	-2.05 (0.46)	<0.0001	0.654 (0.47)	0.17					0.10
	11	0.42 (0.26)	0.0031	-1.77 (0.30)	<0.0001	1.17 (0.97)	0.23					0.07
	14	0.43 (0.27)	0.003	-0.959 (0.36)	0.0099	-1.33 (0.88)	0.13					0.11
	19	0.51 (0.28)	0.001	-1.81 (0.28)	<0.0001	1.51 (0.97)	0.12					0.13
yr	12	0.11 (0.077)	0.0222	-0.497 (0.39)	0.209	2.61 (1.23)	0.03	-0.00963 (0.0083)	0.244	-0.0176 (0.020)	0.3854	0.33
	13	0.13 (0.082)	0.0116	-0.722 (0.18)	0.0002	-2.31 (1.14)	0.09	1.10 (0.54)	0.0416			0.19

Figure 7.4

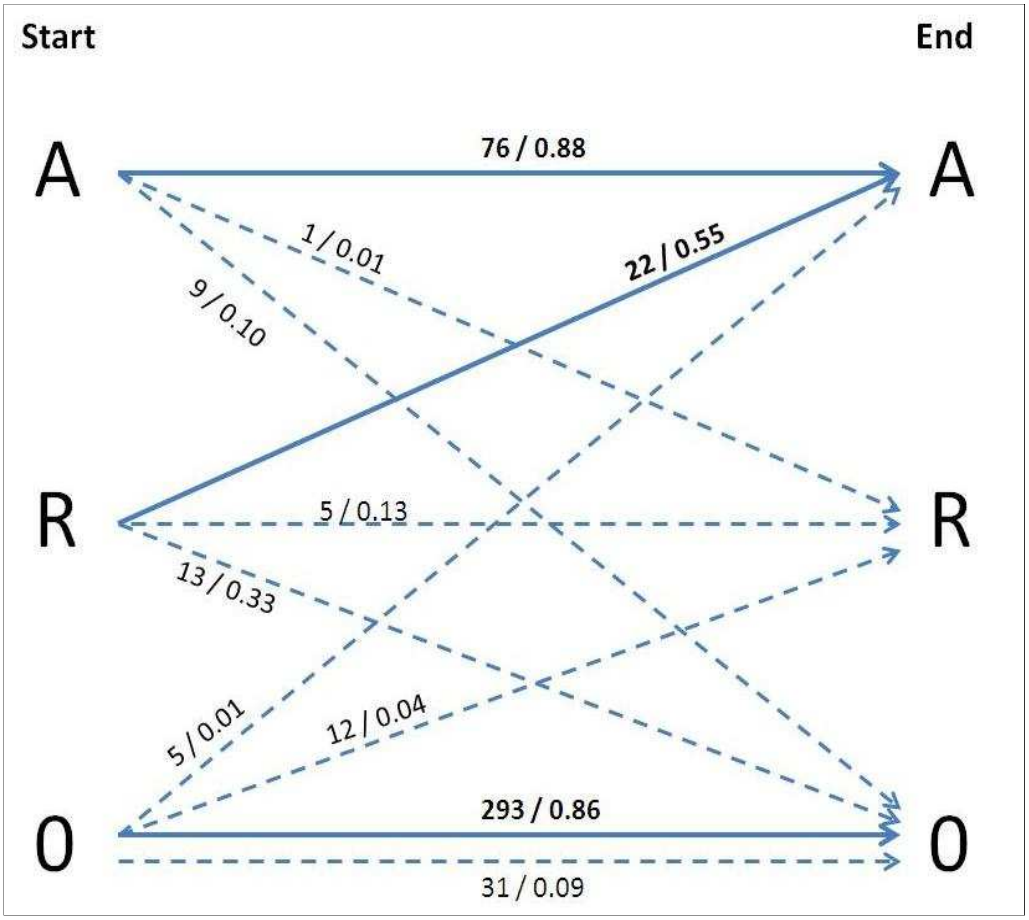

Figure 7.4. Movement pathways by treatment category over the 28 day experiment, showing the number of fish that remained or moved, and the proportion of the initial population this constituted. Solid lines denote fish that exhibited site fidelity to their section (for translocated fish this refers to those that stayed in their new section, A) and dashed lines refer to fish that moved to a different section category.

Table 7.7

Table 7.7. Average growth (% day^{-1}) rates for fish that exhibited site fidelity in relation to the treatment category. Standard deviation is given in parentheses.

Site	A to A, remain	R to A, stay	0 to 0, remain
LSX	na	na	0.57 (0.59)
USM	0.09 (0.19)	0.15 (0.20)	0.32 (0.39)
USU	0.27 (0.27)	0.45 (0.62)	0.16 (0.26)
UWM	0.25 (0.14)	0.46 (0.41)	0.47 (0.33)
MLX	0.44 (0.98)	1.31 (0.64)	1.11 (0.61)
ULU	0.09 (0.23)	na	0.46 (0.54)
UMU	0.17 (0.23)	-0.13 (0.03)	0.18 (0.31)

CHAPTER 8: SUMMARY AND SYNTHESIS

Knut Marius Myrvold

INTRODUCTION

From both a fundamental and applied perspective there is great interest in identifying the factors by which any population is limited, and at what levels density-dependence is operant (Sinclair and Pech 1996, Hixon et al. 2002, Gaillard et al. 2010). For imperiled taxa such as anadromous salmonids a critical step in recovery and management is to identify these factors. Anadromous salmonids have complex life histories and use a vast range of habitats and environments to fulfill their life cycle. Each environment and life stage has its own associated limitations that pose constraints on the individual and the population (Bjornn and Reiser 1991, Quinn 2005).

This dissertation concerned the juvenile stream-rearing stage of steelhead. The primary goal was to identify mechanistic linkages between individual- and population-level demographic parameters and their environment, and to understand how population processes operate to shape individual performance. The study system was a population of Snake River steelhead in Lapwai Creek, Idaho. The population was listed under the Endangered Species Act due to population declines and alterations to its habitat in parts of the watershed (NMFS 2006). Because of the listing, a monitoring program was mandated to evaluate the population trend as well as individual performance. In addition to answering the Lapwai-specific problem, we also used the effort to investigate patterns and processes of interest to the field of ecology.

The preceding chapters were written as stand-alone manuscripts which concerned tests of hypotheses of general ecological relevance, as well as fisheries ecology and management in particular, using the Lapwai Creek steelhead population as a study system. A distinction was made in the introductory chapter between the applied, site-specific problem, and the questions asked in the manuscripts, which had more general relevance to the field of ecology. These components are, however, part and parcel of the same objective, namely to understand which factors govern the stream-rearing cohorts of steelhead. The rationale for attaining a general perspective and reporting the findings as tests of ecological theory was to make the findings applicable to other systems.

Because the dissertation consists of stand-alone manuscripts, there was not a systematic treatment of all the factors that could influence the overall objective. Clearly, a unified treatment of the main findings could yield insights that were not evident or appropriate in the individual chapters. The purpose of this chapter is to summarize and synthesize the findings. I will give an overview of the main patterns in the habitat, individual, and cohort density data; address some alternative factors that were not reported in this dissertation; summarize the main patterns and processes identified in the preceding chapters; synthesize these main findings; and finally address some implications for recovery and management.

PATTERNS IN THE DATA

Densities

Densities of juvenile steelhead varied among sites at any given point in time and within sites over time. The overall pattern was a decline in densities in all the sites over the course of a season, for both yearling and subyearling steelhead. Densities of subyearlings were typically higher than densities of yearlings, but less consistent among years.

The general pattern of higher subyearling and total densities on the second visit than on the first visit was driven by gear selectivity. In most cases, with the exception of lower elevation, mainstem sites (sites LLL and LLU), subyearling steelhead were too small (< 40 mm) to recruit to the sampling gear during the first visit of each season. Despite their presence in the streams they were consequently not accounted for in the density estimates for the first visit(s).

There were consistent patterns in the density differences across years. Densities tended to be higher for both cohorts in the uppermost study sites, and consistently so for yearlings. The lowermost study site LLL, and the lowermost study site on Sweetwater Creek, LSX, tended to have the lowest densities.

Growth rates

Growth rates were consistently higher and less variable for subyearlings than for yearlings, and this pattern was consistent across sites, over the course of a season, and among seasons. Over the course of the sampling season, average subyearling growth rates tended to taper off, with the highest growth typically achieved in August (second growth period, between the second and third visit). During this time the growth rates for yearling steelhead were the lowest.

There was considerable growth variation among yearling individuals in a site, as represented by the error bars. Within a growth period (one month during the course of the study) there was also considerable variation among sites. Whereas most individuals grew on the order of 1.2 % of their body mass per day in some sites, most individuals in other sites lost on average 0.4 % of their body mass per day.

Physical habitat

The in-channel habitat in the uppermost study sites was characterized by coarse substrate, shallow depths, and relatively slower flow velocities. At sites lower on each tributary and below the confluences the same metrics were characterized by finer substrate, deeper and more variable depths, and faster flow velocities.

There was overall more overhanging vegetation in the uppermost sites, but there was variation among the streams due to differential constraints on the channels from levees and land use. Below the confluences (MLX and LSX) and on the mainstem reaches (LLL and LLU) more lateral movement and/or formation of large gravel bars in combination with larger widths caused less overhanging cover. There was evidence of significant redistribution of channel morphology from year to year, owing to high peak runoff-to-baseflow ratio and mobile substrate. The relative rank among the sites in these metrics was overall the same, and reflected higher-level (watershed) constraints.

The drainages above each study site differed greatly with respect to drainage area, topography, geology, land use, and land cover. The lowermost site (LLL) represented the average conditions in the entire watershed, whereas the drainages to sites on each unique tributary were more similar to each other than to those of other unique tributaries. Across unique drainages, more forest cover and more surficial volcanic rock was associated with the uppermost study sites. Further, among the three sites on each tributary, the proportion of steep topography was lower in the uppermost and higher in the lowermost study site, corresponding to the canyon landscapes of the watershed.

Hydrograph

The annual hydrograph for Lapwai Creek was dominated by two main seasons: baseflow conditions from July to October (little or no precipitation), and rain and a mix of snowmelt and rain from November through May. Flood severity within these two seasons was mainly explained by rain on snow events during the wet season in winter and spring, and by precipitation events in summer and fall. Fish sampling occurred during the dry season, and began when flows were low enough to allow efficient electrofishing, which was around mid June in each year.

Temperatures

The thermographs showed similar overall patterns and relative rank from year to year. The hottest temperatures were encountered from mid July through August, with the exception of 2010 when unseasonably cold weather dominated from mid August. Temperatures were the highest in 2012, with average temperatures in some sites exceeding 20 ^{o}C from early July through mid August.

There was a difference between the coolest and warmest site in the order of 4 ^{o}C on average, with the largest difference observed during the warmest part of summer and in late October, and the smallest difference observed during the early summer warming and late summer cooling trends. The warmest study sites were MLX and UML, which both flow through open valleys with very limited shading, have limited lateral movement due to levees, and exposed substrate along the banks. The coolest sites were USU and USM, which are below the diversion dam on Sweetwater Creek, have stable flows due to the minimum flow requirements (BOR 2009), and ample shading from riparian vegetation.

In summary, the patterns of these demographic rates were complex in and of themselves, and substantially more so when considering the rates in relation to each other and the habitat. Therefore, a more formal treatment was in order to understand their interrelationships, which was done in the preceding chapters. The next section discusses the findings from these chapters, and draws on the above summary of the environmental data.

MAIN FINDINGS

At a more integrated level, the preceding chapters investigated the patterns and processes of the relationships among the biotic and abiotic factors encountered in the study system. Below follows a discussion of the main findings from these analyses.

We documented an overall high proportion of mobile steelhead relative to the proportion exhibiting site fidelity (range 58 – 83 % between the seven study sites, at the scale of 700 stream meters). Among the fish that were retained in the study system, most individuals exhibited site fidelity at the scale of 50 m. Habitat (channel configuration) was overall a better predictor of site fidelity than were biotic factors and individuals characteristics. Yearling steelhead were more likely to remain in sections with higher amounts of pool habitats. For subyearling steelhead there was no single factor that explained site fidelity, which was reflected in their overall higher mobility (79 %).

Densities were consistently (i.e. within years and across years) higher in the uppermost study sites, and more variable in the rest. Because such a description is not mechanistic and bears little applicability to other systems, the approach we took to understand the potential processes causing this pattern was to identify the habitat factors responsible. When comparing all models, models that combined watershed-scale topography and instream-scale variables pertaining to flow (velocity and discharge) performed better in describing densities of subyearling steelhead and total densities, whereas the instream-scale model flow velocity was the single best approximating model of yearling densities. A quadratic model of flow velocity was either the single best or among the best approximating instream-scale models for both subyearling and yearling steelhead, depicting a downward concave relationship in both cases.

Self-thinning patterns were statistically significant in only three out of 32 possible cases, and the slopes were shallower than predicted by the territory space-, consumption-, and metabolism hypotheses; however, most cohorts exhibited a negative relationship between mass and density. This shows that the cohorts in most study sites were below the carrying capacity of the environment. Certain abiotic factors could explain a relatively large portion of the variation in the strength of the self-thinning slopes. For subyearling steelhead, the slopes were negatively related to metabolic cost in the warmest months, explaining 44 % to 46 % of the variation, respectively. Physical habitat variables were more important in describing the thinning slopes of yearling steelhead. The variation in thinning slope was best explained by substrate size, corresponding to stronger thinning occurring in the uppermost study reaches.

We found that growth rates in both age classes were negatively related to the total population densities, but that growth rates in one age class were inconsistently affected by the densities of the other age class. Whereas subyearling growth rates were negatively related to yearling densities, the opposite situation was not the case. The best approximating models for both subyearling and yearling steelhead also included individual mass and average mass in each cohort. There was substantial variation in the density dependence among the sites, corresponding to differences in cohort densities and stream productivity. The results demonstrate that density dependence can pose constraints on individual growth rates at low densities (< 1 fish m^{-2}), and underscore the importance of considering age classes separately when studying density dependence in age-structured populations.

Individual growth rates were negatively related to fish mass (slopes of the two best approximating models were both -0.024). Comparing growth rates from 16 different stream reaches throughout the watershed, we found that temperature-induced metabolic cost was the single best approximating model of the variation in individual growth rates. The bioenergetics model showed that mass-specific metabolic costs decreased with mass, but the absolute energetic demands increased over the same size range. Because temperature had a multiplicative effect on metabolic cost, our results suggest that the effect of food limitation increased with fish size. High water temperatures can thus pose energetic bottlenecks and can be a potentially strong mechanism limiting growth in juvenile salmonids in summer, particularly as streams in the region experience warming trends.

In summary, the results show that individuals are probably sampling the habitat conditions at scales previously thought to exceed their capabilities; there exist abiotic controls on the densities of juvenile steelhead that are consistent over time; self-thinning will occur under certain conditions, but that the phenomenon is not necessarily widespread or consistent across a heterogeneous watershed; density-dependence affects cohorts differentially; and temperature is important for population dynamics, because it can impose energetic bottlenecks on entire cohorts of juvenile salmonids.

ALTERNATIVE FACTORS NOT REPORTED IN THE DISSERTATION

No field study can address every possible factor influencing the response metric of interest. Other factors than the ones examined in this dissertation could be of importance to the variation in abundance and performance of steelhead that we observed. These include interspecific competition, predation, recruitment limitation, legacy effects from the Lewiston Orchards Project, water quality, and stochastic events. Other factors deemed unlikely to have any visible effect included predation by birds and mammals and angling. Although not reported in this dissertation, we did investigate most of the likely factors, and these are addressed below.

We investigated the extent to which predation in the early free-swimming phase could be of any importance to cohort size and density variation (Taylor et al. *in preparation*). Predation on juvenile salmonids during the early emergent period has been suggested an important factor in the literature (Quinn 2005). The study was conducted in May and June 2012 and involved the documentation of the presence of steelhead alevins in the stream margins, capture of sculpin (*Cottus sp*.) on site, and examination of the diets of 360 sculpin. We found no evidence of predation on steelhead alevins and fry by sculpin (none of the stomach samples contained salmonids), and concluded that predation at this stage is non-existent.

To address whether densities of subyearlings could be determined by the number of spawning adults (recruitment limitation) or habitat quality once hatched, we attempted to enumerate the distribution and abundance of spawners by conducting visual surveys and radiotagging (Myrvold and Kennedy, *unpublished data*). This effort proved to be significantly hindered by the flow conditions. We were unable to catch adults for tagging due to high discharge during spawning (steelhead ascend the tributary streams of the Clearwater River in March, which is when flows are at their annual maxima). Further, due to poor visibility, or very short periods of ample water clarity, surveying steelhead redds was not feasible at a statistically reliable scale. We concluded that the most likely method to yield reliable numbers of adults and document their distribution is by radiotagging, and that capturing requires operation of a weir.

A post-hoc method involving surveying the relative abundance of post-emergent alevins and fry in stream margins (Myrvold, *unpublished data*) proved to be a useful method for detecting and enumerating fry. Fry surveys could be a useful tool to index upstream spawning events, albeit on a coarse resolution. The main limitation, however, was the inability to linking the observed distributions of juveniles to the number of spawners. We could therefore not elucidate the success of spawning events among the streams.

With the exception of anecdotal accounts (Johnson and Stangl 2000), addressing the potential legacy effects (*via* potential recruitment limitation) from the Lewiston Orchards Project in Upper Sweetwater and Webb creeks was limited by the lack of data from the period prior to the establishment of minimum flows in 2006 (NMFS 2006). We hence had to rely on examining the trends in the juvenile steelhead data. Densities in these streams increased throughout the course of the study, and showed evidence of density-dependent growth. It is likely that these streams see fewer returning adults due to potential legacy effects, but this effect can be compensated for by higher survival in the early juvenile stages. It is therefore difficult to accurately quantify the extent to which these potential legacy effects act on the parr stage.

Stochastic events such as flash floods or extreme flooding following rain on snow can significantly affect the size of entire cohorts. However, due to their infrequent occurrence such events were not effectively documented with the study design. Therefore, rather than a formal treatment in the analyses we relied on our knowledge about these events as auxiliary accounts when analyzing the data.

Finally, we did not investigate the effects of interspecific competition on the abundance and performance of juvenile steelhead. Among the species present, coho, pikeminnow, and redside shiner have the most similar diet and feeding niche as steelhead. Among these three species, we found redside shiner having the widest sympatric overlap with steelhead in space and time (Myrvold, unpublished data). Redside shiner are known to affect steelhead behavior, particularly at high temperatures (Reeves et al. 1987, Tinus and Reeves 2001), and could therefore theoretically have an effect on the reported results. However, the extent of sympatric habitat use was restricted to the lowermost study sites and primarily the months of June, July, and August, and the numbers of redside shiner were typically low compared to steelhead numbers. We therefore concluded that these effects were minor, if any.

SYNTHESIS

In discussing the patterns and processes of the size and change of juvenile steelhead cohorts, it is useful to consider the general factors that constrain population sizes. As noted in the previous chapters, identifying the principal determinants of population abundance is one of the main questions in ecology, and also one of the most widely disputed (Nicholson 1933, Andrewartha and Birch 1954). The discussion has centered on the question of whether and how populations are regulated at their upper limits by factors that slow down the intrinsic rate of increase (Begon et al. 1996, Hixon et al. 2002). While it is clear that density dependent processes are necessary to *regulate* a population (Murdoch 1994, Turchin 1995), their importance in *determining* abundance is much more contingent on the species' life history characteristics and the environment it inhabits, in which factors that act independent of population density can strongly limit its size. Abundance is hence determined by the combined effect of all factors and processes that act on the population, dependent or independent of its density (Begon et al. 1996, Sinclair et al. 2005).

At the most general level, it then seems likely that abiotic factors such as channel morphology, flow regime, and temperature control the initial cohort size through constraints on the distribution of suitable spawning grounds, determine the suitability of the channel habitat for fry and parr, and impose constraints on the standing stock irrespective of its density later in ontogeny (Jensen and Johnsen 1999, Hicks and Hall 2003, Quinn 2005, Fausch 2010). These factors are operant regardless of population density, and hence limit the abundance and in turn the potential for density-dependent processes. Further, these factors are all dynamic in space and time, and represent gradients rather than discrete conditions (Gibson 2002, Ebersole et al. 2006, Anderson et al. 2008). Consequently we would expect variation in individual performance and cohort densities in relation to the abiotic controls.

For survivors in a given environment, density-dependent processes further regulate the cohort size, in turn affecting the conditions for individuals. Regulation only occurs when the population growth rate depends on its own density (Turchin 1995, Sinclair and Pech 1996, Sibly and Hone 2002). Whereas mortality and reproduction *directly* affect the numbers of individuals, other responses such as density-dependent changes in individual growth rate or movement, are *indirect*, and must lead to changes in mortality rate or reproductive success if they are to affect population size (Rose et al. 2001). In juvenile stream salmonids, growth rate has been shown to be a significant factor in determining ontogenetic status, life-history strategies, and ultimately, survival of individuals (Ward et al. 1989, Holtby et al. 1990, Metcalfe 1998, Kahler et al. 2001, Satterthwaite et al. 2010). Density-dependent growth is hence a fundamental mechanism of population regulation in organisms with flexible and indeterminate growth (Sogard 1997, Rose et al. 2001, Einum et al. 2006), and the effects can be visible even at low densities (Jenkins et al. 1999).

Ontogenetic shifts can also cause changes in densities that are not a direct result of current density-dependent processes or environmental conditions (Bjornn and Reiser 1991). In anadromous species the outmigration of one cohort frees up the habitat for remaining cohorts, hence decreasing the competition and improving the conditions for individual growth. Over the course of their juvenile life history, steelhead and other stream salmonids have defined and oftentimes stage-specific requirements (Nislow and Armstrong 2012). What constitutes good habitat for one cohort does not necessarily mean it is equally good for another (Rosenfeld and Boss 2001).

Based on these general principles, we can propose a sequence for the determination, limitation, and regulation of juvenile cohorts in the Lapwai Creek study system.

The initial cohort size (of free-swimming fry) is the product of the number of spawners, suitability of the spawning habitat, and the success of the spawning events. Particularly, the number of alevins is the product of the number of redds and the success of each redd. We found that predation during this stage is of little or no importance, so that the newly emerged fry are governed to a larger degree by the abiotic conditions. Redistribution of alevins to holding habitats and territories (Elliott 1994, Quinn 2005) is thought to occur in May as the hydrograph tapers off (Taylor et al. in preparation). During this period, discharge and channel flow velocity are important factors that can affect the survival and distribution of individuals (Holtby and Healey 1986, Bjornn and Reiser 1991). We began the monitoring of juveniles once the streams were about to reach summer baseflow, and were consequently sampling after this major redistribution had occurred.

When the snowmelt and late spring precipitation stop, the streams in Lapwai rapidly approach baseflow, and the stream temperatures increase sharply. The period of optimal temperatures for growth (12-17 ^{o}C) can hence be rather short, as observed in 2010. High temperatures alone can pose energetic bottlenecks, and more so in the presence of competition. When densities are high, competition increases as juveniles grow in size and individual demands increase. We did observe self-thinning patterns in a few cases when cohorts were at the carrying capacity of the environment, and this pattern was more evident with increasing thermal stress. Further, with yearling fish present, subyearlings showed depressed growth rates. In cases where densities were lower (i.e. not saturated relative to the capacity of the habitat), growth opportunities for the individual are ample, and density dependence may not manifest in increased mortality or emigration. However, we did observe density-dependent growth even at low densities. This likely owes to asymmetric competition among individuals (Abbott and Dill 1989, Höjesjö et al. 2002), which is evident when examining the individual growth variation.

In determining the relative importance of density-dependent and –independent factors on the abundance of juveniles, the short answer is that it depends highly on the context and the life stage. The strength of the density-dependent processes hence depends on the initial cohort size and the prevailing abiotic conditions, temperature in particular. The initial cohort size is determined by a combination of spawner abundance and –distribution, and their success. The distribution of spawners and their success depend, in addition to the number of spawners, largely on the availability of suitable substrate, which are controlled by the flow regime and the physiographic setting of the stream segment.

MANAGEMENT IMPLICATIONS

Although the focus of this dissertation was to test hypotheses of fundamental interest, the findings have applied value in that they can inform management of steelhead and other stream salmonids. Before going into the specific guidelines, it can be useful to review why and how the Lapwai Creek steelhead population was a useful study system. First, the study system was useful for studying the relationship between population size and individual performance through compensation. When the habitat quality is ample, but densities are low for other reasons, the plasticity in the indeterminate growth pattern of salmonids causes the individuals present to achieve measurably better growth. Secondly, with most water bodies being impacted by competing demands for water (Poff and Zimmerman 2010), the Lapwai Creek watershed provided a realistic study system, with visible changes to the channel and floodplain habitats, and direct changes to the flow regime. Finally, despite substantial alterations, the watershed still holds naturally reproducing, wild steelhead, which show evidence of natural population processes.

Any management strategy is faced with the challenge that the scale of the solution has to match the scale of the problem in order to be effective. Being situated above eight hydropower dams on the Snake and Columbia rivers, in a region facing a changing climate- and precipitation regime (Barnett et al. 2004, 2005, Isaak et al. 2010), the challenges appear daunting when considering the viability of the Lapwai steelhead population. However, getting back to the key point that limiting factors at each stage must be identified in a mechanistic manner for effective management and recovery, each study of each stage can contribute to the overall understanding of the problem, and aid in the recovery of populations.

Results from this work set up some important guidelines for the juvenile stream-rearing stage. Due to compensatory mechanisms and indeterminate growth in salmonid populations, there is not a 1:1 relationship between the number of fry and parr, and between smolts and returning adults (Rose et al. 2001). Lower abundances result in less competition and improved individual fitness, which could ameliorate the effect on reduced numbers on population-level vital rates (Holtby et al. 1990, Sogard et al. 2009, Satterthwaite et al. 2010). A corollary to this is to not artificially stock populations that show evidence of density dependence in their vital rates, not to mention the effects of genetic introgression.

The results show a strong influence of temperature on individual performance as well as population-level processes. Management actions that can reduce excess thermal stress (Poole and Berman 2001, Olden and Naiman 2010) such as facilitating upland land use practices that increase the snow storage capacity (such as ample canopy cover; Jutila et al. 1999), riparian shading (Hicks et al. 1991, Mellina and Hinch 2009), and in-stream structures that provide deep pools (Nielsen et al. 1994). These management strategies do not match the scale of the fundamental problem of overall warming and altered precipitation regimes (Barnett et al. 2004), however, restoring degraded channels have the added benefit of improving thermal regimes.

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APPENDIX 1

Energy density (ED, J/g wet weight) values by taxonomic groups used in the bioenergetic model. The values for energy density and wet to dry ratio were obtained from the cited references either directly, averaged over the widest range of published values for the taxonomic group (a), or borrowed from the closest possible taxonomic level (b).

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PHYLUM/ Class	*Order*	*Family*	*Life stage*	*Ratio dry:wet*		*ED wet*		*Notes*	*Ref.*
PHYLUM ANNELIDA									
Hirudinea	Annelida	Hirudinea	Any	0.250	a	5795	a	Based on *Erpobdella octoculata*, *Glossiphonia complanata*, and *Theromyzon rude*	1
Oligochaeta	Annelida	Oligochaeta	Any	0.095	a	2042	a	Based on *Lumbricus* sp., *Limnodrilus hoffmeisteri*, *Dero limosa*, *Branchiodrilus semperi*, and *Megascolex mauritii* (3)	2,3
PHYLUM ARTHROPODA									
Arachnida	Arachnida	Arachnida	Any	0.214	b	9686	b	Borrowed from terrestrial class Arthropoda	3
Arachnida	Hydracarina	Hydracarina	Any	0.160		4342		Based on *Limnochares* spp.	1
Collembola	Collembola	Collembola	Any	0.214	b	9686	b	Borrowed from terrestrial class Insecta	3
Crustacea	Amphipoda	Amphipoda	Any	0.200	a	3305	a	Based on *Hyalella azteca* and *Gammarus lacustris* (1)	1,3
Crustacea	Decapoda	Decapoda	Any	0.250	b	4506		Borrowed from Isopoda	3
Crustacea	Isopoda	Isopoda	Any	0.250		3142		Based on *Sphaeroma rugicauda*	3
Insecta	Coleoptera	Amphizoidae	Adult	0.290		6387		Borrowed from adult Coleoptera	1
Insecta	Coleoptera	Chrysomelidae	Unknown	0.400		8748		Based on *Chrysochus auratus* (terrestrial)	3
Insecta	Coleoptera	Chrysomelidae	Larva	0.200	b	4317	b	Borrowed from larva Coleoptera	1
Insecta	Coleoptera	Coleoptera	Larva	0.200		4317	a	Based on *Agabus bifarius* (Dytiscidae)	1
Insecta	Coleoptera	Coleoptera	Adult	0.290		6387			5
Insecta	Coleoptera	Curculionidae	Larva	0.200	b	4317	b	Borrowed from larva Coleoptera	1
Insecta	Coleoptera	Curculionidae	Adult	0.353		6947			6
Insecta	Coleoptera	Elmidae	Larva	0.200	b	4317	b	Borrowed from larva Coleoptera	1
Insecta	Coleoptera	Elmidae	Adult	0.290	b	6387	b	Borrowed from adult Coleoptera	5
Insecta	Coleoptera	Hydrophilidae	Larva	0.290	b	6387	b	Borrowed from adult Coleoptera	5
Insecta	Coleoptera	Psephenidae	Larva	0.200	b	4317	b	Borrowed from larva Coleoptera	1
Insecta	Coleoptera	Staphylinidae	Adult	0.290	b	6387	b	Borrowed from adult Coleoptera	5
Insecta	Dermaptera	Dermaptera	Adult	0.214	b	9686	b	Borrowed from terrestrial class Insecta	3
Insecta	Diptera	Ceratopogonidae	Larva	0.190	b	4392	b	Borrowed from larva Chironomidae	1,7
Insecta	Diptera	Chironomidae	Unknown	0.200	b	2745		Average of adult and juvenile Chironomidae	3
Insecta	Diptera	Chironomidae	Pupa	0.205	a	5041	a	Based on *Ablabesmyia pulchripennis* and *Camptochironomus tentans*	1

Insecta	Diptera	Chironomidae	Larva	0.190	a	4392	a	Based on *Psectrotanypus guttularis*, *Camptochironumus tentans*, and *Phytotendipes barbipes*	1,7
Insecta	Diptera	Chironomidae	Adult	0.080		1747		Based on *Camptochironumus tentans*	1
Insecta	Diptera	Diptera	Unknown	0.124	b	2565		Average of juvenile and adult Diptera	3
Insecta	Diptera	Diptera	Pupa	0.205	a	5041	a	Based on *Ablabesmyia pulchripennis* (Chironomidae), *Camptochironumus tentans* (Chironomidae), and *Aedes canadensis* (Culicidae)	1
Insecta	Diptera	Diptera	Larva	0.168	a	2872	a	Based on *Psectrotanypus guttularis* (Chironomidae), *Camptochironumus tentans* (Chironomidae), *Phytotendipes barbipes* (Chironomidae), and *Tubifera* sp. (Syrphidae) (1); based on Chironomidae, Limoniidae, and Athericidae (3)	1,3
Insecta	Diptera	Diptera	Adult	0.080		1747		Based on *Camptochironumus tentans* (Chironomidae)	1
Insecta	Diptera	Dixidae	Larva	0.168	b	2872	b	Borrowed from larva Diptera	1,3
Insecta	Diptera	Dolichopodidae	Larva	0.168	b	2872	b	Borrowed from larva Diptera	1,3
Insecta	Diptera	Empididae	Larva	0.168	b	2872	b	Borrowed from larva Diptera	1,3
Insecta	Diptera	Ephydridae	Larva	0.168	b	2872	b	Borrowed from larva Diptera	1,3
Insecta	Diptera	Psychodidae	Larva	0.168	b	2872	b	Borrowed from larva Diptera	1,3
Insecta	Diptera	Simuliidae	Pupa	0.205	b	5041	b	Borrowed from larva Diptera	1,3
Insecta	Diptera	Simuliidae	Larva	0.168	b	2872	b	Borrowed from larva Diptera	1,3
Insecta	Diptera	Simuliidae	Adult	0.080	b	1747	b	Borrowed from adult Diptera	1
Insecta	Diptera	Stratiomyidae	Larva	0.190		1676		Based on *Stratiomys* spp.	1
Insecta	Diptera	Tipulidae	Larva	0.168	b	2872	b	Borrowed from larva Diptera	1,3
Insecta	Ephemeroptera	Baetidae	Unknown	0.182		4703		Borrowed from larva Baetidae	3
Insecta	Ephemeroptera	Baetidae	Larva	0.182	a	4706	a	Based on *Baetis* and *Callibaetis*	1,7
Insecta	Ephemeroptera	Ephemerellidae	Larva	0.153		3266		Based on *Ephemerella*	7
Insecta	Ephemeroptera	Ephemeroptera	Larva	0.240		4706	a	Based on *Baetis* and *Callibaetis*	1,7
Insecta	Ephemeroptera	Ephemeroptera	Adult	0.220		5073		Based on *Callibaetis* (Baetidae)	1
Insecta	Ephemeroptera	Heptageniidae	Larva	0.154	a	3882	a	Based on *Rhithrogena*, *Ecdyonurus*, and *Epeorus*	7
Insecta	Ephemeroptera	Leptophlebiidae	Larva	0.240	b	4706	b	Borrowed from Ephemeroptera	1,7
Insecta	Ephemeroptera	Leptophlebiidae	Adult	0.220	b	5073	b	Borrowed from Ephemeroptera	1
Insecta	Hemiptera	Aphididae	Any	0.240	b	5210	b	Borrowed from order Hemiptera	1
Insecta	Hemiptera	Cicadellidae/Cercopidae		0.240	b	5210	b	Borrowed from order Hemiptera	1

Insecta	Hemiptera	Corixidae	Any	0.360		8076		based on *Callicorixa audeni* (Corixidae)	1
Insecta	Hemiptera	Gerridae	Any	0.240	b	5210	b	Borrowed from order Hemiptera	1
Insecta	Hemiptera	Hebridae	Any	0.240	b	5210	b	Borrowed from order Hemiptera	1
Insecta	Hemiptera	Hemiptera	Any	0.240	a	5210	a	Based on *Callicorixa audeni* (Corixidae) and *Plea* (Pleidae)	1
Insecta	Hemiptera	Mesoveliidae	any	0.240	b	5210	b	Borrowed from order Hemiptera	1
Insecta	Hemiptera	Veliidae	Any	0.240	b	5210	b	Borrowed from order Hemiptera	1
Insecta	Hymenoptera	Hymenoptera	Adult	0.240		5134			5
Insecta	Lepidoptera	Lepidoptera	Larva	0.214	b	3176	b	Borrowed from aquatic class Insecta	3
Insecta	Lepidoptera	Lepidoptera	Any	0.214	b	6431	b	Average of adult and larva Lepidoptera/ as borrowed from Insecta	
Insecta	Lepidoptera	Lepidoptera	Adult	0.214	b	9686	b	Borrowed from terrestrial class Insecta	3
Insecta	Odonata	Zygoptera	Unknown	0.204		4220		Based on *Lestes malabaricus*	3
Insecta	Odonata	Zygoptera	Larva	0.220	a	5032	a	Based on *Lestes disjunctus*, *Lestes congener*, and *Enallagma boreale*	1
Insecta	Orthoptera	Acrididae	Any	0.220	b	4228	b	Borrowed from adult Orthoptera	5
Insecta	Orthoptera	Orthoptera	Adult	0.220		4228			5
Insecta	Plecoptera	Nemouridae	Larva	0.229		5110			7
Insecta	Plecoptera	Perlodidae	Larva	0.157	a	3610	a	Based on *Perlodes* and *Isoperla*	7
Insecta	Plecoptera	Perlodidae	Adult	0.214	b	9686	b	Borrowed from terrestrial class Insecta	3
Insecta	Plecoptera	Plecoptera	Larva	0.179	a	3905	a	Based on *Perlodes, Isoperla, Leuctra,* and Nemouridae	7
Insecta	Plecoptera	Plecoptera	Any	0.197	b	6796	b	Average of adult and larva Plecoptera	7
Insecta	Plecoptera	Plecoptera	Adult	0.214	b	9686	b	Borrowed from terrestrial class Insecta	3
Insecta	Trichoptera	Glossosomatidae	Larva	0.226	b	5376	b	Borrowed from larva Trichoptera	1,7
Insecta	Trichoptera	Helicopsychidae	Larva	0.226	b	5376	b	Borrowed from larva Trichoptera	1,7
Insecta	Trichoptera	Hydropsychidae	Unknown	0.188		4066		Based on *Macronema pseudoneura*	3
Insecta	Trichoptera	Hydropsychidae	Larva	0.173		4354			7
Insecta	Trichoptera	Hydroptilidae	Larva	0.226	b	5376	b	Borrowed from larva Trichoptera	1,7
Insecta	Trichoptera	Phryganeidae	Larva	0.190		4227	a	Based on *Phryganea cinerea*	1
Insecta	Trichoptera	Psychomyiidae	Larva	0.226	b	5376	b	Borrowed from larva Trichoptera	1,7
Insecta	Trichoptera	Rhyacophilidae	Larva	0.153		3972			7

Insecta	Trichoptera	Trichoptera	Pupa	0.160	a	3757	a	Based on *Anabolia* (Limnephilidae) and *Phryganea cinerea* (Phryganeidae)	1
Insecta	Trichoptera	Trichoptera	Larva	0.226	a	5376	a	Based on *Phryganea cinerea* (Phryganeidae), *Philarcus quaeris* (Limnephilidae), *Limnephilus rhombicus* (Limnephilidae), *Limnephilus* sp. (Limnephilidae), *Anabolia* (Limnephilidae), and *Triaenodes tarda* (Leptoceridae) (1); based on Rhyacophilidae, Hydropsychidae, Sericostomatidae, and Limnephilidae (7)	1,7
Insecta	Trichoptera	Trichoptera	Adult	0.295	a	7048	a	Based on *Philarctus quaeris* (Limnephilidae)	1
Arthropoda	Insecta (general, aquatic)			0.214	a	3176		Ratio obtained as average of this species list	
Arthropoda	Insecta (general, terrestrial)			0.214	a	9686		Ratio obtained as average of this species list	
Arthropoda (general, aquatic)				0.214	a	3314		Ratio obtained as average of this species list	
Arthropoda (general, terrestrial)				0.214	a	9686		Ratio obtained as average of this species list	
PHYLUM CHORDATA									
Actinopterygii	Fish	Bridgelip Sucker	Adult	0.235	b	5010	b	Borrowed from sculpin	4
Actinopterygii	Fish	Fish unknown	Unknown	0.235	b	5010	b	Borrowed from sculpin	4
Actinopterygii	Fish	Longnose Dace	Adult	0.235	b	5010	b	Borrowed from sculpin	4
Actinopterygii	Fish	Sculpin	Adult	0.235		5010	a		4
PHYLUM MOLLUSCA							a		
Gastropoda	Mollusca	Gastropoda	Any	0.290		1561	a	Based on *Lymnaea stagnalis* (1); general to Gastropoda (3)	1,3
Pelecypoda	Mollusca	Pelecypoda	Any	0.290	b	2113		Ratio borrowed from Gastropoda	3
UNKNOWN					b				
Unknown	Unknown	Unknown	Any	0.214	a	4829	a	Averaged values across all ratios and ED wet*	

* Note that the average ratio based on the taxa table is used for this category but energy density used in the actual diets is weighted by frequency

APPENDIX 2

Model-specified equations, variables, and associated parameters used in the bioenergetics modeling of subyearling steelhead.

Appendix 2 references

Beauchamp, D.A., Stewart, D.J. & Thomas, G.L. 1989. Corroboration of a bioenergetics model for sockeye salmon. Transactions of the American Fisheries Society 118: 597-607.

Elliott, J.M. 1976a The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. Journal of Animal Ecology 45: 923-948.

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Glova, G.J. & McInerney, J.E. 1977. Critical swimming speeds of coho salmon (*Oncorhynchus kisutch*) fry to smolt stages in relation to salinity and temperature. Journal of the Fisheries Research Board of Canada 34: 151-154.

Hanson, P., Johnson, T., Kitchell, J. & Schindler, D.E. 1997. Fish bioenergetics [version] 3.0. Madison, WI: University of Wisconsin Sea Grant Institute

Kitchell, J.F., Stewart, D.J. & Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). Journal of the Fisheries Research Board of Canada 34: 1922-1935.

Railsback, S.F. & Rose, K.A. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. Transactions of the American Fisheries Society 128: 241-256.

Rand, P.S., Stewart, D.J., Seelbach, P.W., Jones, M.L. & Wedge, L.R. 1993. Modeling steelhead population energetics in Lakes Michigan and Ontario. Transactions of the American Fisheries Society 122: 977-1001.

Stewart, D.J. & Ibarra, M. 1991. Predation and production by salmonine fishes in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 48: 909-922.

Thornton, K.W. & Lessem, A.S. 1978. A temperature algorithm for modifying biological rates. Transactions of the American Fisheries Society 107: 284-287.

Term	*Explanation*	*Unit*	*Value*	*Reference*
CONSUMPTION (Thornton & Lessem 1978)				
C	Specific consumption rate	g/g/d		
Cmax	Maximum specific feeding rate	g/g/d		
p	Proportion of max. consumption (range 0-1)	-		
f(T)	Temperature dependent function	-		
T	Water temperature	°C		Empirical data, this study
W	Fish mass	g		Empirical data, this study
CA	Intercept of the mass dependence function for a 1 g fish at optimum temperature	-	0.628	Elliott 1976a as cited in Rand et al. 1993
CB	Coefficient of the mass dependence	-	-0.3	Elliott 1976a as cited in Rand et al. 1993
CQ	Temperature for CK1, approximates Q10	°C	3.5	Railsback & Rose 1999
CTO	Water temp. corresponding to 0.98 of the max. consumption rate at increasing curve	°C	25	Railsback & Rose 1999
CTM	Water temp. (>CTO) at which dependence is still 0.98 of the max. rate	°C	22.5	Railsback & Rose 1999
CTL	Temperature for CK4	°C	24.3	Railsback & Rose 1999
CK1	Proportion of Cmax at lower temperature threshold	-	0.2	Railsback & Rose 1999
CK4	Proportion of Cmax at upper temperature threshold	-	0.2	Elliott 1976a as cited in Rand et al. 1993
RESPIRATION (Kitchell et al. 1977)				
R	Specific rate of respiration	g/g/d		
W	Fish mass	g		Empirical data, this study
f(T)	Temperature dependence function	-		
T	Water temperature	°C		Empirical data, this study
S	Proportion of assimilated energy lost to specific dynamic action	-		
RA	Intercept of the allometric mass function	g/g/d	0.013	Railsback & Rose 1999,
RB	Slope of the allometric mass function	-	-0.217	Rand et al. 1993
RQ	Rate at which the function increases over relatively low water temps.	1/°C	2.2	Railsback & Rose 1999
RTO	Optimum temp. for respiration (highest)	°C	22	Railsback & Rose 1999
RTM	Maximum (lethal) water temp.	°C	26	Railsback & Rose 1999
RTL	Cutoff temp. at which activity relationship changes	°C	0	Railsback & Rose 1999

RK1	Swimming speed intercept above RTL	cm/s	0	Railsback & Rose 1999
RK4	Mass dependence for swimming speeds	-	0.13	Beauchamp et al. 1989
ACT	Activity multiplier	cm/s	1.3	Railsback & Rose 1999
BACT	Temp.-dependence coefficient for swimming speed-water temp. function below RTL	1/°C	0.0405	Rand et al. 1993
SDA	Specific dynamic action	-	0.172	Rand et al. 1993
WASTE LOSSES (EGESTION AND EXCRETION) (Elliott 1976b)				
FA	Intercept of the proportion of consumed energy egested vs. water temp. and ration	-	0.212	Rand et al. 1993
FB	Coefficient of water temp. dependence of egestion	-	-0.222	Rand et al. 1993
FG	Coefficient for feeding level dependence (P-value) of egestion	-	0.631	Rand et al. 1993
UA	Intercept of the proportion of consumed energy excreted vs. water temp. and ration	-	0.0314	Rand et al. 1993
UB	Coefficient of water temp. dependence of excretion	-	0.58	Rand et al. 1993
UG	Coefficient for feeding level dependence (P-value) of excretion	-	-0.299	Rand et al. 1993
PREDATOR ENERGY DENSITY Equation 2 in Hanson et al. (1997)				
Epred	Energy density of predator	J/g	5763	Glova & McInerney 1977
a	Intercept of allometric mass function	J/g	5763	Stewart & Ibarra 1991
b	Slope of allometric mass function	-	0.9862	Stewart & Ibarra 1991
Eprey	Energy density of prey	J/g	4324	Empirical data, this study

Footnotes: dash (-) denotes dimensionless values. Bolded terms denote variables that are being estimated or inputted values specified for the individual fish or modeling scenario.

APPENDIX 3

Dates for the fish sampling from 2010 to 2012 (month/day).

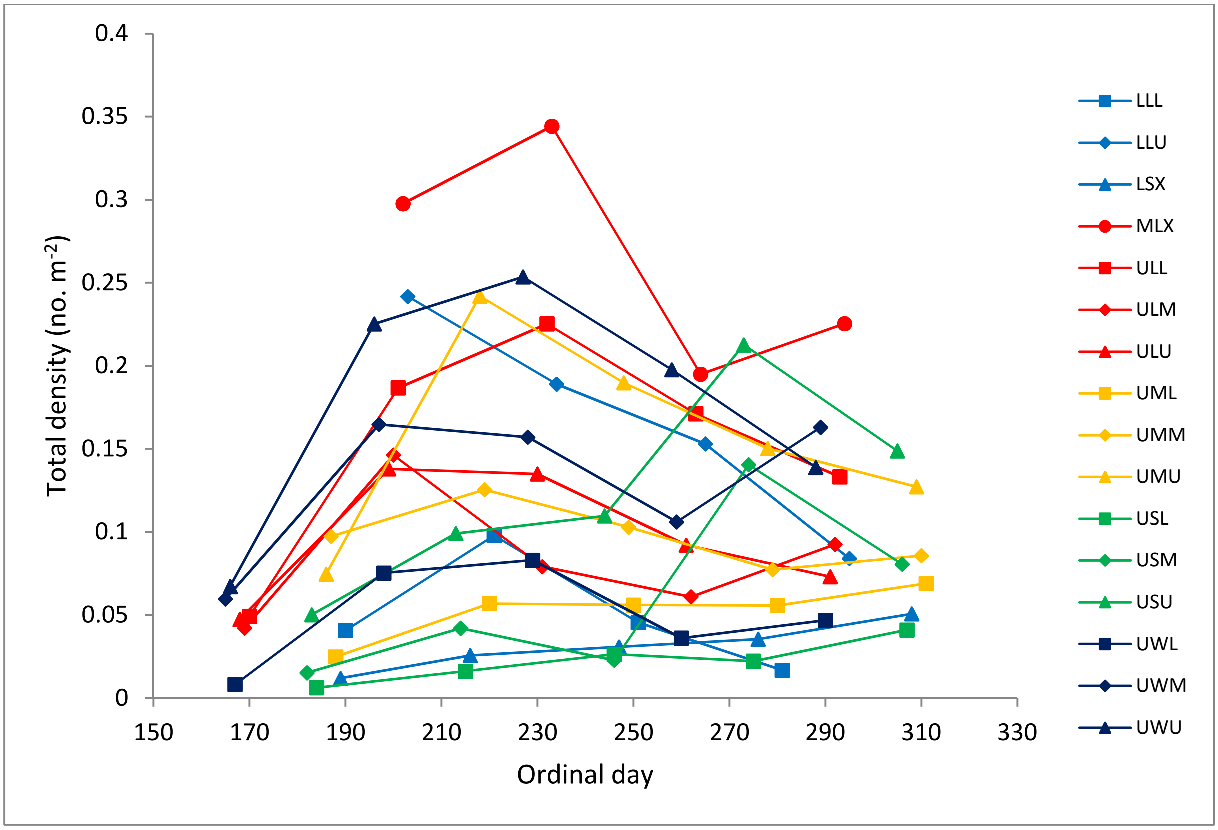
Site	2010	2011	2012
LLL	7/9	7/19	
LLL	8/9	8/18	
LLL	9/8	9/17	
LLL	10/8	10/18	
LLL	11/8	11/17	
LLU	6/21	7/3	6/28
LLU	7/22	8/3	7/26
LLU	8/22	9/2	8/19
LLU	9/22	10/2	9/20
LLU	10/22	11/2	10/18
LSX	7/8	7/15	6/22
LSX	8/4	8/14	7/20
LSX	9/4	9/13	8/15
LSX	10/3	10/14	9/14
LSX	11/4	11/12	10/12
MLX	6/22	7/2	6/26
MLX	7/21	8/3	7/24
MLX	8/21	9/1	8/17
MLX	9/21	10/1	9/18
MLX	10/21	11/1	10/16
ULL	6/19	7/1	
ULL	7/20	8/2	
ULL	8/20	8/31	
ULL	9/20	9/30	
ULL	10/20	10/31	
ULM	6/18	6/30	
ULM	7/19	8/1	
ULM	8/19	8/30	
ULM	9/19	9/29	
ULM	10/19	10/29	
ULU	6/17	6/29	6/25
ULU	7/18	7/31	7/23
ULU	8/18	8/29	8/16
ULU	9/18	9/28	9/17
ULU	10/18	10/28	10/15
UML	7/7	7/18	
UML	8/8	8/17	
UML	9/7	9/16	
UML	10/7	10/17	
UML	11/7	11/16	
UMM	7/6	7/17	6/19
UMM	8/7	8/16	7/17
UMM	9/6	9/15	8/13
UMM	10/6	10/16	9/11
UMM	11/6	11/14	10/9
UMU	7/5	7/16	6/18
UMU	8/6	8/15	7/16
UMU	9/5	9/14	8/12
UMU	10/5	10/15	9/10
UMU	11/5	11/13	10/8
USL	7/3	7/14	
USL	8/3	8/13	
USL	9/3	9/12	
USL	10/2	10/13	
USL	11/3	11/11	
USM	7/1	7/13	6/21
USM	8/2	8/12	7/19
USM	9/3	9/11	8/14
USM	10/1	10/11	9/13
USM	11/2	11/10	10/11
USU	7/2	7/12	6/20
USU	8/1	8/11	7/18
USU	9/1	9/10	8/14
USU	9/30	10/10	9/12
USU	11/1	11/9	10/10
UWL	6/16	6/28	
UWL	7/17	7/29	
UWL	8/17	8/28	
UWL	9/17	9/27	
UWL	10/17	10/27	
UWM	6/14	6/27	6/27
UWM	7/16	7/28	7/25
UWM	8/16	8/27	8/18
UWM	9/16	9/26	9/19
UWM	10/16	10/26	10/17
UWU	6/15	6/26	
UWU	7/15	7/27	
UWU	8/15	8/26	
UWU	9/15	9/25	
UWU	10/15	10/25	

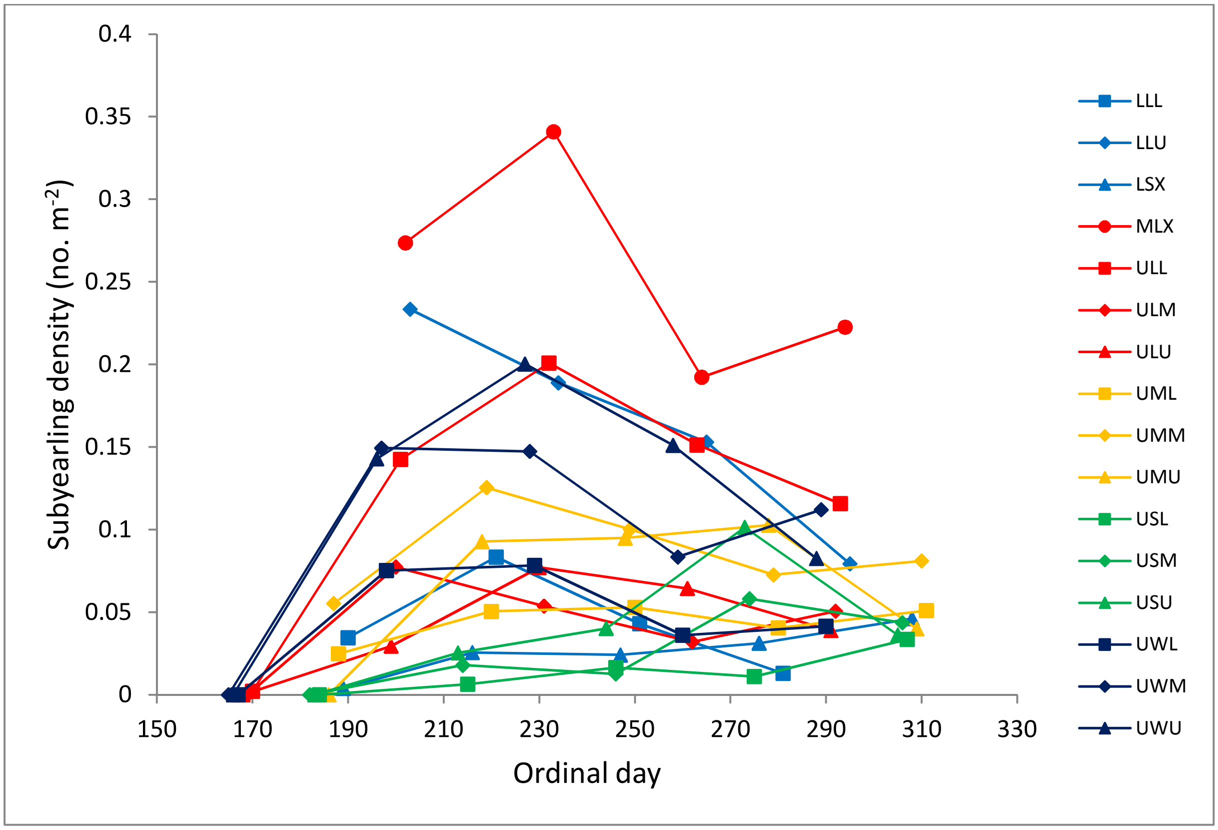
APPENDIX 4

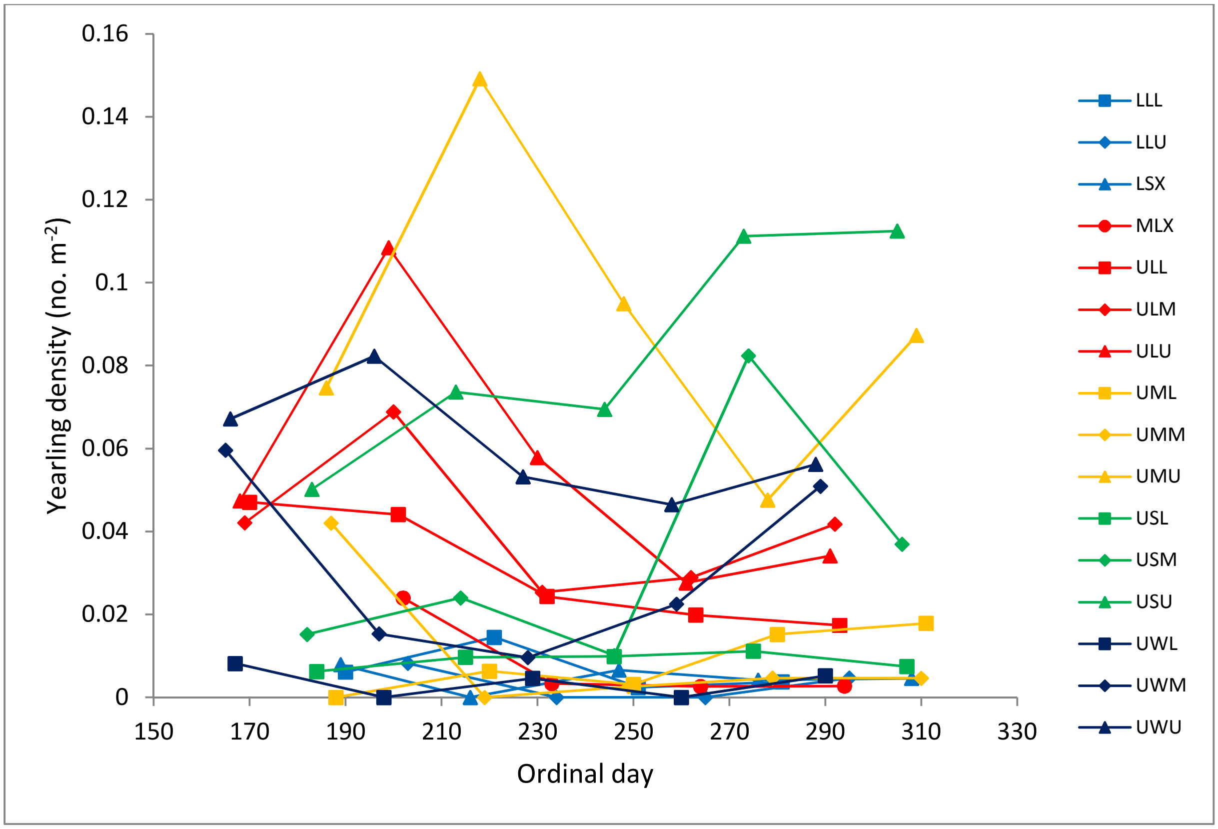
Densities (no. m^{-2}) of juvenile steelhead by study site in 2010 as calculated using the weighted maximum likelihood estimator of Carle and Strub (1978) for removal data. One figure is given for each of the total densities (subyearlings and yearlings combined), subyearling densities, and yearling densities. Cohort class is indicated in the y-axis label.

Appendix reference

Carle, F. L., and M. R. Strub. 1978. A new method for estimating population size from removal data. Biometrics 34:621-630.


0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Total density (no. m^{-2})
150
170
190
210
230
250
270
290
310
330
Ordinal day
LLL
LLU
LSX
MLX
ULL
ULM
ULU
UML
UMM
UMU
USL
USM
USU
UWL
UWM
UWU


0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Subyearling density (no. m^{-2})
150
170
190
210
230
250
270
290
310
330
Ordinal day
LLL
LLU
LSX
MLX
ULL
ULM
ULU
UML
UMM
UMU
USL
USM
USU
UWL
UWM
UWU

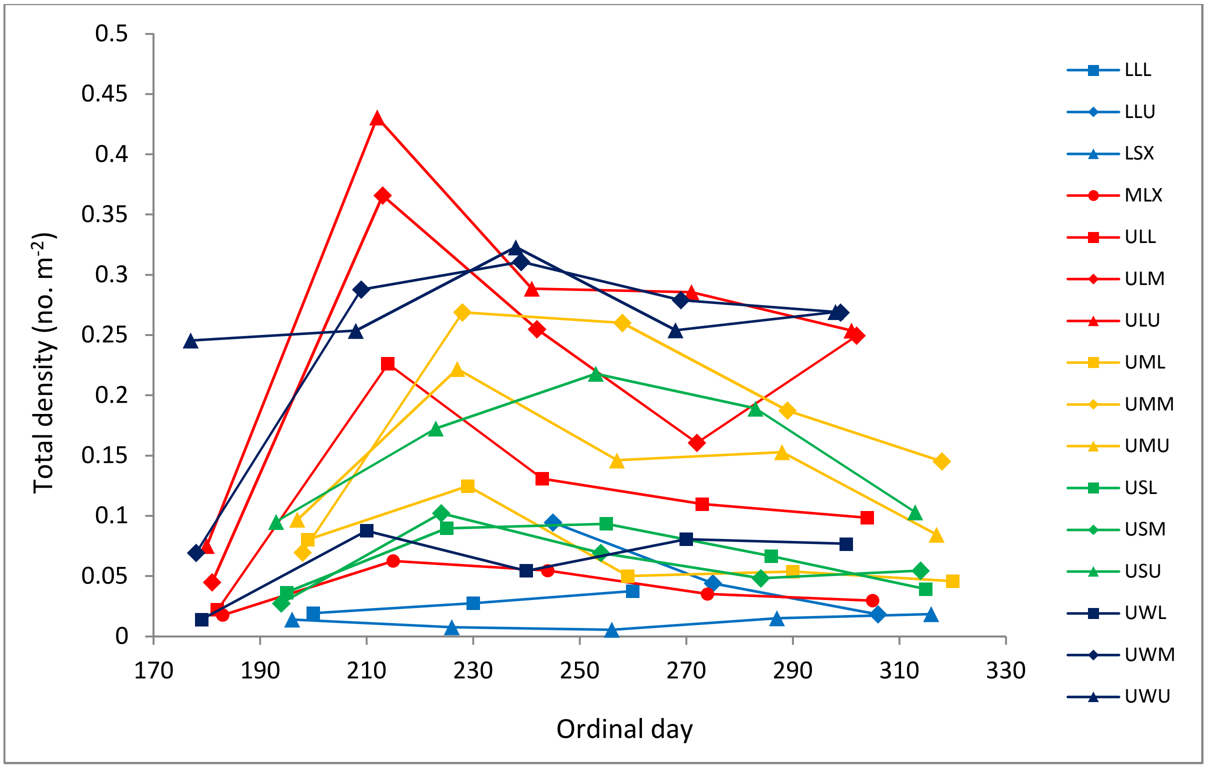

Yearling density (no. m^{-2})
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
150
170
190
210
230
250
270
290
310
330
Ordinal day
LLL
LLU
LSX
MLX
ULL
ULM
ULU
UML
UMM
UMU
USL
USM
USU
UWL
UWM
UWU

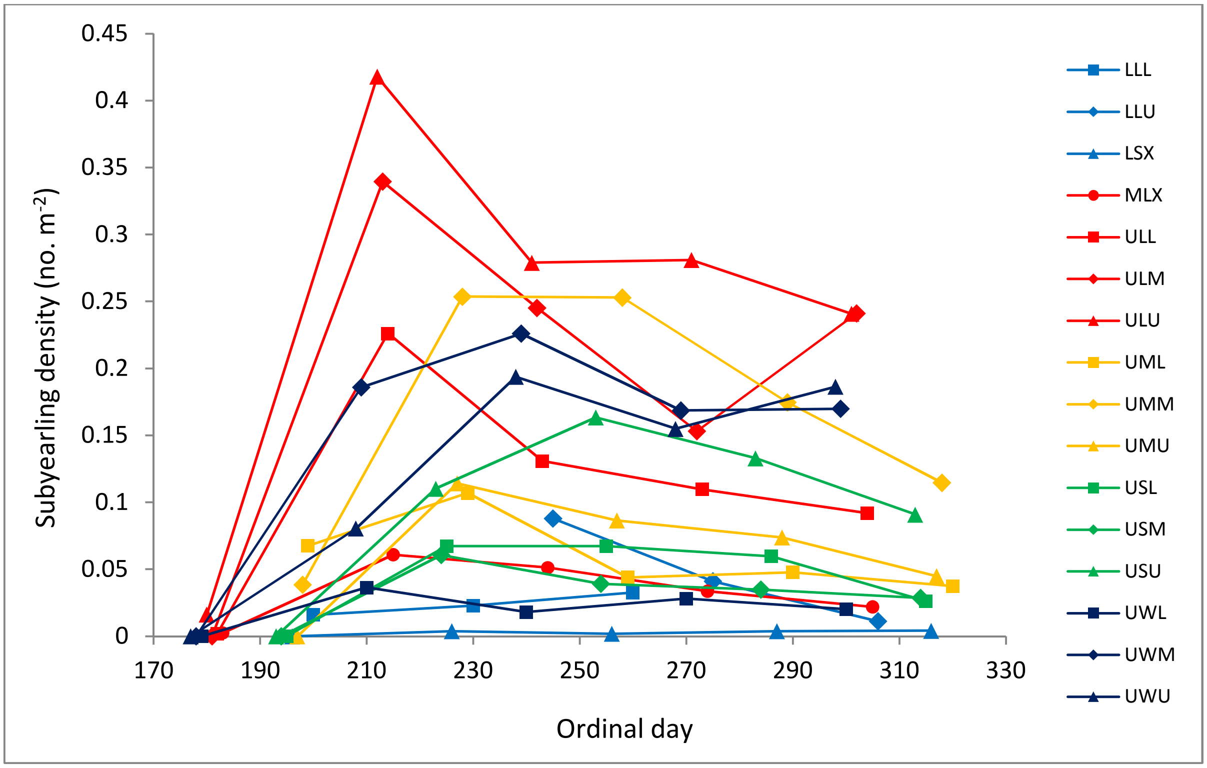
APPENDIX 5

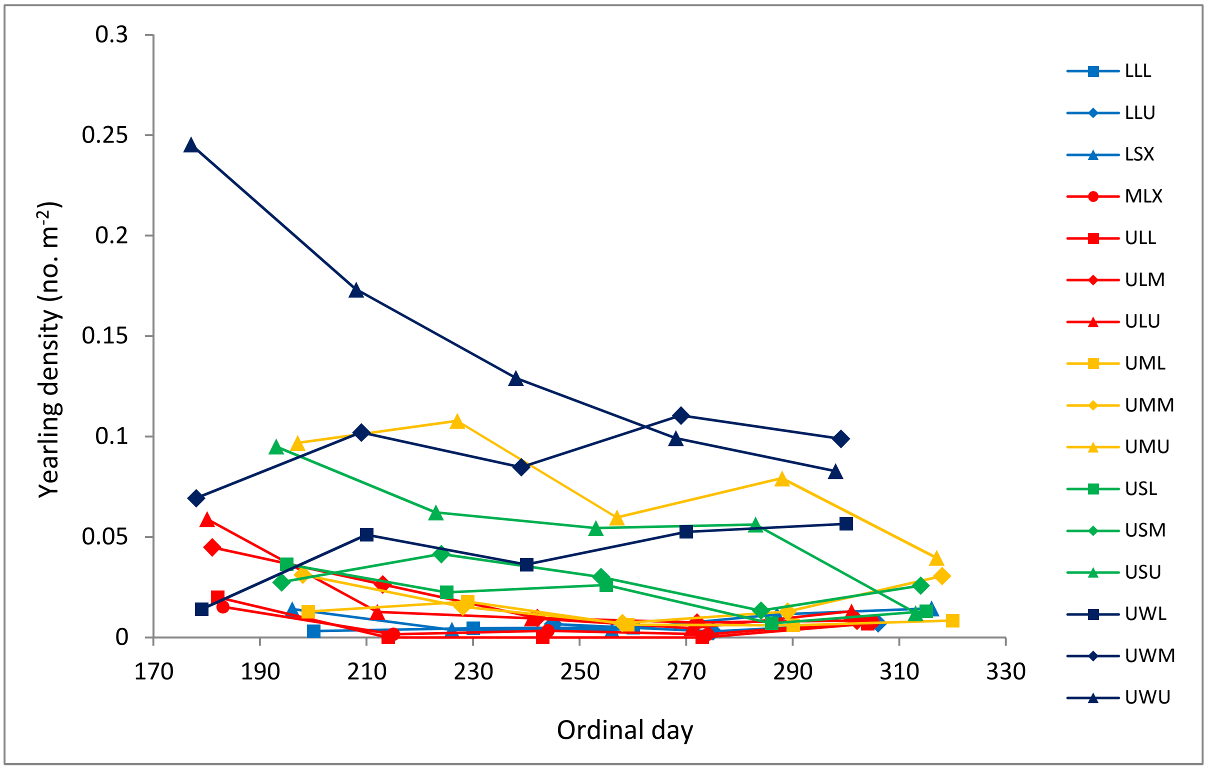
Densities (no. m^{-2}) of juvenile steelhead by study site in 2011 as calculated using the weighted maximum likelihood estimator of Carle and Strub (1978) for removal data. One figure is given for each of the total densities (subyearlings and yearlings combined), subyearling densities, and yearling densities. Cohort class is indicated in the y-axis label.

Appendix reference

Carle, F. L., and M. R. Strub. 1978. A new method for estimating population size from removal data. Biometrics 34:621-630.


Total density (no. m^{-2})
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
170
190
210
230
250
270
290
310
330
Ordinal day
LLL
LLU
LSX
MLX
ULL
ULM
ULU
UML
UMM
UMU
USL
USM
USU
UWL
UWM
UWU


Subyearling density (no. m^{-2})
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
170
190
210
230
250
270
290
310
330
Ordinal day
LLL
LLU
LSX
MLX
ULL
ULM
ULU
UML
UMM
UMU
USL
USM
USU
UWL
UWM
UWU

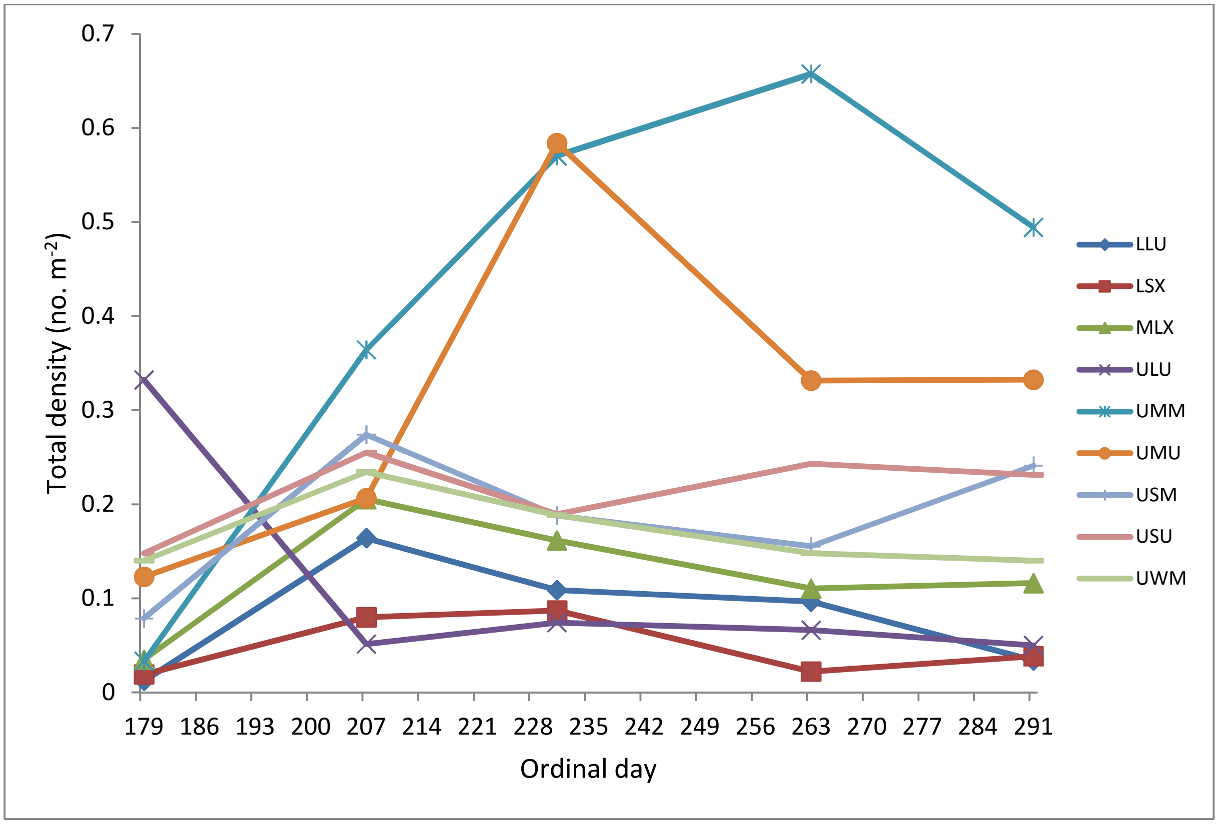

0.3
0.25
0.2
0.15
0.1
0.05
0
Yearling density (no. m-2)
170
190
210
230
250
270
290
310
330
Ordinal day
LLL
LLU
LSX
MLX
ULL
ULM
ULU
UML
UMM
UMU
USL
USM
USU
UWL
UWM
UWU

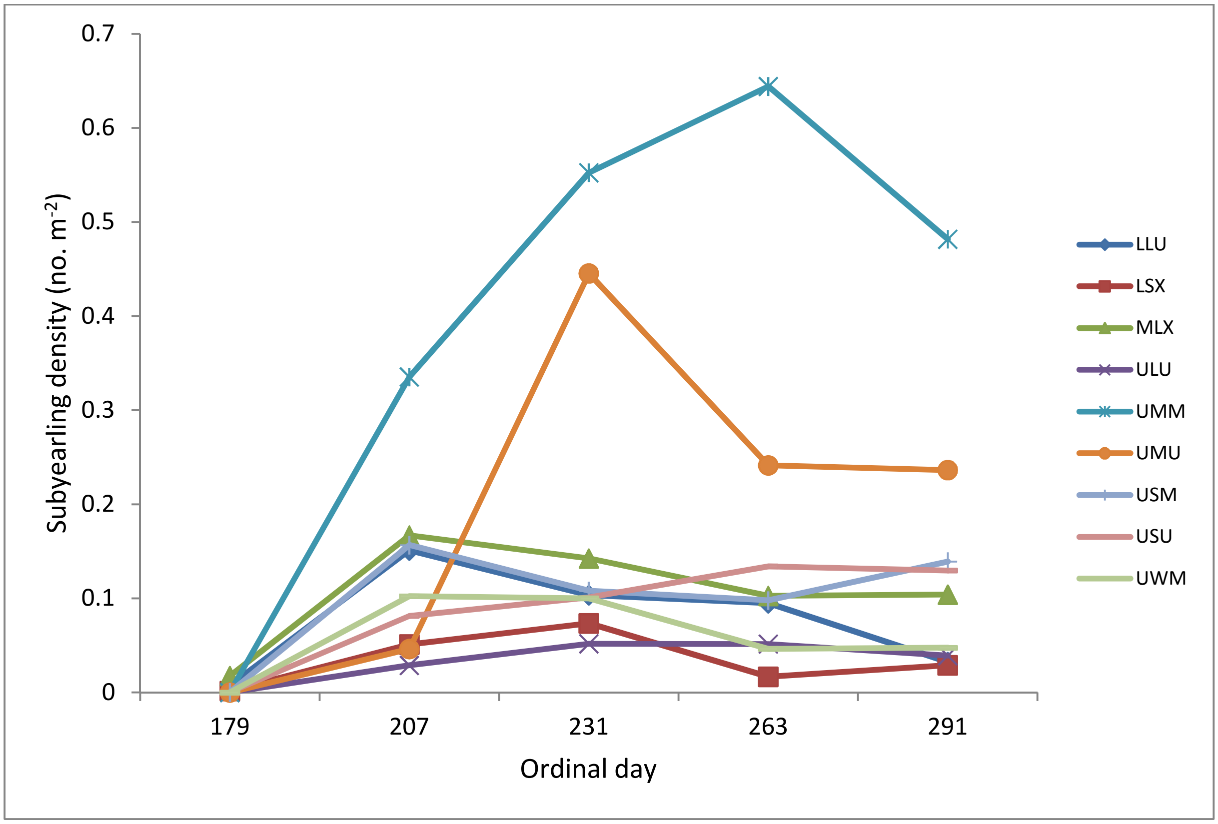
APPENDIX 6

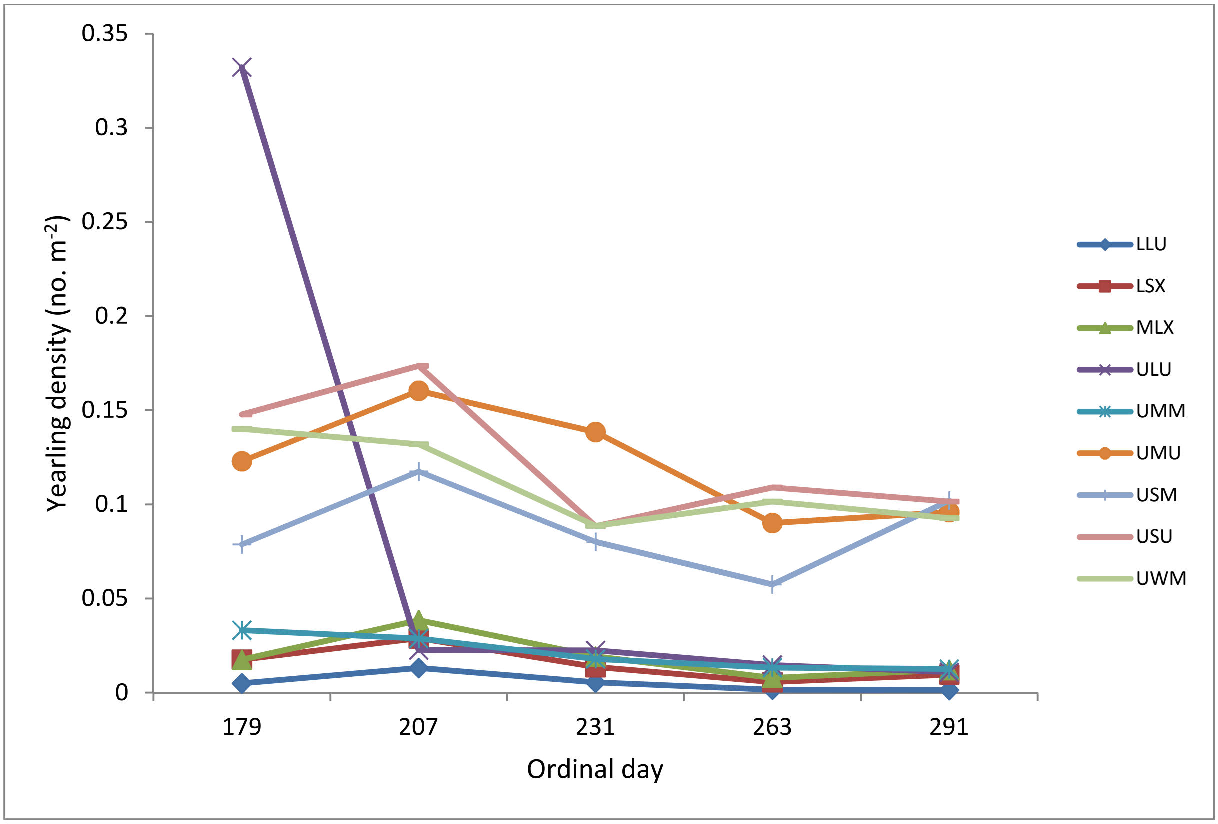
Densities (no. m^{-2}) of juvenile steelhead by study site in 2012 as calculated using the weighted maximum likelihood estimator of Carle and Strub (1978) for removal data. One figure is given for each of the total densities (subyearlings and yearlings combined), subyearling densities, and yearling densities. Cohort class is indicated in the y-axis label.

Appendix reference

Carle, F. L., and M. R. Strub. 1978. A new method for estimating population size from removal data. Biometrics 34:621-630.


Total density (no. m^{-2})
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
179 186 193 200 207 214 221 228 235 242 249 256 263 270 277 284 291
Ordinal day
LLU
LSX
MLX
ULU
UMM
UMU
USM
USU
UWM

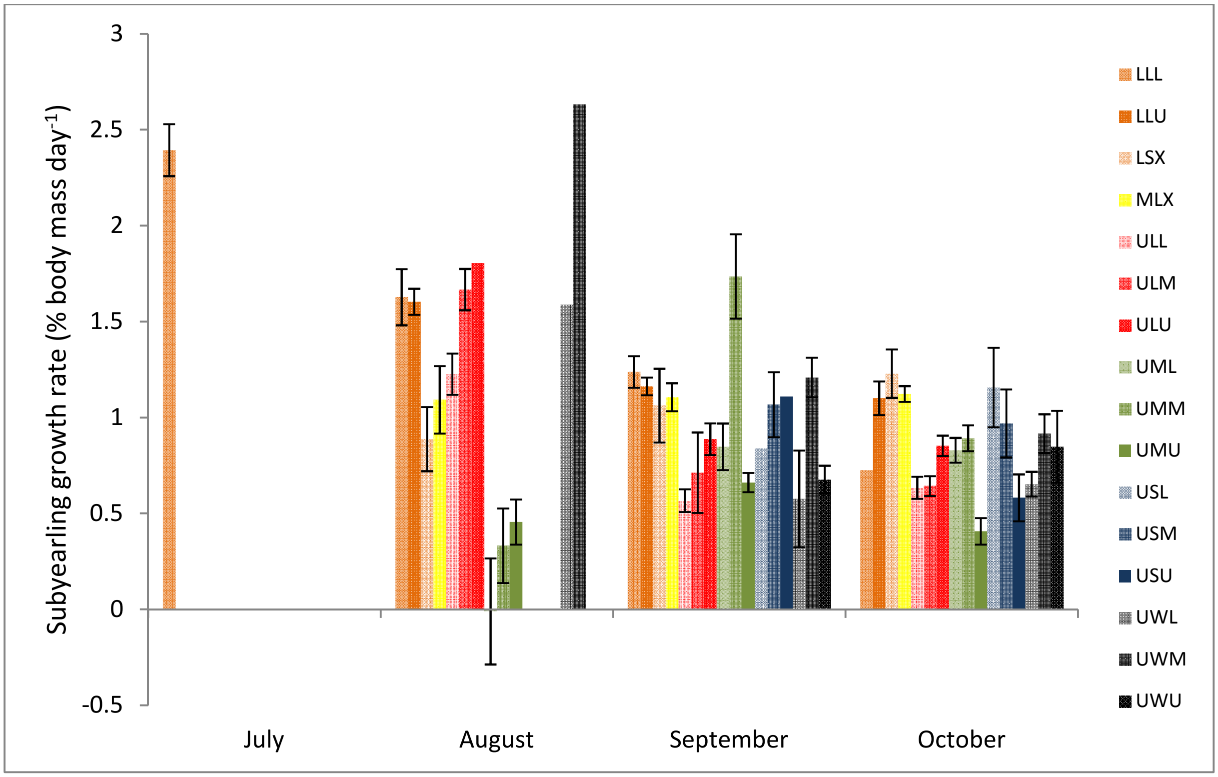

Subyearling density (no. m^{-2})
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
179
207
231
263
291
Ordinal day
LLU
LSX
MLX
ULU
UMM
UMU
USM
USU
UWM

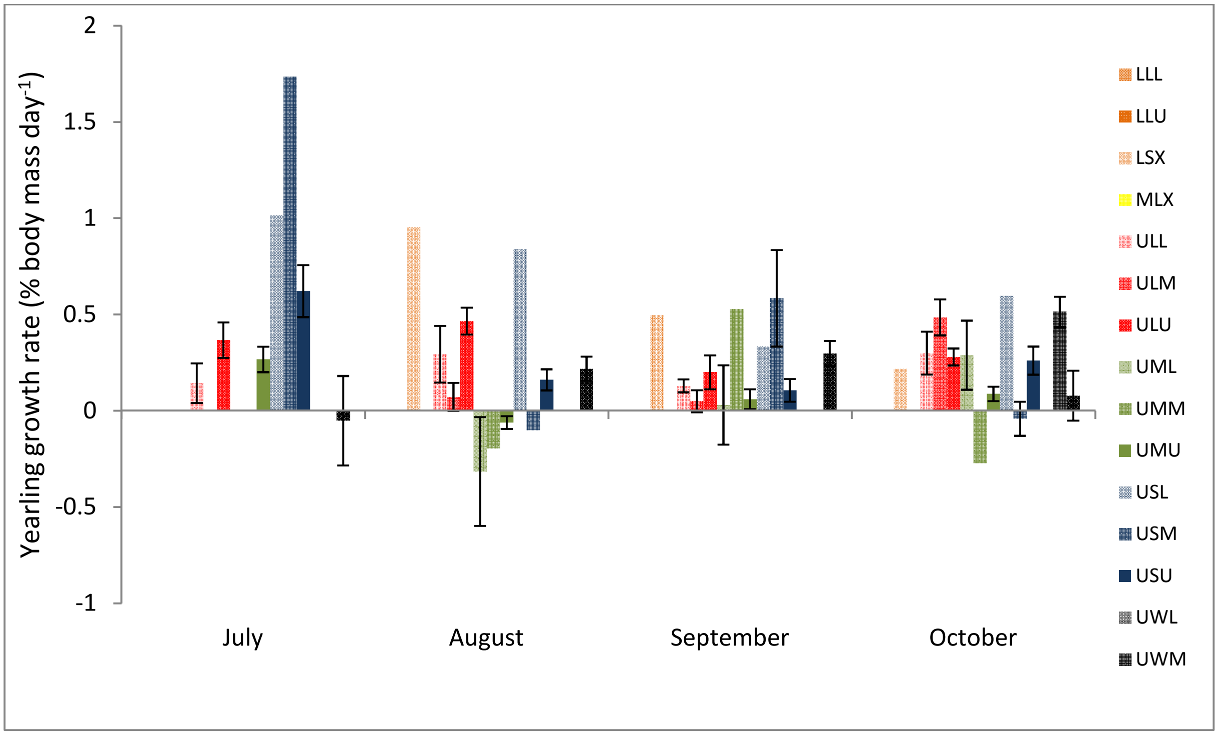


0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Yearling density (no. m^{-2})
179
207
231
263
291
Ordinal day
LLU
LSX
MLX
ULU
UMM
UMU
USM
USU
UWM

APPENDIX 7

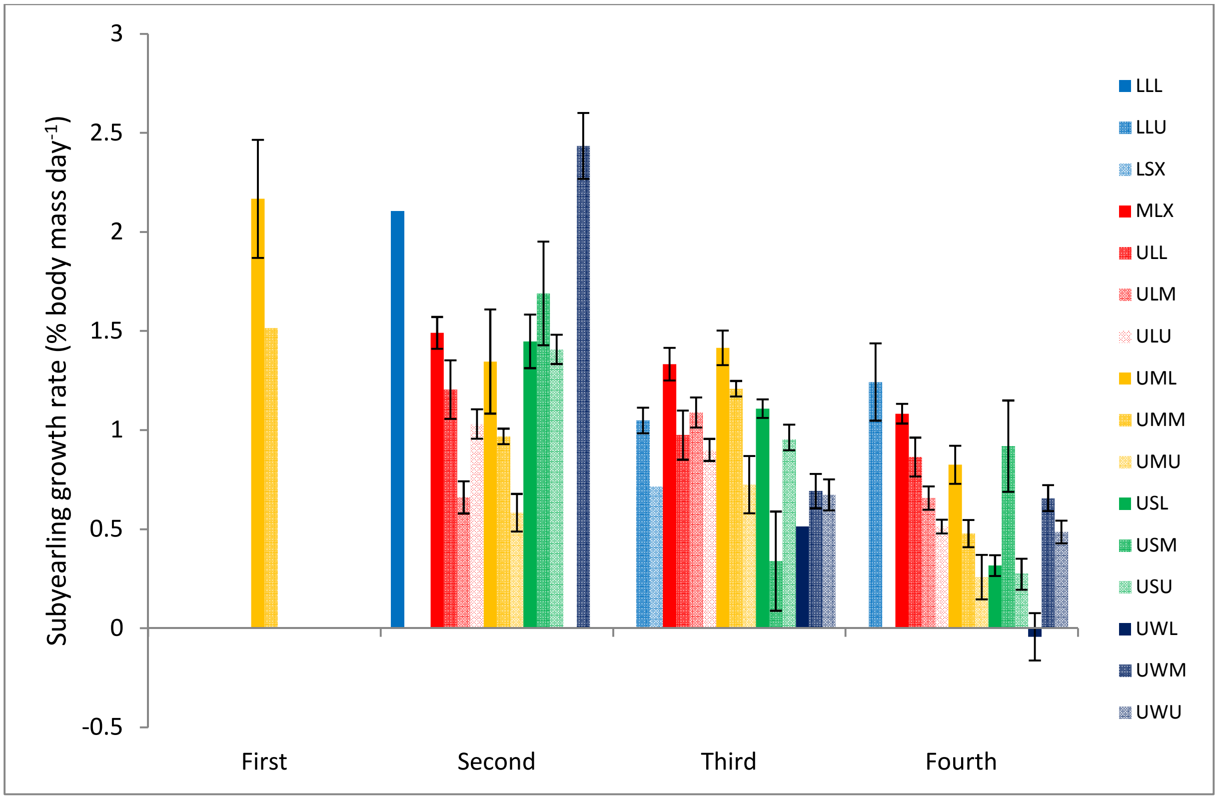
Growth rates (% body mass day^{-1}) of individually tagged juvenile steelhead by study site in 2010. One figure is given for subyearlings and one figure is given for yearling growth rates. Cohort class is indicated in the y-axis label. Error bars represent standard error.

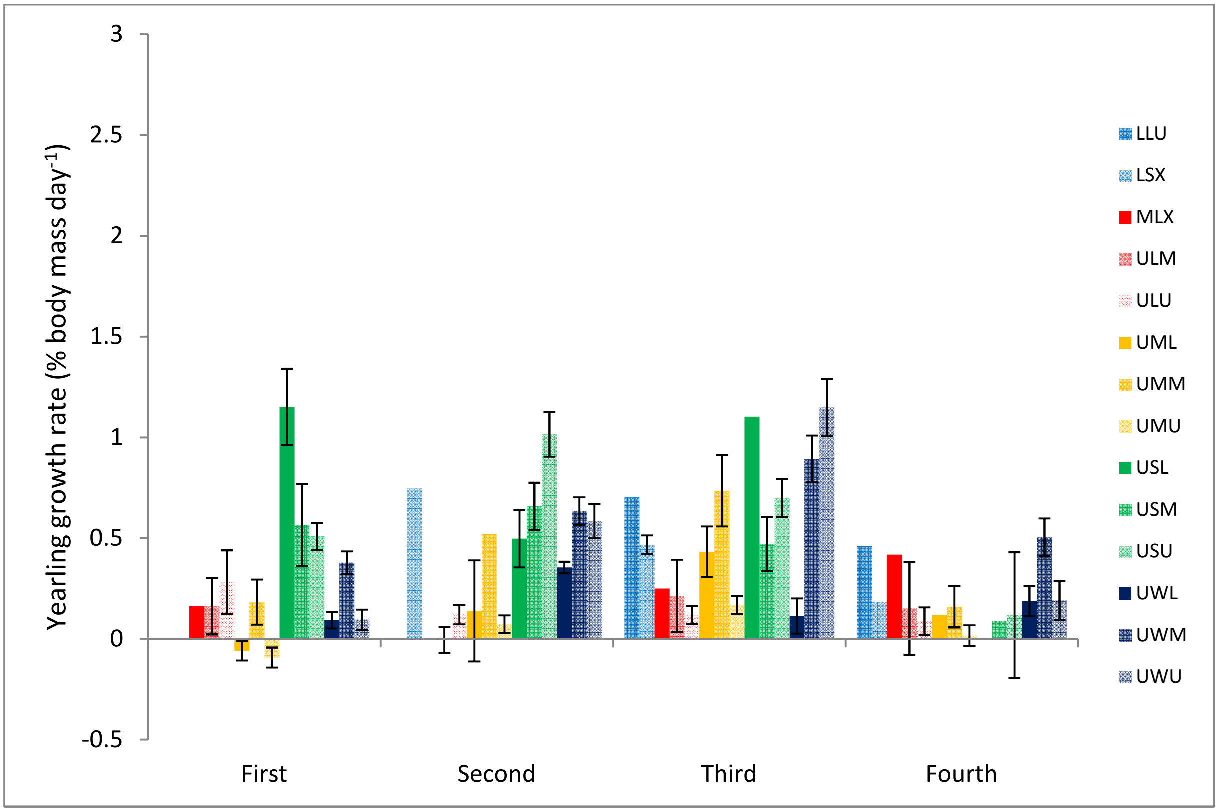

Subyearling growth rate (% body mass day^{-1})
3
2.5
2
1.5
1
0.5
0
-0.5
July
August
September
October
LLL
LLU
LSX
MLX
ULL
ULM
ULU
UML
UMM
UMU
USL
USM
USU
UWL
UWM
UWU


Yearling growth rate (% body mass day^{-1})
2
1.5
1
0.5
0
-0.5
-1
July
August
September
October
LLL
LLU
LSX
MLX
ULL
ULM
ULU
UML
UMM
UMU
USL
USM
USU
UWL
UWM

APPENDIX 8

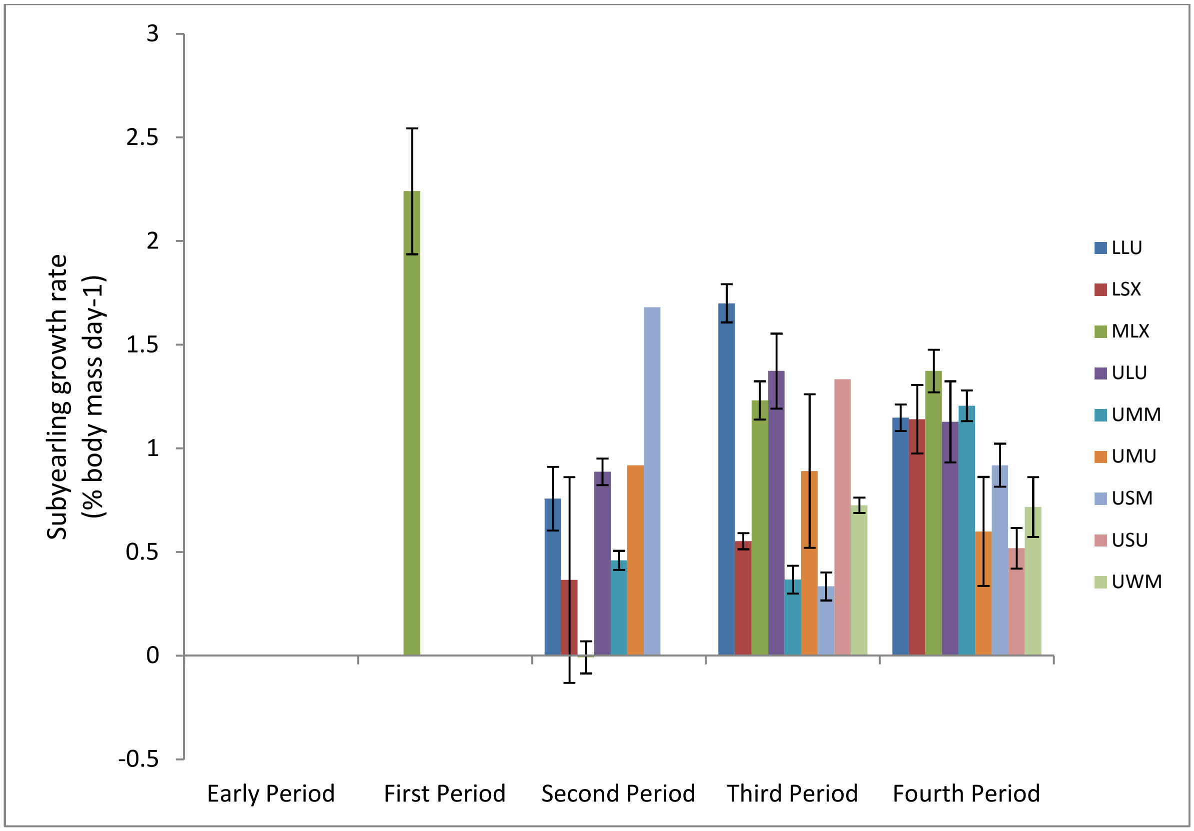
Growth rates (% body mass day^{-1}) of individually tagged juvenile steelhead by study site in 2011. One figure is given for subyearlings and one figure is given for yearling growth rates. Cohort class is indicated in the y-axis label. Error bars represent standard error.

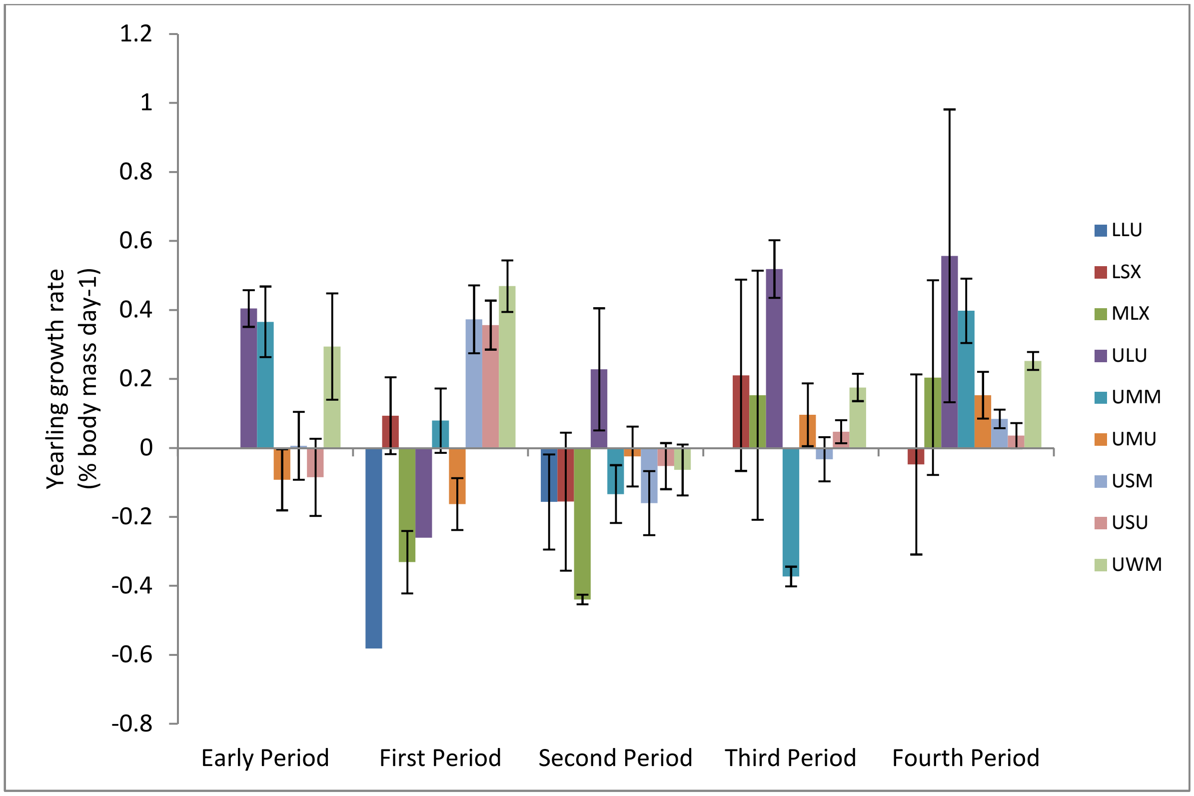

Subyearling growth rate (% body mass day^{-1})
3
2.5
2
1.5
1
0.5
0
-0.5
First
Second
Third
Fourth
LLL
LLU
LSX
MLX
ULL
ULM
ULU
UML
UMM
UMU
USL
USM
USU
UWL
UWM
UWU


Yearling growth rate (% body mass day^{-1})
3
2.5
2
1.5
1
0.5
0
-0.5
First
Second
Third
Fourth
LLU
LSX
MLX
ULM
ULU
UML
UMM
UMU
USL
USM
USU
UWL
UWM
UWU

APPENDIX 9

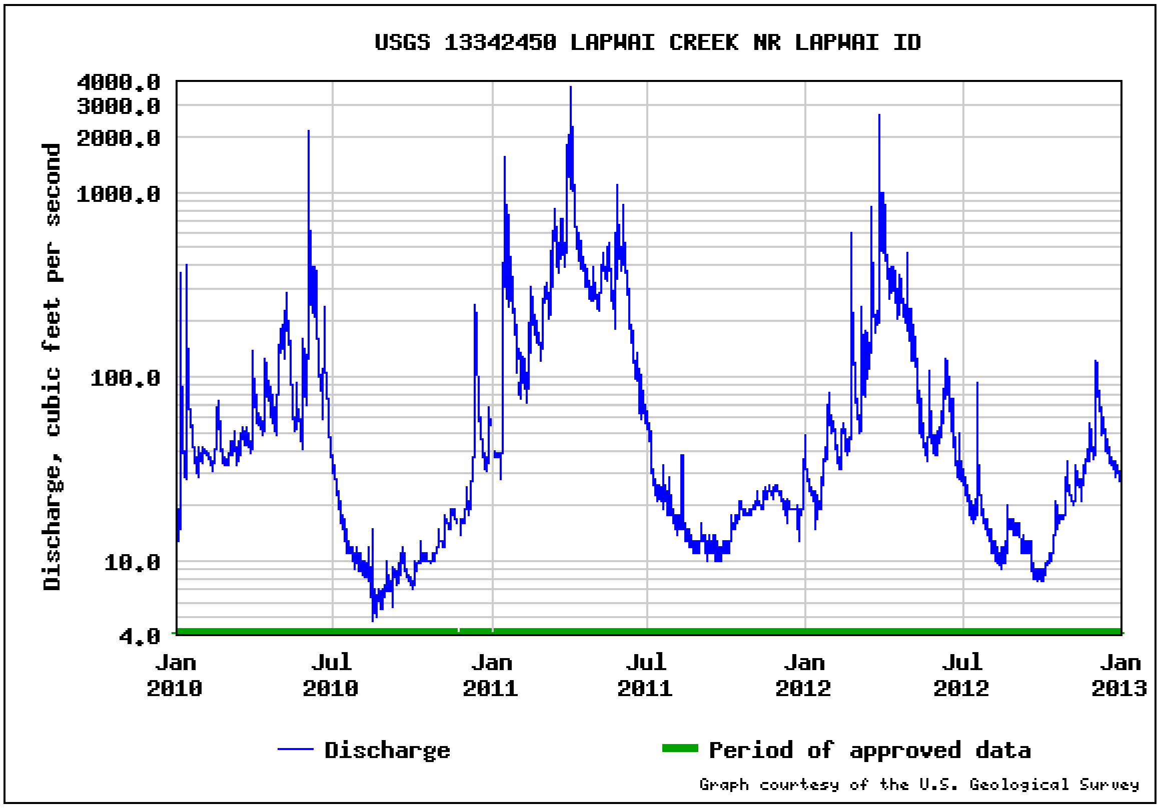
Growth rates (% body mass day^{-1}) of individually tagged juvenile steelhead by study site in 2012. One figure is given for subyearlings and one figure is given for yearling growth rates. Cohort class is indicated in the y-axis label. Error bars represent standard error. Early period refers to a visit in May 2012 where the purpose was to measure growth rates.


Subyearling growth rate
(% body mass day-1)
3
2.5
2
1.5
1
0.5
0
-0.5
Early Period
First Period
Second Period
Third Period
Fourth Period
LLU
LSX
MLX
ULU
UMM
UMU
USM
USU
UWM


Yearling growth rate
(% body mass day-1)
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
Early Period
First Period
Second Period
Third Period
Fourth Period
LLU
LSX
MLX
ULU
UMM
UMU
USM
USU
UWM

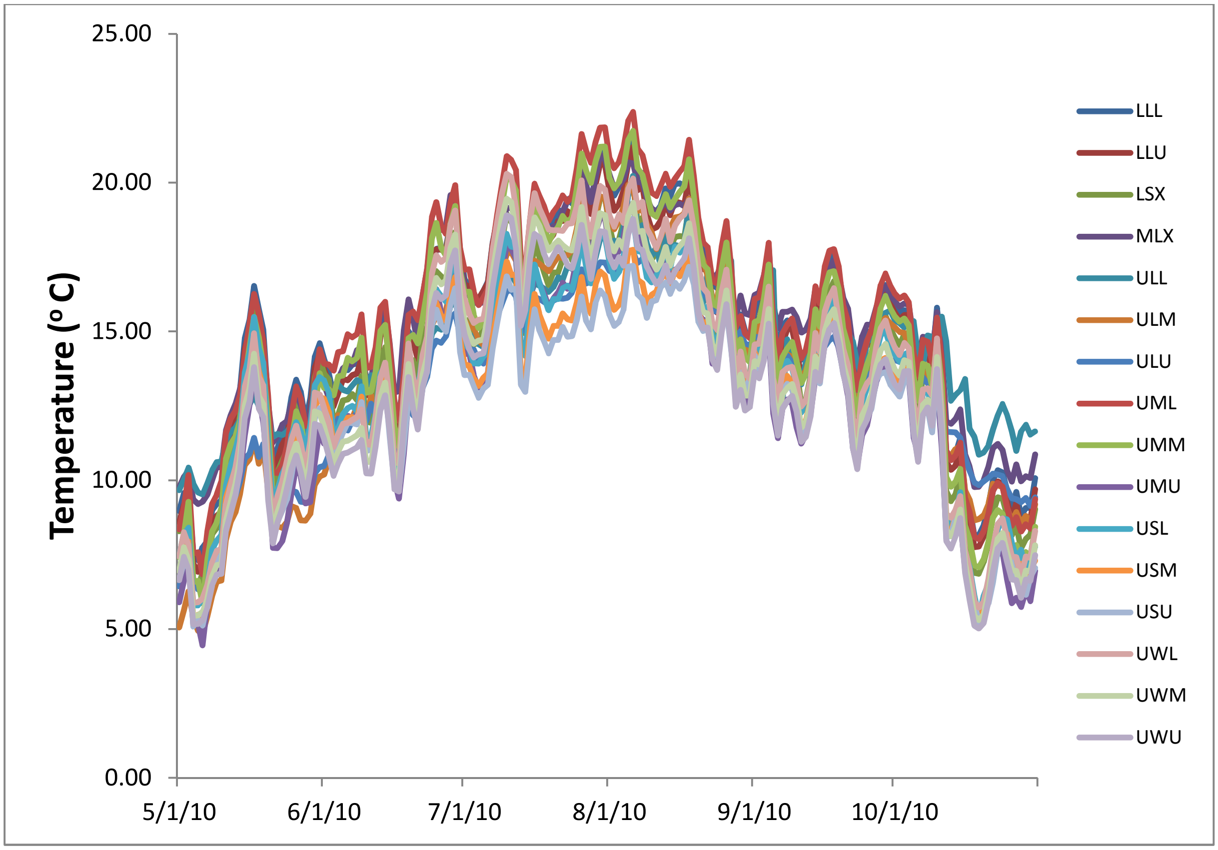
APPENDIX 10

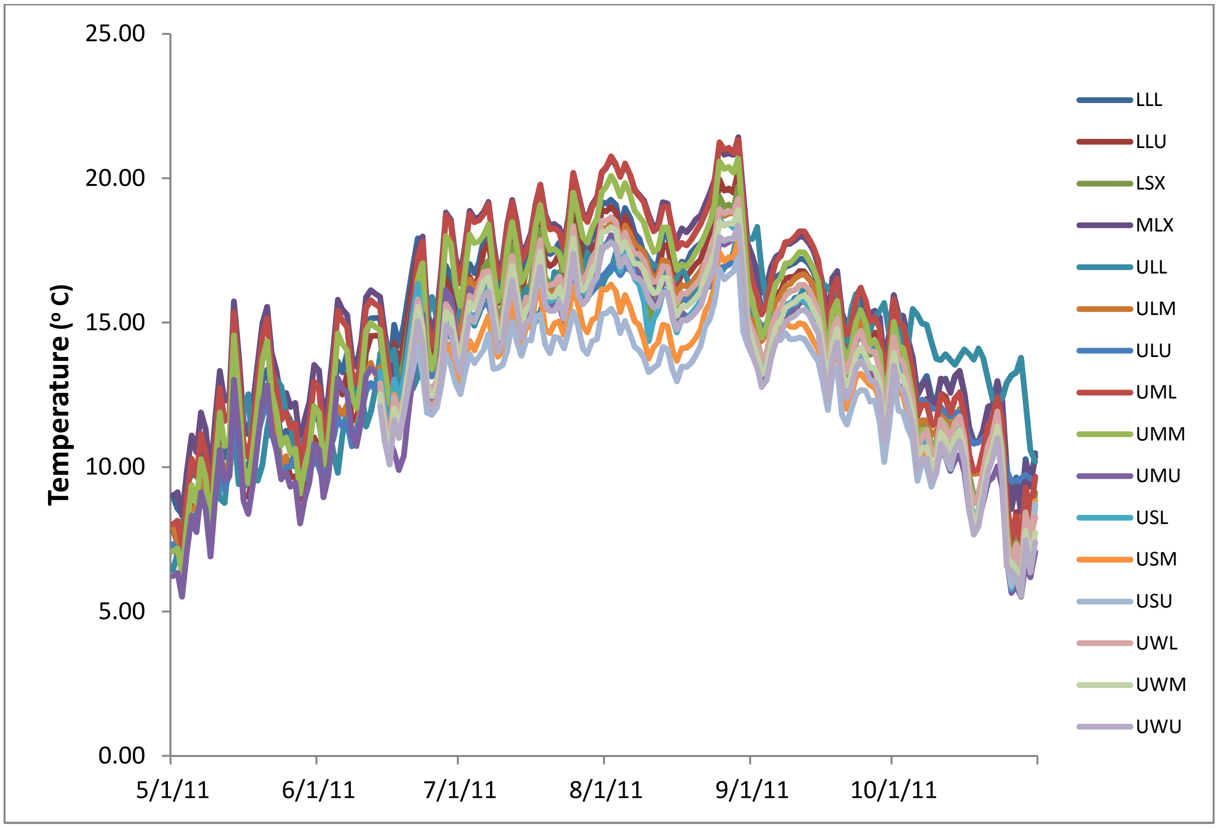
Hydrograph (cubic feet s^{-1}) for the United States Geological Survey gauging station 13342450 Lapwai Creek. The station is located near the mouth, and data are reported from 1.1.2010 to 12.31.2012. All data are approved. Note logarithmic scale on the y-axis.

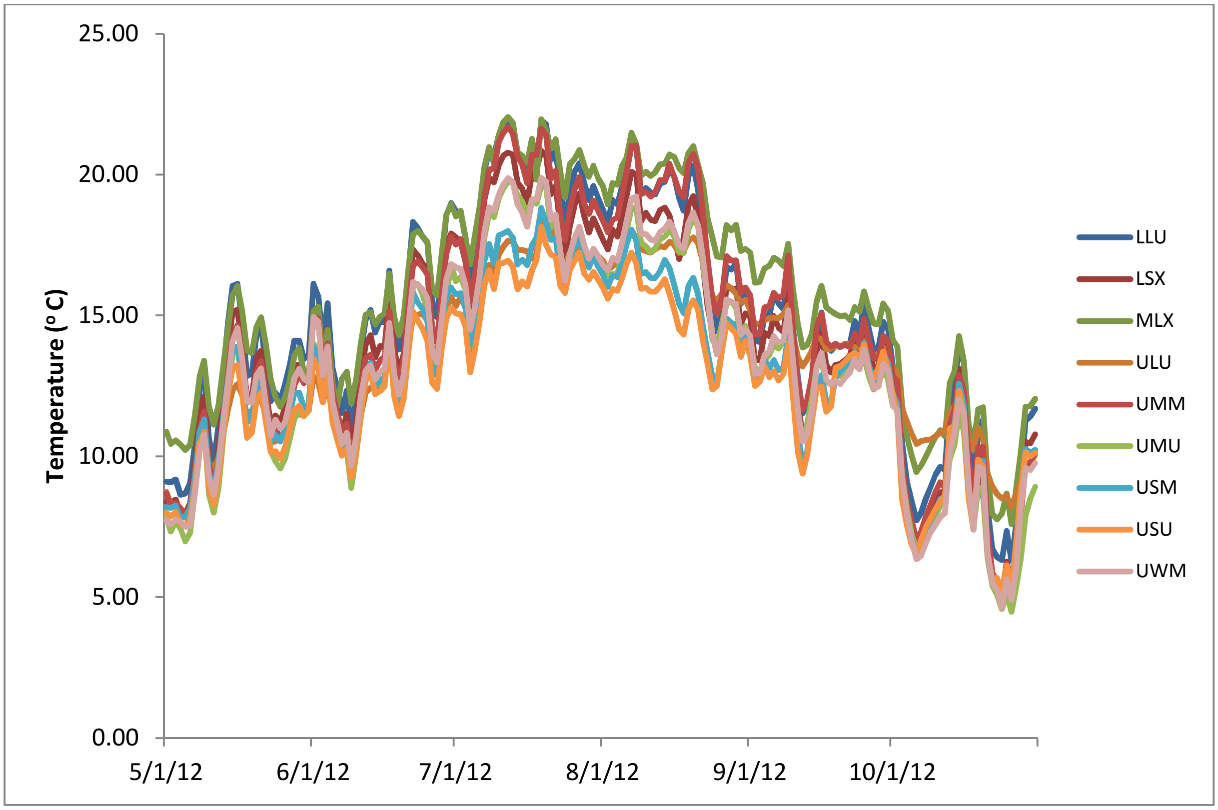

USGS 13342450 LAPWAI CREEK NR LAPWAI ID
Discharge, cubic feet per second
4000.0
3000.0
2000.0
1000.0
100.0
10.0
4.0
Jan 2010
Jul 2010
Jan 2011
Jul 2011
Jan 2012
Jul 2012
Jan 2013
Discharge
Period of approved data
Graph courtesy of the U.S. Geological Survey

APPENDIX 11

Average daily temperatures (^{o} C) from May 1st through October 31st for each of the 2010, 2011, and 2012 sampling seasons. Sampling season is indicated on the x-axes.


25.00
20.00
15.00
10.00
5.00
0.00
Temperature (º C)
5/1/10
6/1/10
7/1/10
8/1/10
9/1/10
10/1/10
LLL
LLU
LSX
MLX
ULL
ULM
ULU
UML
UMM
UMU
USL
USM
USU
UWL
UWM
UWU


25.00
20.00
15.00
10.00
5.00
0.00
Temperature (º C)
5/1/11
6/1/11
7/1/11
8/1/11
9/1/11
10/1/11
LLL
LLU
LSX
MLX
ULL
ULM
ULU
UML
UMM
UMU
USL
USM
USU
UWL
UWM
UWU


25.00
20.00
15.00
10.00
5.00
0.00
Temperature (° C)
5/1/12
6/1/12
7/1/12
8/1/12
9/1/12
10/1/12
LLU
LSX
MLX
ULU
UMM
UMU
USM
USU
UWM

APPENDIX 12

Characteristics of the drainages above each study site, showing the total area, proportion of the area which consists of unconsolidated lithology, elevation of the study site (the lowermost point in the drainage), the mean and maximum elevation, slope characteristics, and the proportions of volcanic rock, forest cover, agricultural land, and urban (housing and pavement).

Site	Total area (km^2)	Area uncon-solidated (km^2)	% uncon-solidated	Site elev. (m)	Max elev. (m)	Mean drainage elev. (m)	Mean Slope (%)	% area slope > 30 %	% area slope > 50	% area surficial volcanic rock	% forest cover	% ag	% urban
LLL	634.23	152.99	24.1	279	1530	988	20	25	8.28	71.3	32	32.7	4.68
LLU	582.80	110.36	18.9	320	1530	1030	20	25	8.83	76.0	35	30.4	4.57
LSX	190.96	53.57	28.0	390	1530	1073	22	27	8.53	63.4	45	17.9	3.56
MLX	367.77	41.72	11.3	354	1466	1039	19	23	9.34	85.3	31	37.0	5.06
ULL	143.60	7.91	5.51	448	1411	1058	18	20	10.6	94.7	22	46.3	6.61
ULM	127.65	1.17	0.92	524	1411	1106	17	20	11.8	98.9	24	47.4	6.06
ULU	99.84	0.00	0.00	692	1411	1161	14	14	8.74	99.8	23	54.2	5.88
UML	190.76	14.23	7.46	411	1466	1103	19	23	9.29	85.9	43	31.2	3.93
UMM	146.25	10.77	7.37	469	1466	1146	19	23	8.95	83.8	51	23.5	3.54
UMU	92.19	0	0	629	1466	1289	16	18	9.00	90.1	66	16.1	2.75
USL	100.89	39.20	38.9	448	1518	1015	24	31	8.91	53.9	35	26.7	4.12
USM	73.41	18.07	24.6	527	1518	1109	26	35	10.7	65.4	48	18.4	3.80
USU	69.40	15.90	22.9	573	1518	1134	26	34	10.5	66.6	50	18.5	3.85
UWL	79.17	8.66	10.9	439	1530	1213	20	23	9.15	77.4	64	6.47	2.37
UWM	77.90	8.57	11.0	485	1530	1225	20	23	8.94	77.2	65	6.57	2.35
UWU	75.71	7.65	10.1	524	1530	1241	19	22	8.62	77.8	66	6.16	2.38

APPENDIX 13

Summary table of habitat conditions in the study reaches for the three years of sampling. N refers to number of point measurements, vel. = velocity, sub. = substrate, comb. = combination of velocity < 0.15 ms^{-1} and depth < 6 cm, LWD = Large woody debris (piece of wood > 100 cm in length and 5 cm in diameter), overhang. = overhanging vegetation above point measurement sector. SD refers to the standard error of the preceding metric, and prop. refers to the proportion of the point measurements having the characteristic.

Year	Site	n	Width (m)	SD	Depth (cm)	SD	Vel. (m/s)	SD	Sub. (mm)	SD	Comb. count	Prop.	LWD count	Overhang.count	Prop.
2010	LLL	70	5.11	2.25	22	12	0.34	0.25	129	61	35	0.5	6	20	0.29
	LLU	85	5.36	1.49	21	11	0.31	0.20	113	47	17	0.2	2	31	0.36
	LSX	100	4.82	1.22	20	15	0.42	0.23	108	70	2	0.02	12	45	0.45
	MLX	100	3.70	0.99	17	12	0.24	0.20	105	73	5	0.05	13	31	0.31
	ULL	85	4.79	1.86	13	8	0.14	0.15	128	98	26	0.31	1	27	0.32
	ULM	85	4.04	0.77	10	8	0.16	0.13	141	77	35	0.41	1	30	0.35
	ULU	100	3.82	1.20	12	8	0.19	0.16	213	186	21	0.21	0	19	0.19
	UML	100	2.66	1.22	9	5	0.08	0.09	119	66	36	0.36	5	36	0.36
	UMM	100	4.11	1.18	7	4	0.13	0.10	124	96	48	0.48	2	15	0.15
	UMU	95	3.56	1.02	11	5	0.15	0.14	238	226	16	0.17	1	32	0.34
	USL	100	2.98	1.25	23	13	0.41	0.28	137	180	2	0.02	0	61	0.61
	USM	100	3.97	2.21	31	16	0.29	0.27	86	56	1	0.01	5	66	0.66
	USU	100	3.06	0.68	19	9	0.46	0.30	107	73	1	0.01	7	49	0.49
	UWL	65	2.54	0.81	12	12	0.11	0.11	85	48	54	0.83	1	28	0.43
	UWM	95	2.77	0.98	11	9	0.14	0.13	103	58	21	0.22	20	28	0.29
	UWU	95	2.41	0.72	11	9	0.16	0.15	159	98	25	0.26	11	0	0.00
2011	LLL	95	8.81	1.53	26	21	0.30	0.28	122	32	9	0.09	4	14	0.15
	LLU	100	6.77	1.46	14	7	0.35	0.25	157	57	7	0.07	23	37	0.37
	LSX	100	4.80	1.27	19	11	0.44	0.27	136	46	4	0.04	16	33	0.33
	MLX	100	6.56	2.25	16	10	0.28	0.24	117	56	3	0.03	6	25	0.25
	ULL	100	4.97	1.02	10	6	0.17	0.14	139	56	17	0.17	61	29	0.29
	ULM	100	4.77	1.65	15	11	0.16	0.15	126	34	13	0.13	5	34	0.34
	ULU	100	4.84	1.40	12	7	0.22	0.22	207	122	10	0.1	0	28	0.28
	UML	100	4.19	1.51	17	11	0.18	0.16	126	45	10	0.1	14	32	0.32
	UMM	100	4.37	1.09	10	5	0.25	0.18	146	53	16	0.16	3	18	0.18
	UMU	100	3.43	0.95	11	7	0.17	0.18	246	163	16	0.16	0	49	0.49
	USL	90	3.13	0.65	24	15	0.40	0.26	108	69	11	0.12	3	48	0.53

	USM	100	3.02	1.17	29	22	0.33	0.29	64	51	3	0.03	32	47	0.47
	USU	100	2.79	0.43	20	8	0.44	0.24	138	66	2	0.02	7	42	0.42
	UWL	100	4.37	0.89	12	9	0.27	0.24	125	50	17	0.17	12	46	0.46
	UWM	100	3.34	0.84	19	12	0.28	0.23	144	92	8	0.08	78	37	0.37
	UWU	100	3.47	1.32	21	13	0.26	0.23	134	56	3	0.03	3	26	0.26
2012	LLU	100	6.95	1.73	14	6	0.39	0.25	186	111	7	0.07	23	28	0.28
	LSX	100	5.05	1.10	19	11	0.41	0.24	165	103	4	0.04	11	24	0.24
	MLX	100	4.43	0.92	19	10	0.26	0.22	141	105	5	0.05	5	22	0.22
	ULU	100	4.54	1.07	11	5	0.24	0.18	176	179	13	0.13	1	39	0.39
	UMM	100	4.68	0.65	10	4	0.23	0.17	149	66	22	0.22	2	16	0.16
	UMU	100	3.68	0.81	14	8	0.22	0.20	184	106	8	0.08	1	43	0.43
	USM	100	3.25	1.00	26	18	0.34	0.28	100	54	2	0.02	17	63	0.63
	USU	100	2.92	0.52	16	9	0.34	0.22	195	149	6	0.06	11	63	0.63
	UWM	100	3.40	0.80	19	13	0.32	0.27	165	126	2	0.02	47	43	0.43

APPENDIX 14

Summary table of habitat conditions in the margins of study reaches for the three years of sampling. N refers to number of point measurements, comb. = combination of velocity < 0.15 ms^{-1} and depth < 6 cm, slowest velocity = the average of all the slowest of each margin measurement pair per transect, and overhang. = overhanging vegetation above point measurement sector. SD refers to the standard error of the preceding metric, and prop. refers to the proportion of the point measurements having the characteristic.

Year	Site	n	Depth (cm)	SD	Velocity (m/s)	SD	Comb. count	Prop.	Slowest velocity avg (m/s)	SD	Overhang. count	Prop.
2010	LLL	28	20	14	0.19	0.16	16	0.57	0.06	0.07	12	0.43
	LLU	34	20	12	0.22	0.17	8	0.24	0.11	0.12	20	0.59
	LSX	40	19	15	0.31	0.18	2	0.05	0.23	0.15	26	0.65
	MLX	40	14	9	0.18	0.20	4	0.10	0.11	0.16	21	0.53
	ULL	34	14	8	0.11	0.15	13	0.38	0.04	0.06	19	0.56
	ULM	34	10	8	0.15	0.11	15	0.44	0.09	0.09	14	0.41
	ULU	40	10	7	0.15	0.15	13	0.33	0.06	0.06	11	0.28
	UML	40	7	3	0.07	0.08	16	0.40	0.05	0.06	15	0.38
	UMM	40	8	5	0.12	0.11	19	0.48	0.07	0.07	10	0.25
	UMU	38	10	4	0.09	0.11	9	0.24	0.02	0.03	18	0.47
	USL	40	20	14	0.32	0.26	2	0.05	0.21	0.21	34	0.85
	USM	40	23	9	0.22	0.25	1	0.03	0.14	0.19	40	1.00
	USU	40	16	9	0.34	0.26	1	0.03	0.21	0.16	27	0.68
	UWL	26	9	11	0.08	0.09	28	1.08	0.03	0.05	13	0.50
	UWM	38	10	10	0.10	0.12	13	0.34	0.04	0.04	19	0.50
	UWU	38	10	10	0.12	0.14	14	0.37	0.04	0.05	0	0.00
2011	LLL	38	25	25	0.26	0.24	6	0.16	0.10	0.10	14	0.37
	LLU	40	11	5	0.22	0.16	5	0.13	0.14	0.11	25	0.63
	LSX	40	16	12	0.36	0.26	4	0.10	0.23	0.19	20	0.50
	MLX	40	15	9	0.27	0.28	2	0.05	0.17	0.13	16	0.40
	ULL	40	10	7	0.15	0.13	12	0.30	0.08	0.09	19	0.48
	ULM	40	13	12	0.14	0.13	8	0.20	0.08	0.09	17	0.43
	ULU	40	10	6	0.14	0.17	7	0.18	0.06	0.08	18	0.45
	UML	40	14	9	0.14	0.13	6	0.15	0.08	0.09	14	0.35
	UMM	40	8	4	0.17	0.16	15	0.38	0.08	0.08	13	0.33
	UMU	40	10	5	0.12	0.16	8	0.20	0.06	0.06	24	0.60
	USL	36	22	14	0.38	0.26	5	0.14	0.22	0.21	26	0.72

	USM	40	26	21	0.25	0.23	1	0.03	0.16	0.16	32	0.80
	USU	40	17	9	0.33	0.25	2	0.05	0.19	0.13	23	0.58
	UWL	40	12	10	0.28	0.25	11	0.28	0.10	0.10	28	0.70
	UWM	40	16	13	0.18	0.15	7	0.18	0.09	0.10	20	0.50
	UWU	40	19	13	0.19	0.21	2	0.05	0.10	0.10	13	0.33
2012	LLU	40	12	6	0.29	0.20	6	0.15	0.16	0.09	16	0.40
	LSX	40	17	13	0.32	0.20	3	0.08	0.20	0.14	17	0.43
	MLX	40	17	11	0.23	0.24	4	0.10	0.17	0.21	13	0.33
	ULU	40	9	4	0.16	0.15	10	0.25	0.07	0.09	28	0.70
	UMM	40	8	4	0.16	0.12	15	0.38	0.09	0.08	15	0.38
	UMU	40	11	6	0.18	0.17	6	0.15	0.11	0.14	25	0.63
	USM	40	21	13	0.24	0.23	1	0.03	0.15	0.14	37	0.93
	USU	40	13	9	0.26	0.24	5	0.13	0.14	0.13	35	0.88
	UWM	40	18	13	0.28	0.26	1	0.03	0.15	0.14	25	0.63