

Influence of early life growth and precipitation zone on survival to adulthood in wild Steelhead Trout (*Oncorhynchus mykiss*) in the Skagit River basin, WA

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Chapter 1: Overview of the decline, life history, and management of wild Steelhead Trout, *Oncorhynchus mykiss*, in Puget Sound

The Decline of Wild Steelhead in Puget Sound

Since 1990, total run sizes of wild winter Steelhead Trout, *Oncorhynchus mykiss*, have declined precipitously in the Puget Sound basin (Hard et al. 2007, Ford et al. 2010). In 2007, wild Puget Sound Steelhead were listed as threatened under the U.S. Endangered Species Act (Rausch 2007). The pre-1900 annual modal run size of Puget Sound winter-run Steelhead was estimated at 622,000 individuals, but more current estimates (between years 1980 and 2004) comprised only 1%–4% of this value (Gayeski et al. 2011). The decline in Puget Sound Steelhead is due to a combination of factors, including loss of the Steelhead life history, loss of freshwater habitat, and interference from hatchery Steelhead propagation (Busby et al. 1996, Hard et al. 2007, Gayeski et al. 2011). Furthermore, environmental conditions in both the nearshore (Moore et al. 2010) and the high seas of the Pacific Ocean influence marine survival of anadromous salmonids (Ward 2000, Welch et al. 2000, Welch et al. 2004, Acheson et al. 2012, Welch et al. 2011).

The overall decline in wild Puget Sound Steelhead is probably a result of historical anthropogenic events that have been compounded by more recent natural and anthropogenic events (Cederholm et al. 2000). The increasing rate of freshwater habitat loss due to urban and rural land development, interspecific competition with hatchery fish, and deleterious changes in climate and oceanic conditions probably destabilizes populations that had been previously impacted by fishery overharvest across multiple generations of stocks. This scenario combines

some of the general mechanisms that have probably led to the continued decline in wild Puget Sound Steelhead populations.

Very little, to no, quantitative information exists that comprehensively and conclusively identifies factors that affect survival and production of wild Puget Sound Steelhead. For example, no recent quantitative data specific to the freshwater life cycle of wild Puget Sound Steelhead were found during a review of the recent literature. Therefore, current factors that influence mortality rates during the juvenile life stage, such as growth, remain unknown in the Puget Sound. In the absence of empirical biological information, efforts to recover anadromous salmonids in Puget Sound may be hampered by ineffectiveness in targeting factors that control survival and productivity.

Life History of Wild Steelhead in the Puget Sound

The plasticity in life history expression by *O. mykiss* in the anadromous zone is unparalleled in other anadromous salmonids, and can confound effective management of threatened wild Steelhead. Wild *O. mykiss* are different from most other anadromous salmonids in that, between the parr and adult stages of life, individuals have the potential to adopt a number of different life history strategies, but can switch to express alternative life histories at any time. For example, some individuals may express a fully anadromous life history throughout life by migrating as premature smolts to marine environments, where they experience increased risk of predation associated with marine environments, but in turn grow fast to a large size-at-maturity (Steelhead Trout). In contrast, others might never migrate to saltwater, and instead spend their entire life in freshwater where, due to limited resources, they will attain a smaller size-at-maturity while avoiding the increased predation pressures of marine life (resident Rainbow

Trout). Still, others can express both life histories if they attain maturity in freshwater habitats (e.g., age 4 or greater) but then emigrate to marine environments to increase gametic production. These individuals are probably more likely to survive early phases in marine environments than most other Steelhead smolts due to their comparatively older age and larger size because larger size enables them to more effectively avoid predation and prey on large, energy-rich food items. Regardless of the life history type expressed, individuals of each form are obligate freshwater spawners, and are therefore capable of reproducing with *O. mykiss* that express other life history types, which may cause errors in production and abundance estimates of the anadromous form.

Mature wild Puget Sound Steelhead return from the ocean to natal river basins during all months, but most return between November and April and spawn prior to or during spring snowmelt or runoff between March and June (Hard et al. 2007). Steelhead construct nests (redds) at locations with ample subsurface flow using small to large gravels (Wydoski and Whitney 2003), and fertilized eggs incubate between 3 weeks and nearly 2 months, depending primarily on water temperature, but also dissolved oxygen concentration (Quinn 2005). Steelhead fry (between 25 and 30 mm fork length [FL]) emerge from redd sites (Deschutes River, OR, Zimmerman and Reeves 1999), move to stream margins, and feed on small invertebrates drifting in the stream current. At approximately age 2 or 3, juvenile Steelhead undergo physiological changes (smolting) that prepare them for a life of growth and maturation in saltwater. Most wild Puget Sound Steelhead smolt emigrate to saltwater during their second or third spring (age 2 or 3) (Busby et al. 1996), although some emigrate as early as their first spring or as late as their fifth spring. After arriving in saltwater, wild Puget Sound Steelhead smolts swim rapidly away from shallow estuarine habitats and navigate through the Puget Sound to the Strait of Juan de Fuca and into the Pacific Ocean (Hartt and Dell 1986, Welch et al. 2004,

Moore et al. 2010, E. Connor, Seattle City Light, personal communication). Most maturing wild Puget Sound Steelhead spend 1 or 2 years in marine environments; however, marine residence in some individuals can range from 4 months (e.g., half-pounder) to more than 4 years, and some adults complete multiple spawning runs in a lifetime. Oceanic distribution data on Steelhead are sparse, but it is known that maturing Steelhead range east as far as the Sea of Japan. Most maturing Steelhead, however, spend a majority of their marine life in the productive Gulf of Alaska and North Central Pacific Ocean regions (Atcheson et al. 2012). It is also possible that some maturing Steelhead from Puget Sound basins do not emigrate to the open ocean, but instead reside in Puget Sound before returning to spawn in natal streams (Busby et al. 1996).

Management of Wild Steelhead in the Skagit River Basin

Land and Water Management

The Skagit River basin is the largest tributary to the Puget Sound, produces the highest proportion of wild winter-run Steelhead annually (on average 37% of the total Puget Sound population, Ford et al. 2010), and historically contained significant numbers of summer-run Steelhead. The recent decline in wild Skagit River Steelhead returns seems less severe than that observed in many other Puget Sound populations (Hard et al. 2007); however, reduced run sizes have resulted in continual reductions in sport and tribal fisheries, and reductions in fisheries have had little to no effect on improving run sizes (B. Barkdull, Washington Department of Fish and Wildlife, personal communication). Probable causes of the decline in wild Skagit River basin Steelhead include various forms of habitat alteration, harvest impacts, hatchery impacts, flow alterations, and poor oceanic conditions. Two large hydroelectric projects are located in the Skagit basin, including two dams in the Baker River sub-basin operated by Puget Sound Energy,

and three dams in the upper Skagit River operated by Seattle City Light. Although utility managers have invested relatively large amounts of resources to guide restoration efforts to improve fish passage and habitat, the Baker River project directly limits the upstream spatial distribution of anadromous *O. mykiss*, and the regulation of flows from both hydroelectric projects diminish hydraulic and geomorphic dynamics that would otherwise fluctuate widely. In free-flowing systems, native hydrologic dynamics increase the complexity of habitats and enable the flux of energy and vital nutrients between aquatic and terrestrial systems. Thus, at least some native physical attributes have been altered or severed in the Skagit River basin, especially in the zones most heavily influenced by project management operations. However, impacts of land and project management have not been conclusively linked to the decline in wild Skagit basin Steelhead. Furthermore, a large portion of riverine habitat in the Skagit basin, the Sauk River sub-basin, is not affected by regulated flows, and most of the headwaters in this sub-basin are located on protected U.S. Forest Service and National Park lands. However, historical and current timber harvest practices and residential development are still prevalent in the lower portion of the Sauk River sub-basin. In the Skagit River basin as a whole, most of the medium elevation, lower-basin tributaries continue to be affected by land use, such as logging, commercial and residential development, and farming, whereas most of the high elevation, upper-basin tributaries remain relatively undisturbed by these factors.

Fishery Management and Monitoring

Research and monitoring programs have increased the overall amount of empirical data available on wild Skagit River Steelhead smolt populations. In 1990, the Washington Department of Fish and Wildlife (WDFW) initiated a combination screw/scoop-fry and smolt-

trapping program approximately 27 kilometers upstream from the Skagit River delta in the Skagit River mainstem. These traps operate annually from early winter through early summer and specifically target the quantification of Chinook Salmon, *O. tshawytscha*, and Coho Salmon, *O. kisutch*, smolt production (Kinsel et al. 2008). However, Steelhead smolt are also captured and sampled in these traps during their spring emigration. Trapping efficiency for Steelhead smolts has not yet been conclusively determined at these traps, which constrains the ability to accurately estimate smolt recruitment. It is assumed that the combined trap system in the Skagit River mainstem yields a limited, size-biased catch of emigrating Steelhead smolts, as larger smolts (e.g., greater than 200 mm FL) are able to escape from the trap or avoid being captured during trap operation, and therefore are probably underrepresented in the sample (M. Zimmerman, Washington Department of Fish and Wildlife, personal communication).

Regardless of trap inefficiencies, it appears that Steelhead smolt migration timing is influenced by the hydrologic regime, as smolt catch increases near the middle of April, peaks in the middle of May, and essentially ceases by late June (Washington Department of Fish and Wildlife, unpublished data). Between 1990 and 2011, peak emigration of smolts corresponded with the final ascents of spring peak flows, and the smolt migration essentially ceased just prior to the end of the peak flow period. Based on smolt trap frequency distributions, most smolts captured at the Skagit River mainstem traps appear to be age 2 or 3. However, due to the biased nature of smolt size catch data and differences in size-at-age, caution should be exercised when interpreting these results.

Probable size-selective capture at the Skagit River mainstem smolt traps has precluded Steelhead smolt production estimates. Therefore, Puget Sound salmonid fishery co-managers with the Upper Skagit Indian Tribe and WDFW were granted resources to augment the smolt-

trapping program to obtain more directed, less biased Steelhead smolt production information. In early spring of 2012, prior to the peak Steelhead smolt migration, screw traps were deployed in three tributaries, and trapping efficiency and size-selectivity studies were initiated. Preliminary results indicated that these traps were not significantly size-selective, but more rigorous size-selectivity studies are needed to provide conclusive evidence (C. Kinsel, Washington Department of Fish and Wildlife, personal communication). Nevertheless, at a minimum this program should provide refined estimates of Steelhead smolt production in selected tributaries to the Skagit River mainstem, and may eventually inform overall production estimates in the Skagit River basin.

Size and age structure information is vitally important to the effective management of fishes (Isley and Grabowski 2007), and this is especially true for wild Steelhead during the early stages of life (Ward et al. 1989, Ward 2000, Bond et al. 2008). Evaluation of size-at-age and the complete growth history of individuals can inform estimates of growth and survival, and guide research efforts to improve growth and survival where needed in the basin. Scales reveal the complete growth history of salmonids, and use of scales over otoliths is advantageous in that the age and growth history of each fish can be measured, and fish need not be sacrificed (Devries and Frie 1996). However, if only scales are evaluated, a one-year underestimation in age can occur, especially for late-emerging fish inhabiting cold water in unproductive habitats (Davis and Light 1985). Scale samples of wild Skagit River basin adult Steelhead caught using various methods between 1985 and 2012 (tribal fishery and ceremony, sport fishery, and biological sampling) were analyzed by WDFW to evaluate smolt and adult age composition in Skagit River Steelhead (Washington Department of Fish and Wildlife, unpublished data). Based on these samples, 75% of wild adults from brood years 1980 to 2010 were age 2 when they entered salt

water, 23% were age 3, 1% were age 1, and 1% were age 4. The proportion of ocean ages for adult steelhead that smolted at age 2 was 48% ocean age 1, 47% ocean age 2, and 5% ocean age 3. Adults that smolted at age 3 spent 1 (46%), 2 (49%), or 3 (5%) full years at sea. Thus, the most common combined freshwater-saltwater age among pooled years was age 2.1 or 2.2. On average, adults that smolted at a younger age (freshwater age 1 or 2) spent more time in the ocean, resulting in a larger size-at-maturity, whereas those that smolted at an older age (freshwater age 3 or 4) spent less time in the ocean, attaining a smaller size-at-maturity (Washington Department of Fish and Wildlife, unpublished data). Hooten et al. (1987) and Ward and Slaney (1988) observed similar life history-dependent size and growth patterns in Steelhead populations on Vancouver Island, British Columbia. It is important to recognize that, as opposed to the aforementioned studies, which used weirs and traps to capture adults and smolts near the river mouth, Skagit River basin adult samples were obtained using methods and levels of effort that varied spatially and temporally within a much larger basin. Nevertheless, size at any age can be estimated by employing back-calculation methods with steelhead scales (Ward et al. 1989), and growth rate frequencies from different life stage samples (steelhead sampled at the fry, parr, smolt, and adult stages) can be evaluated to determine the relative role of early life growth and corresponding environmental conditions on survival to later life stages (i.e., size-selective mortality) (Ward 2000, Bond et al. 2008).

For anadromous salmonids, marine mortality is high (Ricker 1976; Beamish and Mahnken 2001), and size-selective mortality is prevalent during early marine life stages (Beamish et al. 2004, Melnychuck et al. 2007 Cross et al. 2008, Duffy and Beauchamp 2011, Miller et al. 2011, Tomaro et al. 2012). This study evaluated consequences of early life growth in terms of survival to smolt or adult stages. The primary objective of this study was to

determine whether significant size-selective mortality (SSM) in Steelhead could be detected between freshwater stages and returning adults; and if so, how the magnitude of SSM varied among reaches categorized by three different riverine environments (precipitation zones: snow, mixed rain-snow, or rain). Secondly, I used a bioenergetics-modeling framework to investigate how underlying environmental factors affect freshwater growth and thus survival during critical growth periods for juvenile Steelhead in the Skagit River basin.

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Chapter 2: The relative roles of early life growth and precipitation zone on survival to adulthood in wild Steelhead Trout in the Skagit River basin, WA

Abstract

Wild Steelhead Trout, *Oncorhynchus mykiss*, in the Puget Sound are currently in decline, and very little is known about the early life history of these threatened fish. This study evaluated consequences of early life growth in terms of survival to smolt or adult stages. The objectives of this study were to determine whether significant size-selective mortality (SSM) in Steelhead could be detected between freshwater stages and returning adults; and if so, how the magnitude of size selectivity varied among reaches categorized by three different precipitation zones (snow, mixed rain-snow, or rain). Wild Steelhead in the Skagit River basin were sampled as juveniles, smolts, and adults, and scales were measured to compare back-calculated freshwater growth rates and size distributions of rearing juveniles with individuals that survived from an earlier life stage to the smolt and adult stages. Linear regression of scale radius (SR) and fork length indicated that SR was a reasonable predictor of fork length during freshwater residency. Back-calculated size-at-annulus estimates indicated that fish sampled as adults grew significantly faster to age 1, 2, and 3 annuli compared to fish sampled as juveniles, and faster to the age 2 and 3 annuli compared to fish sampled as smolts. Within precipitation zones, fish sampled as juveniles were consistently smaller at each freshwater annulus compared to those same freshwater annuli on fish sampled as adults. An increased disparity in size-at-annuli 2 and 3 between fish sampled as juveniles, smolts, and adults suggests that fast growth during the period at which Steelhead smoltify is vitally important to survival to adulthood. These findings provide evidence that survival among life stages is an important dynamic in wild Steelhead, and can be attributed, in

part, to size attained at earlier life stages. Efforts for recovery of threatened Puget Sound Steelhead could benefit by considering growth- and size-selective mortality in freshwater environments, and identifying factors that limit early life growth at a finer scale of habitat, for example among sub-basins or precipitation zones.

Introduction

During the previous two decades, wild adult Steelhead Trout, *Oncorhynchus mykiss*, have declined precipitously in the Puget Sound basin (Hard et al. 2007, Ford et al. 2010), and in 2007, this evolutionary significant unit was listed as threatened under the US Endangered Species Act (Rausch 2007). Possible reasons for the decline include loss of the Steelhead (anadromous) life history form, loss of freshwater habitat, interference from artificial (hatchery) Steelhead propagation, and changes in ocean productivity (Busby et al. 1996, Cederholm et al. 2000, Welch et al. 2000, Hard et al. 2007, Gayeski et al. 2011). However, a scarcity of empirical information continues to limit our understanding of the mechanistic factors that influence the decline of wild Puget Sound Steelhead.

Survival to adulthood in many fishes is partially dependent on growth rate during early life, as larger, faster growing individuals are better able to survive size-selective pressures, such as predator avoidance, and increased gape size enables consumption of higher energy prey (Sogard 1997). Juvenile growth rate and smolt size vary among species of anadromous salmonids, but also among different life history types within a species. For anadromous salmonids, marine mortality is high (Ricker 1976; Beamish and Mahnken 2001), and size-selective mortality is prevalent during early marine life stages (Beamish et al. 2004, Melnychuck et al. 2007 Cross et al. 2008, Duffy and Beauchamp 2011, Miller et al. 2011, Tomaro et al. 2012). Juvenile Steelhead generally rear longer in freshwater than other species of Pacific salmon, and most Steelhead smolts emigrate after growing 2-3 years in freshwater environments (Busby 1996), then move rapidly offshore to oceanic waters (Miller et al. 1983, Hartt and Dell 1986, Moore et al. 2010). Because of their extended freshwater rearing, Steelhead could undergo

critical growth periods in one or more freshwater (Ward et al. 1989; McCarthy et al. 2009) or marine life stages (Ward 2000; Bond et al. 2008).

Previous studies of wild coastal Steelhead indicated that juvenile growth can influence survival at different freshwater or marine life stages (Ward et al. 1989, Bond et al. 2008). For Steelhead in the Keogh River, British Columbia, smolt-to-adult returns (SARs) were strongly correlated to smolt size (i.e. freshwater growth) during years 1976 to 1990 (Ward et al. 1989). However, the relation between smolt size and marine survival disappeared during 1991-1996, and marine survival declined significantly (Ward 2000). Heterogeneity in freshwater feeding and growth among habitats within a watershed (e.g. McCarthy et al. 2009), combined with the potential influence of smolt size on marine survival (Ward et al. 1989, Bond et al. 2008) suggest that riverine habitats could play an important role in growth, survival, and viability of Steelhead populations.

Current biological information on the early life stages of Puget Sound Steelhead is scarce. For example, few recent studies have documented the freshwater ecology and early life history of these fish to the degree that historical studies did (e.g., Meigs and Pautzke 1941). Therefore, current factors that influence mortality rates in freshwater and marine environments remain unknown in Puget Sound populations. Local fishery management has recently increased efforts to enable wild Steelhead smolt production estimates in the Skagit River basin. This program focuses on outmigrating smolts, which will facilitate estimates of egg-to-smolt survival (M. Zimmerman, Washington Department of Fish and Wildlife, personal communication). However, monitoring programs based on single life stages cannot necessarily identify the mechanisms or life stages that most influence production throughout the life cycle (Zabel and Achord 2004). In the absence of empirical biological information from multiple life stages, efforts to maintain or

recover anadromous salmonid populations in the Puget Sound may be hampered by ineffectiveness at identification of factors that control survival from early to later life stages (e.g., Ward 2000).

Information is also limited on how different habitats might contribute to increased or decreased survival among life stages. However, a recently completed companion study in the Skagit River basin indicated that habitat associated with three different precipitation zones (snow, mixed snow and rain, and rain-dominated precipitation zones) could influence the seasonal importance of rearing habitats for juvenile salmonids (Lowery et al. 2013). These results could have implications for how survival is affected by differential habitat availability and use in the Skagit River and other basins in the Puget Sound region.

The objectives of this study were to determine whether size-selective mortality (SSM) could be detected at one or more early phase freshwater life stages in Steelhead or between freshwater stages and returning adults, and if so, did the magnitude of SSM vary among habitats in different precipitation zones. This study was conducted on wild Steelhead in the Skagit River basin, the most productive watershed for Steelhead in the Puget Sound. I expected that fish sampled as surviving adults would be larger at ages 1, 2, and 3 compared to fish sampled during earlier life stages as juveniles and smolts. Secondly, I expected that size-at-age would vary among different precipitation zones, and would correspond with faster early life growth and reduced SSM in mixed rain-snow zone sites, and lower growth and increased SSM in more extreme physical environments in the snow and rain precipitation zones.

Study Area

The Skagit River basin, which includes the mainstem Skagit and Sauk rivers and numerous tributaries, is the largest drainage in the Puget Sound region and the second largest in the Salish Sea. The basin drains approximately 8,544 km² from the west side of the North Cascades of Washington State and the Canadian province of British Columbia. Annual precipitation in the basin ranges from 90 cm/year at sea level to 460 cm/year at 3,275 m on Glacier Peak (Beechie et al. 2005). The Skagit River drainage supports the largest populations of anadromous salmonids in the Puget Sound, including Chinook *Oncorhynchus tshawytscha*, Coho *O. kisutch*, Chum *O. keta*, and Pink Salmon *O. gorbuscha*, and Steelhead. Other Salmonid species in the study area include resident Rainbow Trout *O. mykiss*, sea-run and resident Coastal Cutthroat Trout *O. clarkii clarkii*, sea-run and resident Bull Trout *Salvelinus confluentus*, and Mountain Whitefish *Prosopium williamsoni*.

Elevation and precipitation zone influence the hydrologic and water temperature regimes in the drainage (Beechie 1992), and could influence the seasonal importance of rearing habitats for juvenile salmonids (Lowery et al. 2013). Peak annual stream discharge in the snow precipitation zone is influenced by snowmelt, and in the rain precipitation zone by rainstorms. A majority of the Skagit River basin, however, is located in the transitional precipitation zone (mix rain-snow), where peak annual discharge can be influenced by a mixture of both rain and snow precipitation (Figure 1). Two large hydroelectric projects block upstream fish passage in the Skagit River basin, including two dams in Puget Sound Energy's Baker River Project (above rkm 91), and three dams in Seattle City Light's Skagit River Project (above rkm 156). However, the Skagit River Project is located above natural barriers to migration that were considered the upstream limit of native anadromous salmonid distribution (Smith and Anderson 1921).

Methods

To detect SSM during the freshwater phase in wild Steelhead, scales from fish sampled at different life stages, as juveniles, smolts, and adults, were measured to back-calculate size-at-ages 1, 2, and 3 during the freshwater phase. Estimation of freshwater size-at-age among life stage sample groups enabled comparisons of size distributions and growth rates at each stage. Water temperature and stream flows associated with geophysical factors effect juvenile salmonid growth rates (e.g., Wipfli and Baxter 2010); therefore, size-at-age was compared by life stage group among snow, mix rain-snow, and rain precipitation zones. Freshwater growth at ages 1, 2, and 3 observed from the adult life stage sample group was used as the benchmark for the amount of growth required, at each freshwater age, to increase the probability of survival to adulthood.

Juvenile Sampling

Juvenile Steelhead were sampled for assessment of growth during the earliest stages of life. Juveniles (ages 0 – 3 years) were defined as immature anadromous or non-anadromous *O. mykiss* that were sampled while rearing in a variety of freshwater habitats. Twenty-four sites were selected for a companion study using a spatially balanced allocation scheme (general random tessellation stratified [GRTS]) within the spatial range of Chinook Salmon distribution in the Skagit River basin (Stevens and Olsen 2004, Lowery et al. 2013) (Figure 1). Adult Chinook Salmon and Steelhead populations maintain similar ranges of distribution throughout the study area. Sampling was conducted at or in the vicinity of each GRTS-selected site; therefore, juvenile samples represented growth associated with a diversity of habitats occupied by Steelhead.

Juveniles were captured from stream margin transects up to 400 m long at each sample site using single-pass upstream backpack electrofishing without block nets (Bateman et al. 2005) (Smith Root Model 12-B, 400-1000 v, standard pulse 80 Hz, 500 μ s). Electrofishing practices followed protocols prescribed by the Washington Department of Fish and Wildlife (WDFW) (Temple and Pearsons 2005), and all activities involving vertebrates conformed to the University of Washington Office of Animal Welfare IACUC protocol #3286-20. Captured salmonids were anesthetized with buffered MS-222 and measured for fork length (FL to within 1 mm), and weight (to within 0.1 g), and scale samples were taken from the area above the lateral line between the dorsal and adipose fins (Devries and Frie 1996) of juvenile *O. mykiss* greater than 54 mm FL. Scale formation in Steelhead generally occurs after individuals reach a FL of 30 – 35 mm (Bond et al. 2008). Sample sizes from captured juvenile Steelhead at each site were allotted by functional size groups in an effort to retain ten individuals per size group per site, and to ensure proportional representation of fish size distributions in later analyses (FL: 56 – 65 mm, 66 – 111 mm, 112 – 169 mm, 170-209 mm, \geq 210 mm) (Table 1). Seven additional juveniles of 43 – 52 mm FL from a 2009 sample were used to quantify scale circuli on smaller fish as a reference. Processed fish were allowed to regain equilibrium in a recovery bath and released when able to safely swim away.

Coastal Cutthroat Trout and Steelhead are sympatric within portions of the study area, and distinguishing between juveniles of the two species using morphological traits alone can be difficult (Campton and Utter 1985). However, morphological and genetic studies indicated that Steelhead, Coastal Cutthroat, and hybrids between these two species are reasonably well distinguished in the field (Baumsteiger et al. 2005, Kennedy et al. 2009). Juvenile Steelhead were differentiated from juvenile Coastal Cutthroat Trout using external characteristics that

morphologically differentiate between pure forms (non-hybrids) of each species (e.g., presence of orange cutthroat “slashes” along the lower jaw, maxillary length, spotting intensity, body color, and body depth) (Behnke 1992, Williams et al. 2007, Kennedy et al. 2009). While not dominant, juvenile Coastal Cutthroat were relatively abundant at some sample sites in the Skagit River basin, including Hansen Creek (sites 1 and 27), East Fork Nookachamps Creek (site 30), Finney Creek (site 32), and the Suiattle River (site 3). Only minor numbers of juvenile Coastal Cutthroat Trout were sampled from Jackman Creek (site 18), Day Creek (site 20), and Buck Creek (site 19) sample sites (Figure 1).

Smolt Sampling

Steelhead smolts were sampled for assessment of growth during the intermediate stage of life. During most years since 1990, the WDFW has sampled emigrating Steelhead smolts from the Skagit River basin in a side-by-side dual-trap system (one scoop and one screw trap) located at river kilometer (rkm) 24 in the Skagit River mainstem (site 33, Figure 1). The traps sample only a small fraction of the wetted width of the Skagit River mainstem, and were deployed to capture and facilitate production estimates for smaller anadromous smolts, such as Chinook and Coho Salmon. Based on size-selectivity of the traps at capturing Coho and Chinook Salmon, these mainstem traps probably only capture smaller Steelhead smolts (Kinsel et al. 2008). However, these data were included in size-at-age analysis because size distributions from this smolt trap were similar to those at other smolt traps in the basin. Steelhead smolts captured in smolt traps (February – June 2012) represented immature anadromous Steelhead that had successfully reared, survived to the smolt stage, and were intercepted during the peak smolt saltwater emigration period (smolts age 1–5). During trap operation, a sub-sample of smolts

were measured (FL), and starting in 2011, scale samples were obtained from a sub-sampled portion of the smolt catch (Table 1).

Recently, co-managers have increased smolt production monitoring efforts for Steelhead in the Skagit River basin. In 2012, the WDFW installed and operated three additional Steelhead smolt traps in upstream tributaries to the Skagit River, including Bacon (site 31), Illabot (site 26), and Finney (site 32) creeks (Figure 1). These traps were installed to specifically target wild Steelhead smolts in an attempt to enable estimates of production of wild Skagit River Steelhead smolts using mark-recapture methodology. At each trap site, a subset of captured smolts was measured for lengths, and scales were removed from the area above the lateral line between the dorsal and adipose fins (Table 1). A passive integrated transponder (PIT) tag was inserted into the body cavity, and PIT tag mark-recapture data provided preliminary information on smolt trap efficiencies among tributary trap sites. Trap efficiencies during 2012 were estimated at 0.02% for the Skagit River mainstem traps, 2% - 4% at Bacon Creek, 3% - 5% at Finney Creek, and 30% at Illabot Creek. Trapping efficiency tests from mark-recapture data indicated that upstream traps were not significantly size-selective against larger smolt; however, more rigorous studies of size-selectivity at each trap are needed to provide more conclusive results. The increased potential for size-selective capture inefficiencies at the Skagit River mainstem trap precluded estimates of growth and survival between upstream (tributary) and downstream (mainstem Skagit River) smolt traps (C. Kinsel, Washington Department of Fish and Wildlife, personal communication).

Adult Sampling

Adult Steelhead were sampled in freshwater as they returned from saltwater to spawn. Between 2008 and 2012, adult Steelhead migrating to spawning grounds were caught at various locations within precipitation zones in the Skagit River basin. Samples were collected for targeted genetic and age structure sampling as opposed to recreational creel samples (Pflug et al. 2013). Non-lethal catch-and-release angling was conducted between January and August using a variety of angling gear. Care was taken to handle fish as quickly and gently as possible to reduce the amount of stress. All fish were measured (FL), sexed (if possible), and scales were removed. Fish were released when able to safely swim away. Adult Steelhead were also incidentally caught by the Upper Skagit Indian Tribe during the Skagit River Sockeye fishery in 2012.

Scale Analysis

Because this study focused on the influence of early growth on survival, only the freshwater portion of adult scales was measured and used for comparisons with measurements from scales of fish sampled as juveniles and as smolts. Each scale sample was mounted on a gummed card, pressed into a heated acetate tile, and observed under a microscope-mounted digital video camera using image processing software (Image Pro Plus version 4.5.1 Media Cybernetics, Inc., Silver Spring, MD). Further evaluation of each scale image was contingent on whether it met required criteria for sample and image quality. First, each scale sample was assessed for the presence of a clearly defined focus on a non-regenerated scale. Unusually oblong or non-uniform shaped scales can appear as outliers in the FL-SR regression, so these were removed from further processing. Only higher quality acetate impressions, and therefore finer resolution scale images, were used for analysis of early growth.

Scale impressions that met the criteria were photographed using a 1.0x objective in ImageProPlus® digital microscopic photography software (version 4.5.1 Media Cybernetics, Inc., Silver Spring, MD) (Figure 2). Juvenile scale images were taken at 4.0x magnification, whereas scales from smolts and the freshwater regions on adult scales were taken between 0.8x and 3.2x magnification depending on the freshwater radius. All images were calibrated prior to taking measurements in ImageProPlus® using a 3,1 mm Carl Zeiss Jena® Objectmikrometer.

Scale radii (SR) of juveniles and smolts were measured (mm) in Image Pro Plus®, and linear regression analysis with FL was used to determine if SR could be used to predict FL with reasonable accuracy. The resulting relationship between SR and FL was adjusted using a biological intercept of 32 mm FL, assuming that this was the size of first scale formation (L. Campbell, Washington Department of Fish and Wildlife, personal communication; Figure 3; Range: 45 mm – 260 mm FL; $n = 872$; $r^2 = 0.89$; $P < 0.001$).

$$FL \text{ (mm)} = 144.8 * SR \text{ (mm)} + 32.0$$

Fish scales and lengths generally grow in relative proportion to one another. However, due to allometric differences between SR and FL during some periods, the slope of the linear SR-to-FL relationship is not consistent across all fish sizes, and this can often cause the regression to substantially over- or underestimate the size at which the fish form their first scale (Fisher and Pearcy 2005). Therefore, an adjusted biological intercept can be used to represent a more probable size at which recently emerged juveniles first form scales, and a more biologically representative slope and vertical axis intercept. The SR-FL regression can be used in conjunction with a proportional SR-FL ratio estimator to explicitly estimate FL-at-SR (Ward et al. 1989, Bond et al. 2008). However, because the objectives of this study were to evaluate

whether SSM was occurring and if it differed among habitats, size-at-age results were not converted to FL, but instead were reported in terms of SR-at-annuli.

To measure specific benchmarks on the freshwater-growth region of each scale, an automated caliper tool was used to locate circuli (peaks in the image). However, the ability of the caliper tool to identify peaks was highly dependent on image quality, so some circuli on lesser quality images had to be added or subtracted manually from the transect. For each sample, the number of circuli were counted, and the distance between each circulus, between the focus and margin of each annular check, between the focus and the saltwater entry check, between each annulus, and between the last freshwater annulus and size-at-saltwater entry were measured. To verify scale morphology interpretations, scale selection and identification of circuli, annuli, and scale margins were discussed among three trained scale readers. Ages of smolts and adults were previously determined by WDFW otolith laboratory staff and were independently re-evaluated during this study. Age determination methodology was similar to that used in WDFW protocol and was discussed with the lead biologist at the WDFW aging lab (L. Campbell, Washington Department of Fish and Wildlife, personal communication). However, because only freshwater growth was assessed during this study, scales were aged based on full completion of freshwater annuli, whereas most fishery managers use January 1 of each year as a freshwater annulus regardless of completion of a true freshwater annulus (Devries and Frie 1996).

Statistical Analyses

Normality tests (Kolomogorov-Smirnov) were conducted on SR-at-annuli data for the juvenile-, smolt-, and adult-sample groups (hereafter referred to as life stage sample groups). Frequency distributions were normal for SR-at-annuli 1 and 2, but not for annuli 3. Two-way

ANOVA tests were conducted on SR-at-annuli among life stage sample groups and precipitation zones. Tukey HSD tests were conducted where significant differences in SR-at-annuli existed to identify where differences in size-at-age occurred among life stage groups, precipitation zones, or from interactions between the two factors (Zar 1999). Statistical significance α was set at 0.050.

Results

In general, size-selective mortality was measurable between each life stage, and size disparities increased between prior and subsequent life stages at annuli 2 and 3. Within life stage samples, SR-at-annulus 1 was larger in the snow zone than the mixed precipitation or rain zones, but differences were not evident for annuli 2 or 3 (Table 2).

Comparisons of SR-at-annuli among life stage sample groups indicated that, in general, only the faster-growing portion of juvenile and smolt populations in the Skagit River basin survive to adulthood. Significant SSM was evident for Steelhead sampled as juveniles at each annulus, and for fish sampled as smolts at annuli 2 and 3 when compared to fish sampled as adults (Figure 4). At annulus 1, fish sampled as juveniles were significantly smaller than fish sampled as smolts ($P = 0.003$) and as adults ($P < 0.001$), but SR-at-annulus 1 was similar between fish sampled as smolts and adults ($P = 0.123$). At annulus 2, fish sampled as adults were larger than those sampled as smolts ($P < 0.001$), and as juveniles ($P < 0.001$), and fish sampled as smolts were larger than those sampled as juveniles ($P < 0.001$). At annulus 3, fish sampled as juveniles were smaller than those sampled as smolts ($P = 0.026$) and adults ($P < 0.001$), and fish sampled as adults were larger than those sampled as smolts ($P < 0.001$).

Overall, precipitation zone had little or no effect on SR-at-annulus when compared by each life stage sample group (Figure 5). Thus, growth to each annulus was the same among precipitation zones for fish sampled as juveniles, a majority of smolts, and all adults. However, fish sampled as smolts in the snow zone were significantly larger at age 1 than those sampled as smolts in the rain zone ($P = 0.013$).

Life stage sample group explained differences in SR-at-annulus 1 within each precipitation zone ($P = 0.038$; Figure 5). In the snow zone, fish sampled as juveniles were significantly smaller at annulus 1 than those sampled as smolts ($P = 0.022$) and adults ($P = 0.003$). In the mixed rain-snow zone, fish sampled as juveniles were smaller at annulus 1 than those sampled as smolts ($P = 0.017$) and adults ($P = 0.012$). In the rain zone, fish sampled as adults were larger at annulus 1 than those sampled as smolts ($P = 0.001$) and as juveniles ($P < 0.001$).

Life stage sample group also explained differences in SR-at-annulus 2 within each precipitation zone ($P = 0.047$; Figure 5). In the snow zone, fish sampled as adults were larger than those sampled as smolts ($P = 0.003$) and as juveniles ($P < 0.001$). In the mixed rain-snow zone, fish sampled as juveniles were smaller at annulus 2 than those sampled as smolts ($P < 0.001$) and adults ($P < 0.001$), and fish sampled as adults were larger than those sampled as smolts ($P = 0.017$). In the rain zone, fish sampled as juveniles were smaller at annulus 2 than those sampled as smolts ($P = 0.002$) and adults ($P < 0.001$), and fish sampled as adults were larger than those sampled as smolts ($P < 0.001$).

Discussion

This study revealed that significant size-selective mortality operates during both freshwater and marine phases of life for wild Steelhead from the Skagit River Basin. Significant SSM was measurable in terms of the size-at-annulus achieved between each life stage for fish sampled as juveniles, smolts and returning adults. In general, significant size disparities were evident between prior and subsequent life stages at annuli 1, 2, and 3 within each precipitation zone. However, growth and size-at-age differences were less pronounced among precipitation zones than among life stage samples. Survival to adulthood appears to depend on size established during early life stages in freshwater environments, and the combination of stage-specific growth and size-selective mortality could be a primary filtering mechanism for survival to later stages.

A number of studies on wild Steelhead have identified the need to evaluate the influence of growth during early life on survival to later stages (e.g., Ward 2000); however, few studies have directly evaluated the effects of juvenile growth on survival to subsequent stages. Regional studies of wild Steelhead production investigated the role of smolt size on smolt-to-adult return rates with mixed results among decades (Ward and Slaney 1988, Ward et al. 1989, Ward 2000, Welch et al. 2000). Ward (2000) found that smolt size was strongly correlated with survival to adulthood between years 1976 and 1990; however, the smolt size-marine survival relationship disappeared during 1991-1996, and the ensuing chronically low adult returns were not sufficient to sustain replacement. More recently, Bond et al. (2008) provided compelling evidence that faster juvenile growth in coastal lagoons enhanced survival to adulthood in a Steelhead population near the southern extent of the species' range. The findings presented here provide further evidence that survival among life stages is an important dynamic in wild Steelhead, and

can be attributed, in part, to size attained during early life. These results are important because they suggest that a freshwater, habitat-specific growth-effect parameter, in addition to smolt size, might improve accuracy in production estimators for wild Puget Sound Steelhead.

Differences in size-at-age among life stage sample groups reflect differences in growth rates, but differences in size-at-age 1 among sample groups might also result from differential spawning and emergence timing. While most basins in the Puget Sound exhibit relatively cool water temperature regimes (Busby et al. 1996), there is considerable variation in water temperature and streamflow regimes within and among precipitation zones (Beechie et al. 2006), and differences in Steelhead spawning and emergence timing probably correspond with those physical factors (Washington Department of Fish and Wildlife, unpublished data). Therefore, larger size-at-age 1 in fish sampled as adults may indicate selection for faster growth rates (e.g., Kirkpatrick et al. 1990), and metabolism (Millidine et al. 2009), but could also indicate selection for earlier emergence (Einum and Fleming 2000). However, to draw such conclusions, sub-basin-specific data on temporally-explicit growth rates (e.g., otolith microstructure analysis), spawn timing, water temperature, and streamflow data would need to be synthesized to determine the relative importance of each factor on growth and survival.

Differences in growth might also be indicative of different life history strategies. Evidence from this study suggests that survival to adulthood, and possibly life history expression of *O. mykiss*, could be reliant on growth rates established early on in freshwater environments. Ancillary analyses from this study suggested that slower growing juveniles (or later emerging ones) that survive to the age 3 annulus may be prone to lower overall growth throughout life (i.e., do not utilize marine environments for increased growth). Adoption of a resident life history by an iteroparous salmonid at any age does not prohibit adoption of an anadromous life history at a

later age (e.g., Quinn and Myers 2004). The tendency for freshwater residency in salmonids in the anadromous zone depends on a diversity of factors that relate to site fidelity, including food quantity and quality (e.g., Meka et al. 2003, Ridgway 2008), and availability of foraging habitat that provides refuge from predators (e.g., Boss and Richardson 2002).

Regardless of alternative life histories, survival to adulthood by juvenile Steelhead appears to be, in part, a direct result of fast growth during the earlier stages of life. This finding demonstrates the need for representative measurements of growth among life stages of Steelhead, among different life history forms of *O. mykiss*, and corresponding measurements of factors that affect growth and life history in specific habitat types. Identification of freshwater growth and corresponding mechanisms that limit growth in these habitats, for example, water temperature, stream flow regime, feeding rate, prey quality and quantity, habitat condition, and salmonid density, will be required to determine in which habitats juvenile growth might need to be increased to improve survival to adulthood in Steelhead. Growth conditions can be compared to production rate estimates obtained from smolt trapping to determine whether juvenile growth or smolt abundance, or interactions between these two factors, limit the production of adult Steelhead in specific sub-basins.

Size-selective mortality was detected in all age groups, but low sample sizes among precipitation zones reduced the power of statistical tests and precluded a more in-depth analysis of precipitation zone effects. For example, most adult samples were collected in rain and mixed rain-snow precipitation zones in the lower Skagit River, whereas most juvenile samples were collected from sites in the mixed rain-snow precipitation zone in the Sauk/Suiattle rivers.

Furthermore, fish were sampled as smolts from only two sites in the mixed rain-snow zone, and

only one in the snow zone. Thus, size-biased and unbalanced sample sizes, and spatially unbalanced samples may have influenced estimates of precipitation zone-specific SSM.

The adult samples for this study came from different brood years than did those sampled as juveniles and smolts, and thus do not represent a direct comparison of juvenile growth patterns to adult returns for the same cohort of Steelhead. Nonetheless, the adult samples were drawn from multiple brood years and thus represented a generalized pattern of growth associated with successful marine survival compared to the freshwater size distributions and growth patterns measured for juvenile and smolt samples. A useful comparison will be forthcoming when adults from the same broods as those sampled as juveniles and smolts in this study return to spawn, which would be in 2014 for an age 2 smolt. Still, size-selectivity in capture methods should be continuously re-evaluated among different streamflow scenarios for Steelhead smolts at each smolt trap, and due to river channel-trap size discrepancy, continued effort and ingenuity should be applied to smolt production estimates at the lower Skagit River mainstem traps.

Conclusions

Recent findings suggest that environmental conditions in both the nearshore marine (Moore et al. 2010) and the high seas of the Pacific Ocean influence marine survival and production of many anadromous Salmonid stocks in the region (Welch et al. 2000, Welch et al. 2004, Atcheson et al. 2012, Welch et al. 2011). Yet, effective recovery of wild Puget Sound Steelhead will require a quantified understanding of the interactions between physical and biological factors in both marine and freshwater environments. Freshwater growth in Steelhead is important because Puget Sound Steelhead smolts do not appear to spend time foraging and growing in estuarine or brackish water environments. The increasing disparity in size-at-annuli

between fish sampled as juveniles, smolts, and adults at later freshwater ages (annuli 2 and 3) suggests that fast growth during the ages at which Steelhead smoltify (between ages 1 and 2, and 2 and 3) is vitally important to survival to adulthood. This study provides evidence that Puget Sound Steelhead smolt survival in the marine environment is at least partly dependent on growth attained during each stage of development in freshwater.

Increased smolt trapping efforts and evaluation of growth at critical life stages should enable more integrated estimates of wild Steelhead smolt production. Combined with trap-based production estimates, size and age analysis of concurrent juvenile, smolt, and adult samples will provide further insights into the relative influence of juvenile growth rate on the numerical production of adult Steelhead. Sub-basin-specific measurements of probable growth limiting factors will inform recovery efforts because this study implies early growth is an important factor influencing the production of wild Puget Sound Steelhead.

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Chapter 2 Figures And Tables

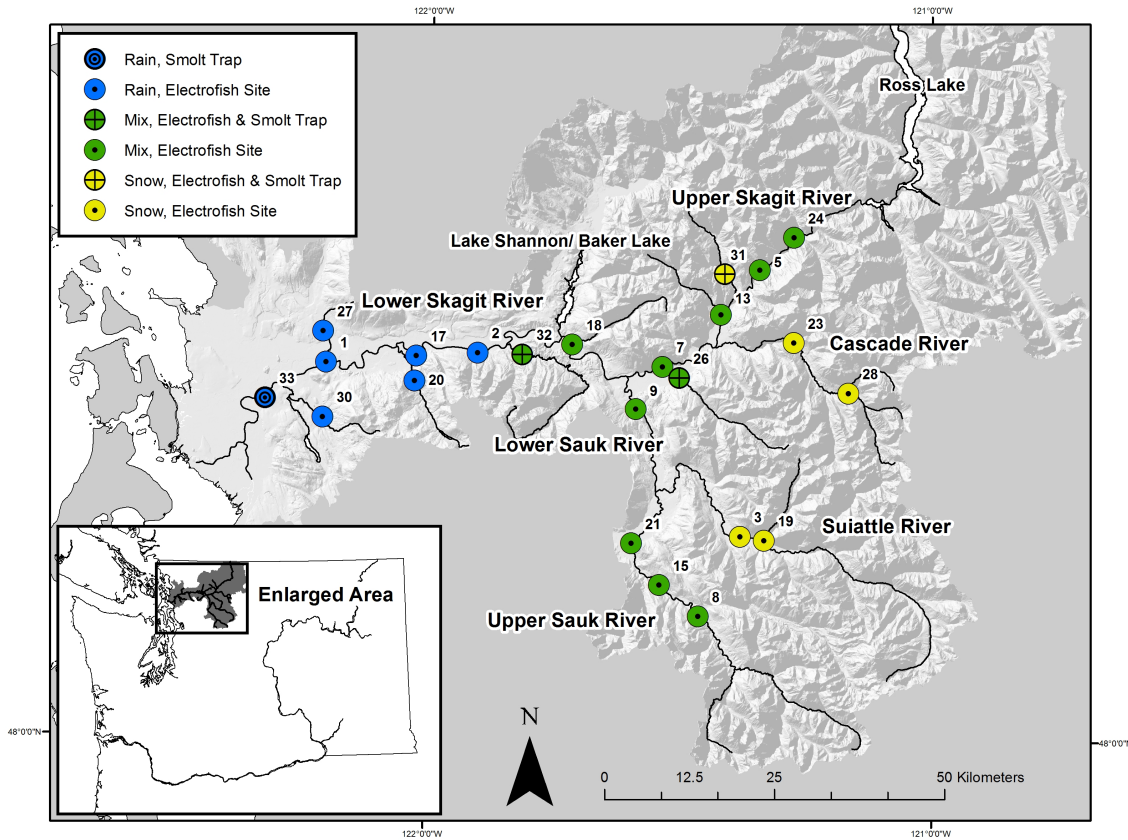


Figure 1. Skagit River basin study area showing electrofishing and smolt trapping sample sites. Sites are color-coded to indicate precipitation zone (rain, mix [mixed rain-snow], and snow), and major basins are delineated in large font captions. Sub-basins are listed for each numbered site in Table 2.

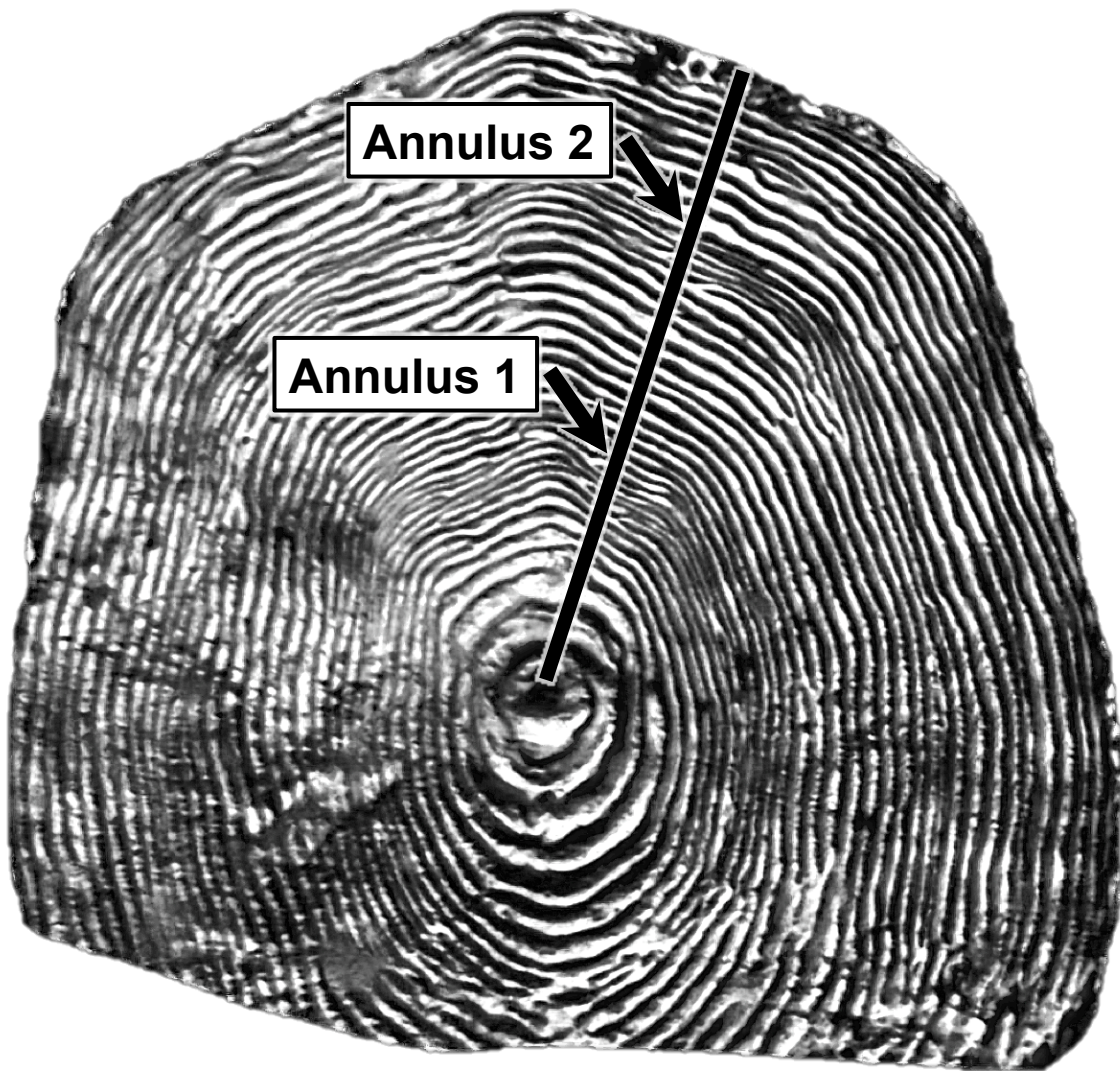


Figure 2. Sample image of annuli measurements on scales from Steelhead sampled as juveniles, smolts, and adults in the Skagit River basin. Each circulus and annulus was demarked using a transect (20° off-axis) caliper tool that automatically detected circuli margins. The transect origin at the center of the scale indicates the focus region, and annuli represented areas where slow growth transitioned to fast growth based on spacing between, and crossing over of circuli.

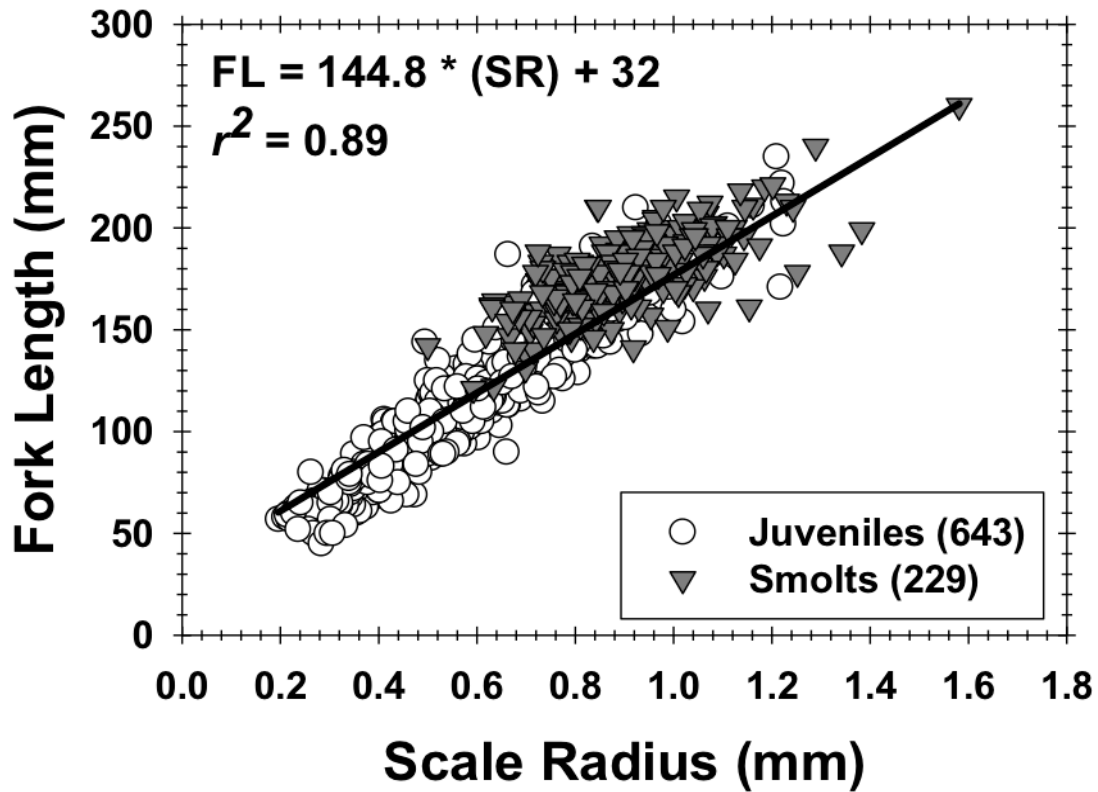


Figure 3. Linear FL and SR relationship established from scales and lengths of Steelhead sampled as juveniles and smolts in the Skagit River basin between 2008 and 2012. The vertical intercept of the regression was adjusted to represent the FL and SR at which the first scale was formed (32 mm FL).

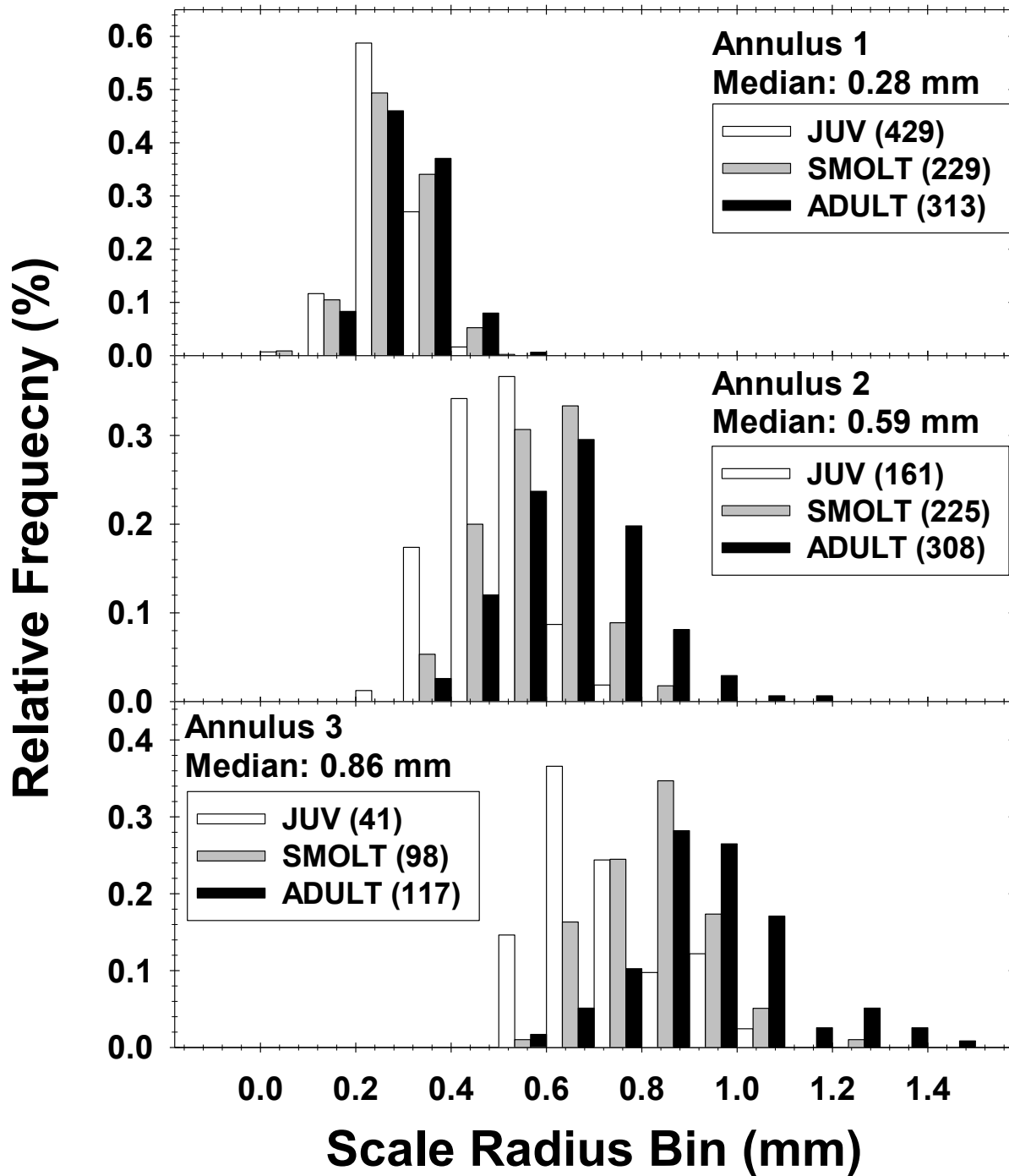


Figure 4. Scale radius frequency distributions at annuli 1 (top), 2 (middle), and 3 (bottom) for fish sampled as juveniles, smolts, and adults in the Skagit River basin. Pooled sample group median scale radius values and sample sizes for each life stage sample group-annulus combination (numbers in legend) are provided for each annulus.

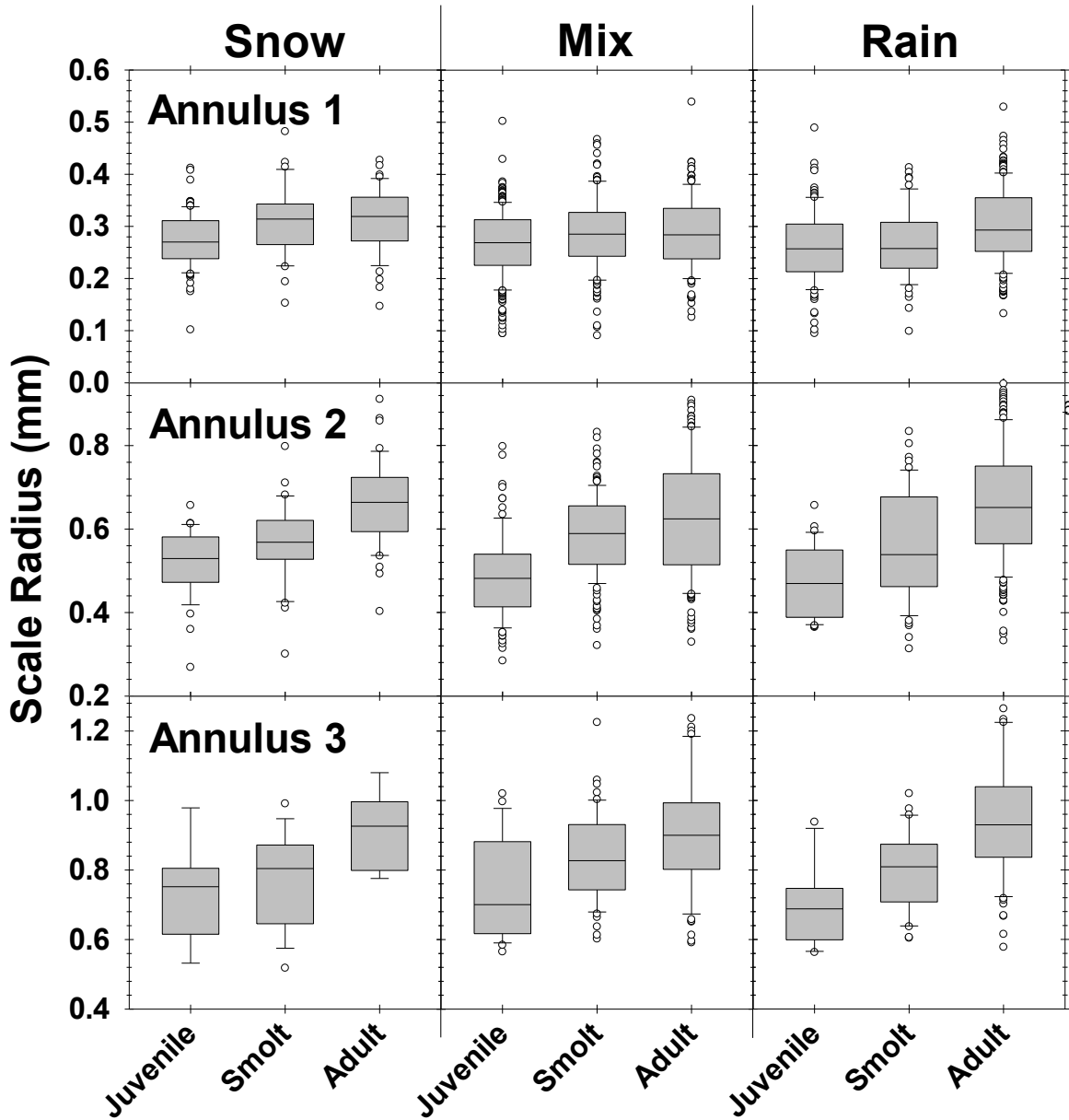


Figure 5. Box plots of scale radius-at-annuli 1, 2, and 3 for life stage sample groups sampled among precipitation zones. Plots indicate median scale radius values (horizontal bar inside box), 25th and 75th percentiles (range of bars), 10th and 90th percentiles (error bars), and outliers (hollow circles).

Table 1. Age-at-capture, sample size, and FL (mean \pm SE) of fish sampled as juveniles and smolts among different precipitation zones in the Skagit River basin. Juveniles were captured during summer and fall of 2011 and winter of 2012, and smolts were captured between January and June of 2012.

| Precipitation Zone | Freshwater Age | Juveniles | | Smolts | |
|--------------------|----------------|-----------|-------------|----------|--------------|
| | | <i>n</i> | FL (mm) | <i>n</i> | FL (mm) |
| Snow | 1 | 65 | 111 \pm 3 | 1 | 131 |
| | 2 | 29 | 155 \pm 3 | 16 | 161 \pm 3 |
| | 3 | 9 | 192 \pm 9 | 11 | 187 \pm 3 |
| | 4 | | | 3 | 207 \pm 5 |
| Mix | 1 | 137 | 105 \pm 2 | 3 | 139 \pm 10 |
| | 2 | 66 | 136 \pm 3 | 84 | 172 \pm 2 |
| | 3 | 22 | 174 \pm 5 | 50 | 191 \pm 2 |
| | 4 | | | 3 | 201 \pm 15 |
| Rain | 1 | 66 | 93 \pm 2 | | |
| | 2 | 25 | 135 \pm 3 | 27 | 166 \pm 2 |
| | 3 | 10 | 154 \pm 4 | 26 | 180 \pm 2 |
| | 4 | | | 4 | 216 \pm 9 |
| | 5 | | | 1 | 260 |

Table 2. Sample sizes and mean SR (\pm SE) at annuli 1, 2, and 3 for wild Steelhead sampled as juveniles, smolts, and adults by precipitation zone, sub-basin, and site in the Skagit River basin.

| Precipitation Zone | Sub-basin | Site Number | Juveniles | | | | | | Smolts | | | | | | Adult Steelhead | | | | | |
|--------------------|----------------------|-------------|-----------|-----------------|-----------|-----------------|-----------|-----------------|-----------|-----------------|-----------|-----------------|-----------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| | | | Annulus 1 | | Annulus 2 | | Annulus 3 | | Annulus 1 | | Annulus 2 | | Annulus 3 | | Annulus 1 | | Annulus 2 | | Annulus 3 | |
| | | | <i>n</i> | SR (mm) | <i>n</i> | SR (mm) | <i>n</i> | SR (mm) | <i>n</i> | SR (mm) | <i>n</i> | SR (mm) | <i>n</i> | SR (mm) | <i>n</i> | SR (mm) | <i>n</i> | SR (mm) | <i>n</i> | SR (mm) |
| Snow | Upper Cascade River | 28 | 14 | 0.25 \pm 0.03 | 3 | 0.47 \pm 0.10 | 2 | 0.62 \pm 0.03 | | | | | | | | | | | | |
| | Buck Creek | 19 | 47 | 0.25 \pm 0.04 | 23 | 0.51 \pm 0.08 | 7 | 0.76 \pm 0.14 | | | | | | | | | | | | |
| | Cascade River | 23 | 17 | 0.29 \pm 0.04 | 4 | 0.54 \pm 0.06 | | | | | | | 9 | 0.29 \pm 0.07 | 9 | 0.65 \pm 0.14 | 2 | 0.80 \pm 0.00 | | |
| | Suiattle River | 3 | 17 | 0.30 \pm 0.07 | 4 | 0.59 \pm 0.01 | | | | | | | 30 | 0.31 \pm 0.06 | 30 | 0.67 \pm 0.09 | 4 | 0.96 \pm 0.14 | | |
| | Bacon Creek | 31 | 8 | 0.30 \pm 0.03 | 4 | 0.53 \pm 0.06 | | | 28 | 0.32 \pm 0.06 | 27 | 0.59 \pm 0.08 | 11 | 0.82 \pm 0.10 | | | | | | |
| Mix | Upper Sauk River | 8, 15, 21 | 107 | 0.28 \pm 0.06 | 34 | 0.51 \pm 0.11 | 7 | 0.76 \pm 0.15 | | | | | | | | | | | | |
| | Diobsud Creek | 13 | 11 | 0.26 \pm 0.04 | 7 | 0.45 \pm 0.04 | 1 | 0.61 | | | | | | | | | | | | |
| | Illabot Creek | 26 | 26 | 0.27 \pm 0.06 | 8 | 0.51 \pm 0.10 | 3 | 0.82 \pm 0.12 | 110 | 0.28 \pm 0.06 | 110 | 0.58 \pm 0.09 | 41 | 0.84 \pm 0.12 | | | | | | |
| | Upper Skagit River | 5, 7, 24 | 7 | 0.25 \pm 0.05 | 1 | 0.57 | – | | | | | | | 29 | 0.29 \pm 0.06 | 29 | 0.61 \pm 0.11 | 17 | 0.90 \pm 0.16 | |
| | Lower Sauk River | 9 | 18 | 0.29 \pm 0.06 | 3 | 0.47 \pm 0.08 | | | | | | | | 42 | 0.29 \pm 0.06 | 42 | 0.64 \pm 0.12 | 17 | 0.90 \pm 0.11 | |
| | Jackman Creek | 18 | 16 | 0.23 \pm 0.07 | 9 | 0.45 \pm 0.14 | 1 | 0.61 | | | | | | | | | | | | |
| | Finney Creek | 32 | 40 | 0.24 \pm 0.07 | 26 | 0.48 \pm 0.10 | 10 | 0.73 \pm 0.15 | 27 | 0.34 \pm 0.07 | 24 | 0.62 \pm 0.10 | 9 | 0.88 \pm 0.15 | 27 | 0.30 \pm 0.07 | 26 | 0.71 \pm 0.17 | 8 | 1.09 \pm 0.22 |
| Lower Skagit River | N/A | | | | | | | | | | | | 34 | 0.28 \pm 0.09 | 33 | 0.60 \pm 0.15 | 13 | 0.87 \pm 0.17 | | |
| Rain | Day Creek | 20 | 11 | 0.27 \pm 0.04 | 1 | 0.45 | – | 1 | 0.75 | | | | | | | | | | | |
| | Upper Hansen Creek | 27 | 29 | 0.27 \pm 0.06 | 8 | 0.44 \pm 0.07 | 1 | 0.59 | | | | | | | | | | | | |
| | Lower Skagit River | 2, 17, 33 | 14 | 0.25 \pm 0.08 | 7 | 0.53 \pm 0.08 | | | 53 | 0.27 \pm 0.07 | 53 | 0.57 \pm 0.13 | 26 | 0.80 \pm 0.11 | 173 | 0.30 \pm 0.07 | 170 | 0.67 \pm 0.14 | 62 | 0.95 \pm 0.17 |
| | Lower Hansen Creek | 1 | 13 | 0.23 \pm 0.05 | 6 | 0.44 \pm 0.09 | 4 | 0.75 \pm 0.14 | | | | | | | | | | | | |
| | EF Nookachamps Creek | 30 | 34 | 0.27 \pm 0.09 | 13 | 0.48 \pm 0.09 | 4 | 0.64 \pm 0.06 | | | | | | 2 | 0.31 \pm 0.03 | 2 | 0.60 \pm 0.02 | | | |

Chapter 3: Size-selective mortality and the relative roles of water temperature, feeding rate, and prey quality on early life growth in wild Steelhead Trout among three tributaries representative of different precipitation zones in the Skagit River, WA

Abstract

Early growth in anadromous salmonids influences survival to adulthood, and varies with thermal experience, feeding rate, and prey quality. I used a bioenergetics modeling framework to investigate how these factors affected growth in juvenile wild Steelhead Trout, *Oncorhynchus mykiss*, among tributary habitats representative of different precipitation zones in the Skagit River basin. I expected that growth at early life stages would be influenced by water temperature, feeding rate, and seasonal prey energy budgets associated with each tributary environment. Bioenergetics model simulations were run for age 1–2 and 2–3 wild Steelhead sampled at three life stages, as juveniles, smolts, and adults. Model simulations indicated that relatively small differences in mean annual feeding rate translated into significant differences in annual growth between life stage. In Bacon Creek, a snow zone tributary, low mean annual prey energy densities inhibited annual growth. In Illabot Creek, a mixed rain-snow tributary with cool water temperatures, low winter water temperatures and prey energy density caused weight loss during winter. In Finney Creek, a mixed rain-snow tributary with warm water temperatures, high composite summertime prey energy density enabled positive growth through the thermally stressful period of summer. Based on substantial disparities in annual growth trajectories among life stage sample groups in Finney Creek, it appears that high energy diets are available only to a small fraction of the population, but those with access have increased growth and probability of survival to adulthood. Tributaries in different precipitation zones contain differing seasonal

composite prey energy densities and water temperature regimes, and these factors interact to affect growth differently among early life stages of Steelhead. Early growth of Steelhead in the Skagit River influences survival to adulthood, and recovery of this threatened species could be enhanced by gaining a more widespread understanding of what limits growth in riverine habitats.

Introduction

In recent decades, wild Steelhead *Oncorhynchus mykiss* in the Puget Sound have declined, and were listed in 2007 as threatened under the U.S. Endangered Species Act (Rausch 2007). Unfortunately, a scarcity of empirical information on Puget Sound Steelhead currently limits our understanding of the mechanistic factors that influence their continued decline. Survival in many fish species is partially dependent on growth rate during early life to minimize the magnitude of size-selective mortality (Sogard 1997). Juvenile growth rate and smolt size vary among species of anadromous salmonids, but also among life history types within a species. Steelhead typically spend 2-3 years rearing in freshwater habitats and achieve larger size than smolts of most other anadromous salmonids (Busby 1996). Therefore, riverine environments have a potentially greater influence on early growth and survival of Steelhead than in most other anadromous salmonids that migrate to saltwater as subyearlings or yearlings. After marine entry in Puget Sound, Steelhead smolts move rapidly out of local marine waters into the open ocean (Miller et al. 1983, Hartt and Dell 1986, Moore et al. 2010). Marine mortality is often high for anadromous salmonids (Ricker 1976, Melnychuck et al. 2007), and may be related to size thresholds during critical early growth periods, (e.g., Beamish and Mahnken 2001, Beamish et al. 2004, Cross et al. 2008, Duffy and Beauchamp 2011, Miller et al. 2011, Tomaro et al. 2012). Therefore, the size achieved in freshwater before the smolt stage might play an integral role in survival to adulthood by wild Puget Sound Steelhead.

Early life growth in anadromous salmonids is an important factor influencing survival to later life stages (Ward et al. 1989, Bond et al. 2008). Water temperatures (McCullough et al. 2009; Mantua et al. 2010; Wenger et al. 2011), food quality and quantity (Wipfli and Baxter 2010), and feeding (Bradford and Higgins 2001) directly affect metabolism, growth, and survival

(Beauchamp 2009). In riverine environments, water temperature and prey sources fluctuate seasonally across the landscape (Wipfli and Baxter 2010), having spatially variable effects on growth performance and subsequent survival. Heterogeneity in freshwater feeding and growth among habitats within a watershed (e.g. McCarthy et al. 2009), combined with the potential influence of early life growth on survival to adulthood (Ward et al. 1989, Bond et al. 2008, Chapter 2), suggest that riverine habitats could play an important role in viability of anadromous salmonid populations. Understanding how environmental factors affect early growth over broad spatial scales is important in large watersheds because growth, and thus survival to later life stages, varies with the river landscape (Schlosser 1991).

Environmental factors associated with different habitats, such as water temperature and prey source, can have a direct influence on early life growth in Steelhead. For example, McCarthy et al. (2009) used bioenergetics modeling to show that feeding rate and growth of juvenile Steelhead varied among different forest cover types associated with differing water temperature regimes and prey sources (aquatic vs. terrestrial invertebrates). Bioenergetics modeling uses energy balance in an average individual to estimate feeding rate based on observed growth, thermal experience, and prey quantity and quality. A bioenergetics modeling framework provides an evaluation of how much energy must be consumed to support growth after satisfying metabolic costs and waste losses. When costs of metabolism and waste are more than the energy acquired through feeding, energy is at a deficit and weight is lost from the fish. Environmental conditions vary over space and time, influencing water temperatures (metabolism) and prey sources (energy inputs) that control feeding and growth. Different combinations of thermal and prey source factors interact to affect growth uniquely in each different habitat. For example, Beauchamp (2009) showed how increasing the composite prey

energy density in the diet can vastly improve growth performance, broaden the temperatures at which maximum growth is experienced, and reduce the chance of thermally induced weight loss. This sensitivity analysis highlighted the need to increase our understanding of how water temperature and prey sources interact to affect growth across the mosaic of habitats that support anadromous salmonids.

Puget Sound Steelhead fishery monitoring and management programs have focused mainly on estimating adult run sizes. In selected basins, yearly counts of Steelhead redds and recently improved smolt trapping efforts have enabled smolt production estimates, but will not necessarily improve understanding of the underlying mechanisms influencing survival to adulthood, and therefore production of adult Steelhead (Zabel and Achord 2004). In the absence of empirical biological information from multiple life stages, efforts to maintain or recover wild Puget Sound Steelhead may be hampered by ineffectiveness in identifying factors that control freshwater and marine survival and productivity (e.g., Ward 2000).

Information is limited regarding how different habitats contribute to increased or decreased growth and survival among life stages. However, a recently completed companion study in the Skagit River basin indicated that the seasonal importance of rearing habitats for juvenile salmonids differed among three precipitation zones (Lowery et al. 2013). These results have implications for how growth of juvenile Steelhead could be affected by differential habitat availability and use in the Skagit River and other basins in the Puget Sound region.

Significant size-selective mortality was observed among juvenile, smolt and adult life stages of wild Steelhead in the Skagit River, and was particularly apparent during annual growth increments between annulus 1 and 2 and between annulus 2 and 3 (Chapter 2). Therefore, the objectives of this study were to evaluate how prey resources and water temperature influenced

growth of wild Steelhead between ages 1 and 2, and ages 2 and 3, and to determine whether environmental and growth patterns varied among tributaries that represented different precipitation zones in the Skagit River basin. Based on back-calculated growth trajectories for different ages of stream-rearing juveniles and smolts from each tributary, bioenergetics simulations were conducted to estimate feeding rate and total annual consumption required to meet the back-calculated annual growth rates of freshwater age 1-2 and 2-3 Steelhead sampled as juveniles, compared to those that survived to the smolt and adult stages. I expected that thermal experience, prey sources, and feeding rate would affect annual growth differentially among age groups of fish sampled at different stages of life in each tributary. Given the prey resources and thermal regime of the tributaries examined, I estimated how much additional energy would be required by the average juvenile Steelhead to achieve the growth and size exhibited by those that survived to the smolt and adult stages. Finally, I expected to find that growth potential would be higher in tributaries representing precipitation zones with moderate thermal regimes and higher composite prey energy densities, and lower in tributaries representing precipitation zones with higher or more variable water temperatures and lower composite prey energy densities.

Study Area

The Skagit River basin, which includes the mainstem Skagit and Sauk rivers and numerous tributaries, is the largest drainage in the Puget Sound region and the second largest in the Salish Sea. The basin drains approximately 8,544 km² from the west side of the North Cascades of Washington State and the Canadian province of British Columbia. Annual precipitation in the basin ranges from 90 cm/year at sea level to 460 cm/year at 3,275 m on Glacier Peak (Beechie et al. 2005). The Skagit River drainage supports the largest populations

of anadromous salmonids in the Puget Sound, including Chinook *Oncorhynchus tshawytscha*, Coho *O. kisutch*, Chum *O. keta*, and Pink Salmon *O. gorbuscha*, and Steelhead. Other Salmonid species in the study area include resident Rainbow Trout (*O. mykiss*), sea-run and resident Coastal Cutthroat Trout *O. clarkii clarkii*, sea-run and resident Bull Trout *Salvelinus confluentus*, and Mountain Whitefish *Prosopium williamsoni*.

Elevation and precipitation zone influence hydrologic and water temperature regimes in different tributaries of the drainage, and could influence the seasonal importance of rearing habitats for juvenile salmonids (Lowery et al. 2013). Peak annual stream discharge in the snow precipitation zone is influenced by snowmelt, and in the rain precipitation zone by rainstorms. A majority of the Skagit River basin, however, is located in the transitional precipitation zone (mixed rain-snow), where peak annual discharge can be influenced by a mixture of both rain and snow precipitation and water temperature regimes vary accordingly (Beechie 1992) (Figure 1). Two large hydroelectric projects block upstream fish passage in the Skagit River basin, including two dams in Puget Sound Energy's Baker River Project (above rkm 91), and three dams in Seattle City Light's Skagit River Project (above rkm 156). However, the Skagit River Project is located above natural barriers to migration that were considered the upstream limit of native anadromous salmonid distribution (Smith and Anderson 1921).

Methods

Annual bioenergetic model simulations were run for Skagit River basin Steelhead sampled at three different life stages, as juveniles, smolts, and adults, using annual back-calculated growth between ages 1 and 2 and ages 2 and 3 for each life stage sample group. Simulations estimated the feeding rate and total biomass of invertebrates required to achieve the

back-calculated annual growth increments of the average juvenile Steelhead compared to those that survived to the smolt or adult stages. Annual growth in weight was estimated by back-calculating length-at-annuli 1, 2, and 3, and then converting length to weight using regression analysis. Seasonal body condition of fish sampled as juveniles was estimated for each age group for comparisons with simulated annual growth trajectories. Model simulations were run for each life-stage sampling group in distinct tributary habitats, including a snow-dominated tributary (Bacon Creek), a cold mixed rain-snow-dominated tributary (Illabot Creek), and a warm mixed rain-snow-dominated tributary (Finney Creek). These three tributaries were selected for intensive evaluation of factors that limit growth because they contained annual growth data for each life stage sample group, and each site was representative of important habitats and environmental conditions used by rearing Steelhead in the Skagit River basin.

Juvenile Sampling

Juvenile Steelhead were sampled in Bacon, Illabot, and Finney creeks during summer and fall 2011, and winter 2012 for assessment of growth during the earliest stages of life (Figure 1). Juveniles (ages 1–3 years) were defined as immature anadromous or non-anadromous *O. mykiss* that were sampled while rearing in each of these tributary habitats.

Juveniles were captured from stream margin transects up to 400 m long in each tributary using single-pass upstream backpack electrofishing (Smith Root Model 12-B, 400-1000 v, standard pulse 80 Hz, 500 μ s) without block nets (Bateman et al. 2005). Electrofishing practices followed protocols prescribed by the Washington Department of Fish and Wildlife (WDFW) (Temple and Pearsons 2005), and all activities involving vertebrates conformed to the University of Washington Office of Animal Welfare IACUC protocol #3286-20. Captured salmonids were

anesthetized with buffered MS-222 and measured for fork length (FL to within 1 mm), and weight (to within 0.1 g), and scale samples were taken from the area above the lateral line between the dorsal and adipose fins (Devries and Frie 1996) of juvenile *O. mykiss* greater than 54 mm FL. Scale formation in Steelhead generally occurs after individuals reach a FL of 30 – 35 mm (Bond et al. 2008). Sample sizes for captured juvenile Steelhead at each site were allotted by functional size groups in an effort to retain ten individuals per size group per site, and to ensure proportional representation of fish size distributions in later analyses (FL: 56 – 65 mm, 66 – 111 mm, 112 – 169 mm, 170-209 mm, \geq 210 mm) (Table 1). Seven additional juveniles of 43 – 52 mm FL from a 2009 sample were used to quantify scale circuli on smaller fish as a reference. Processed fish were allowed to regain equilibrium in a recovery bath and released when able to safely swim away.

Coastal Cutthroat Trout and Steelhead are sympatric within portions of the study area and distinguishing between juveniles of the two species using morphological traits alone can be difficult (Campton and Utter 1985). However, morphological and genetic studies indicated that Steelhead, Coastal Cutthroat, and hybrids between these two species are reasonably well distinguished in the field (Baumsteiger et al. 2005, Kennedy et al. 2009). Juvenile Steelhead were differentiated from juvenile Coastal Cutthroat Trout using external characteristics that morphologically differentiate between pure forms (non-hybrids) of each species (e.g., presence of orange cutthroat “slashes” along the lower jaw, maxillary length, spotting intensity, body color, and body depth) (Behnke 1992, Williams et al. 2007, Kennedy et al. 2009). Negligible numbers of fish identified as Coastal Cutthroat Trout were captured in Finney Creek, and none were captured in Bacon and Illabot creeks.

Smolt Sampling

Steelhead smolts were sampled for assessment of growth during the intermediate stage of life. Recently, co-managers have increased smolt production monitoring efforts for Steelhead in the Skagit River basin. In 2012, the WDFW installed and operated three Steelhead smolt traps in upstream tributaries to the Skagit River, including Bacon, Illabot, and Finney creeks (Figure 1). These traps were installed to specifically target wild Steelhead smolts in an attempt to enable estimates of production of wild Skagit River Steelhead smolts using mark-recapture methodology. At each trap site, a subset of captured smolts was measured for lengths, and scales were removed from the area above the lateral line between the dorsal and adipose fins (Table 1). A passive integrated transponder (PIT) tag was inserted into the body cavity, and PIT tag mark-recapture data provided preliminary information on smolt trap efficiencies among tributary trap sites. Trap efficiencies during 2012 were estimated at 2% - 4% at Bacon Creek, 3% - 5% at Finney Creek, and 30% at Illabot Creek. Trapping efficiency tests from mark-recapture data indicated that upstream traps were not significantly size-selective against larger smolt; however, more rigorous studies of size-selectivity at each trap are needed to provide more conclusive results (C. Kinsel, Washington Department of Fish and Wildlife, personal communication).

During most years since 1990, the WDFW has sampled emigrating Steelhead smolts from the Skagit River mainstem in a side-by-side dual-trap system (one scoop and one screw trap) located at river kilometer (rkm) 24 in the Skagit River mainstem. These traps sample only a small fraction of the wetted width of the Skagit River mainstem, and were deployed to capture and facilitate production estimates for smaller anadromous smolts, such as Chinook and Coho Salmon. Based on size-selectivity of the traps at capturing Coho and Chinook Salmon, the mainstem traps probably only capture smaller Steelhead smolts (Kinsel et al. 2008). Due to the

increased potential for size-selective capture inefficiencies at the Skagit River mainstem trap, evaluation of growth was limited to the tributary smolt trap sites.

Adult Sampling

Adult Steelhead were sampled in freshwater as they returned from saltwater to spawn. Between 2008 and 2012, adult Steelhead migrating to spawning grounds were caught at various locations in the Skagit River basin, including in Finney Creek and in the upper Skagit River basin (Figure 1). No adults were sampled directly in Bacon and Illabot creeks; therefore, I used adult Steelhead captured in the upper Skagit River basin mainstem as adult representatives for these two creeks (Table 1). Samples were collected for targeted genetic and age structure sampling as opposed to recreational creel samples (Pflug et al. 2013). Non-lethal catch-and-release angling was conducted between January and August using a variety of angling gear. Care was taken to handle fish as quickly and gently as possible to reduce the amount of stress. All fish were measured (FL), sexed (if possible), and scales were removed. Fish were released when able to safely swim away.

Scale Analysis

Back-calculation of freshwater size-at-age was conducted on scale samples obtained from each life stage sample group to estimate length-at-age and convert estimated lengths to weights for use in bioenergetics model simulations. Each scale sample was mounted on a gummed card, pressed into a heated acetate tile, and observed under a microscope-mounted digital video camera using image processing software (Image Pro Plus version 4.5.1 Media Cybernetics, Inc., Silver Spring, MD). Further evaluation of each scale image was contingent on whether it met

required criteria for sample and image quality. First, each scale sample was assessed for the presence of a clearly defined focus on a non-regenerated scale. Unusually oblong or non-uniform shaped scales can appear as outliers in the FL-SR regression, so these were removed from further processing. Only higher quality acetate impressions, and therefore finer resolution scale images, were used for analysis of early growth.

Scale impressions that met the criteria were photographed using a 1.0x objective in ImageProPlus® digital microscopic photography software (version 4.5.1 Media Cybernetics, Inc., Silver Spring, MD). Juvenile scale images were taken at 4.0x magnification, whereas scales from smolts and the freshwater regions on adult scales were taken between 0.8x and 3.2x magnification depending on the freshwater radius. All images were calibrated prior to taking measurements in ImageProPlus® using a 3,1 mm Carl Zeiss Jena® Objectmikrometer.

Scale radii (SR) of juveniles and smolts were measured (mm) in Image Pro Plus®, and linear regression analysis with FL was used to determine if SR could be used to predict FL with reasonable accuracy. The resulting relationship between SR and FL was adjusted using a biological intercept of 32 mm FL, assuming that this was the size of first scale formation (L. Campbell, Washington Department of Fish and Wildlife, personal communication; Range: 45 mm – 260 mm FL; $n = 872$; $r^2 = 0.89$; $P < 0.001$).

$$FL \text{ (mm)} = 144.8 * SR \text{ (mm)} + 32.0$$

Fish scales and lengths generally grow in relative proportion to one another. However, due to allometric differences between SR and FL during some periods, the slope of the linear SR-to-FL relationship is not consistent across all fish sizes, and this can often cause the regression to substantially over- or underestimate the size at which the fish form their first scale (Fisher and Pearcy 2005). Therefore, an adjusted biological intercept can be used to represent a more

probable size at which recently emerged juveniles first form scales, and a more biologically representative slope and vertical axis intercept.

To measure specific benchmarks on the freshwater-growth region of each scale, an automated caliper tool was used to locate circuli (contrast peaks in the image). However, the ability of the caliper tool to identify peaks was highly dependent on image quality, so some circuli on lesser quality images had to be added or subtracted manually from the transect. For each sample, the number of circuli were counted, and the distance between each circulus, between the focus and margin of each annular check, between the focus and the saltwater entry check, between each annulus, and between the last freshwater annulus and size-at-saltwater entry were measured. To verify scale morphology interpretations, scale selection and identification of circuli, annuli, and scale margins were discussed among three trained scale readers. Ages of smolts and adults were previously determined by WDFW otolith laboratory staff and were independently re-evaluated during this study. Age determination methodology was similar to that used in WDFW protocol and was discussed with the lead biologist at the WDFW aging lab (L. Campbell, Washington Department of Fish and Wildlife, personal communication). However, because only freshwater growth was assessed during this study, scales were aged based on full completion of freshwater annuli, whereas most fishery managers use January 1 of each year as a freshwater annulus regardless of completion of a true freshwater annulus (Devries and Frie 1996).

Growth and Body Condition Between Ages 1–2 and 2–3

Linear regression estimates of freshwater FL-at-circuli and -annuli were converted to weights (W) at each circuli and annuli for fish sampled as juveniles, smolts, and adults in Bacon,

Illabot, and Finney creeks using a power function regression between FL and W established from field measurements of fish sampled as juveniles (Range: 45 – 235 mm FL; $n = 628$; $r^2 = 0.99$; $P < 0.0001$).

$$W = 0.0000152 * (FL)^{2.94}$$

Mean W-at-circuli and W-at -annuli were then calculated for each life stage sample group in each tributary. Estimated mean W-at-annuli 1, 2, and 3 were used as annual initial (W_i) and final weight (W_f) inputs for bioenergetics model simulations for the period between annulus 1 and annulus 2 (age 1–2), and annulus 2 and annulus 3 (age 2–3) for each life stage sample group in each tributary.

Seasonal mean relative body condition (K) was estimated for fish sampled as juveniles in each tributary to compare simulated W-at-age with seasonal body condition observed from sampled fish for age groups 1–2 and 2–3. Fulton’s condition factor equation was calculated as the ratio between observed and expected weight for a fish of given length (Pope and Kruse 2007).

$$K = (W/L^3) * 100,000$$

Estimated seasonal body condition for age 1–2 and 2–3 juveniles was compared to annual growth trajectories from model simulations to verify whether seasonal increments of simulated W-at-age were similar to W:FL ratios observed in fish measured and weighed in the field.

Water Temperatures

Mean daily water temperatures were used as the thermal experience of Steelhead rearing in Bacon, Illabot, and Finney creeks. Water temperature data loggers (HOBO Water Temperature Pro v2 Data Logger - U22-001) were housed in a PVC case and deployed in each

tributary using steel cable tethers attached to the bank. Loggers recorded water temperature continuously in 20-minute increments between February 17 and July 31, 2011 in Illabot Creek, and between July 1 and August 15, 2011 in Finney Creek, whereas temperature loggers were not available in Bacon Creek; therefore, surrogate water temperatures from a nearby snow zone tributary were used for Bacon Creek.

Temperature data were screened for anomalous data points, which indicated the logger had been flushed from the channel during a high flow event and subsequently exposed during lower flows. Only partial data were downloaded from temperature loggers prior to being lost during high flows (duration of recordings given above). Of the temperature data available, some were suspect and were removed from analysis. However, water temperature loggers had been deployed in 10 additional sites in the Skagit River basin concurrent with those deployed in Illabot and Finney creeks.

Due to the lack of available annual water temperature data, mean daily water temperatures from Illabot and Finney creeks were each regressed separately with concurrent mean daily water temperatures recorded at sites that appeared to follow each water temperature profile (Illabot Creek was correlated with the mouth of Suiattle River [Range of independent temperatures: 1° – 11° C; n = 130; $r^2 = 0.96$; $P < 0.0001$]), and Finney Creek was correlated with lower Sauk River [Range of independent temperatures: 4° – 13° C; n = 48; $r^2 = 0.97$; $P < 0.0001$]). Linear regression equations were then used to estimate mean daily water temperature in Illabot and Finney creeks for the period between April 1, 2011 and March 31, 2012. Water temperature data were not available for Bacon Creek; however, water temperature data collected in Bacon Creek during two days in summer and one day in fall aligned with the those same days along the complete water temperature profile at a similar site, Cascade River Marble, so mean

daily water temperature at Cascade River Marble was used as a surrogate for mean daily water temperature at Bacon Creek for the period between April 1, 2011 and March 31, 2012.

Seasonal Prey Sources

Seasonal prey species composition and seasonal composite prey energy densities were estimated using macroinvertebrates captured seasonally from each tributary in stream drift nets. Seasonal macroinvertebrate prey species composition was used in place of actual seasonal Steelhead diets for running bioenergetics model simulations, and seasonal composite prey energy densities were used as an index of the relative energy density of seasonally available food items in Bacon, Illabot, and Finney creeks.

A macroinvertebrate drift net was used to sample the biovolume and energy composition for functional groups of surface and drifting prey resources as a relative index of energy delivery for a subset of sites. The drift net was deployed upstream of the juvenile electrofishing sample transect prior to electrofishing for juvenile Steelhead, and was collected after processing fish. The frame opening of the drift net was 50 cm wide and 25 cm high, and the netting was made with 150 μm mesh. Holes were drilled around the circumference of a detachable PVC-encased cod end, and were covered with the same 150 μm mesh netting to allow water to pass through the holes. Deployment sites for the drift nets were targeted at stream depths less than 0.50 m with measureable velocity, and were located along stream margins representative, but upstream, of habitats where electrofishing was conducted. Thus, drift nets sampled a small portion of representative feeding habitats along the stream margin available to juvenile Steelhead, and were not targeted for optimal feeding lanes or the thalweg. Mean wetted widths of the stream channel at deployment sites varied seasonally in each tributary (Summer 2011: Bacon Creek = 17 m;

Illabot Creek = 16 m; Finney Creek = 12 m; Winter 2012: Bacon Creek = no data; Illabot Creek = 15 m; Finney Creek = 23 m), so the proportion of the wetted channel that was sampled varied seasonally. Bacon Creek was not sampled for drift during winter, so drift data from a same-aspect, proximate site (Diobsud Creek) were used for winter in Bacon Creek.

Drift nets were deployed to capture both floating and submerged invertebrates drifting passively downstream. Nets were stationed in the channel by attaching rope tethers to a metal bar that was hammered into the streambed so that the lower 20 cm of cross-sectional area of the net opening was securely submerged, and floats were attached to the sides of the net frame, allowing the top 5 cm of the cross-sectional area of the net opening to capture prey drifting on the surface. Velocity (m/s), depth of net location (to the nearest 0.1 m), and deployment duration (to the nearest minute) were recorded at the mouth of the net during deployment and retrieval. Velocity and depth were measured using a flow meter (Swoffer Instruments, Inc., Seattle, Washington USA). Duration of net deployment varied in proportion to the time spent electrofishing and processing captured fish at each site (Culp et al. 1994) (range: 76–167 minutes; mean: 103 minutes; SD: 25 minutes). Upon net retrieval, large organic matter was washed so that any attached invertebrates fell into the cod end of the net, large cleaned organic debris was discarded, and the net was sealed to retain winged insects. All items captured in the net were carefully placed into large plastic vials, labeled, and preserved in 95% ethanol diluted with water.

Invertebrates were sorted into three size categories, ≥ 2 mm, 1–2 mm, and < 1 mm. Organisms smaller than 1 mm were removed from further processing because salmonids feed on the larger size fractions (Filbert and Hawkins 1995, Keeley and Grant 2001). Remaining invertebrates were extracted from debris under a dissecting microscope and separated by order

and life stage (larval or adult). Taxa were then categorized into broader energy groups based on similarity in energy densities (Table 2; low: ~ 3,000 J/g; medium: ~ 4,000 J/g; high: greater than 5,000 J/g) (McCarthy et al. 2009). Aquatic nymphs and larvae were considered low-energy food, aquatic adults and terrestrial larvae were considered medium-energy food, and adult terrestrials were considered high-energy food. Seasonal compositions (proportional biomass contribution to the drift by blotted-wet-weight [g]) of these three energy groups were used as the seasonal diet composition inputs for bioenergetics model simulation runs for each Steelhead life stage sample group in Bacon, Illabot, and Finney creeks. Blotted-dry wet weight (g) of each energy group was converted to energy content (Joules), and the summed amount of joules in each energy group was divided by the total wet-weight (g) of the composite drift sample to estimate the mean energy density (J/g) in macroinvertebrate drift by site and season.

Bioenergetics Modeling

The Wisconsin bioenergetics model (Hanson et al. 1997) with Steelhead parameters from Rand et al. (1993) was used to fit juvenile Steelhead consumption to mean back-calculated annual growth between annuli 1 and 2 and annuli 2 and 3 for juveniles sampled at each site, for those that survived to the smolt stage at each site, and for the pool of adult samples collected from Finney Creek and in the upper Skagit River basin mainstem. Modeling inputs were specific to each tributary, using the seasonal composition of macroinvertebrate drift as a surrogate for diet composition and the thermal experience as described in the previous section. The model estimated total consumption (C [g]) resulting from net energy required to maintain observed growth (G [g]) and corresponding metabolism (M) and waste (W) costs,

$$C = M + W + G$$

This energy-balance equation estimates consumption as a proportion of the theoretical maximum consumption ($\%C_{\max}$) for each species-size combination of interest. Estimates of $\%C_{\max}$ indicate relative feeding rate, which in this study corresponded with seasonal consumption of the composite of macroinvertebrate drift items required to meet estimated annual growth of each age and life stage sample group in Bacon, Illabot, and Finney creeks.

Selection of start and end dates for bioenergetics model simulations depended on the period of interest for modeling growth and consumption. April 1 was selected as the start date for model simulations because this is the general time when annual growth checks were created on scales (annuli). Growth in juvenile Steelhead increased near this date as water temperatures and feeding activity increased. Because I modeled growth and consumption for a complete year of life for Steelhead, the end date was set at March 31. For daily thermal experience of juvenile Steelhead, daily mean water temperatures collected or estimated in each tributary during the period April 1, 2011 to March 31, 2012 were used. Literature values were used for the seasonal predator energy density (J/g) of age 1 or greater *O. mykiss* in the Skagit River (Lowery 2009), and generalized energy density values were used for major categories of prey (McCarthy et al. 2009).

Diets were not sampled from individual fish; therefore, macroinvertebrate drift composition was used as the diet input under the assumption that a fish occupying the cross-sectional area of the submerged net opening could consume each food item (submerged and surficial) drifting past in direct proportion (by weight) to that captured in the drift net (Johnson 2007, Johnson et al. 2013) for organisms larger than 1 mm. The diet composition of Rainbow Trout was similar between winter and spring in another large Puget Sound river basin (Thompson et al. 2011). Therefore, because macroinvertebrate drift was not sampled during

spring, winter drift composition was used as a surrogate for spring drift composition in model simulations.

Year-round bioenergetics model simulations were conducted by tributary with separate model simulations conducted for the growth trajectories of each different life stage sample group. Each simulation spanned an annual growth increment: 365 days between the age 1 and age 2 annuli (age 1–2), and 365 days between the age 2 and age 3 annuli (age 2–3).

Growth Sensitivity Analysis

Growth of salmonids is dependent on a combination of thermal experience, prey quality and quantity, and feeding rate, and as fish size increases, so does their growth sensitivity to these factors (Beauchamp 2009). Temperature-dependent growth curves evaluate the sensitivity of growth potential to thermal experience, composite prey energy density, and feeding rate. The scope for growth decreases as prey energy density or feeding rate decline or as water temperatures deviate further from optimum. An increase in composite prey energy density can increase the total scope for growth and reduces sensitivity to thermal extremes.

Temperature-dependent growth curves were created for 10 g (age 1–2) and 30 g (age 2–3) Steelhead feeding at rates observed during this study in the Skagit River basin (20%, 25%, and 30% C_{max}) to determine sensitivity of growth to environmental factors in each tributary. Sensitivity analysis was conducted to evaluate the scope of summer fast growth given the thermal experience, observed composite prey energy density of macroinvertebrates captured in drift samples during summer, and the mean annual feeding rate estimated from bioenergetics model simulations. Scope of growth for the mean annual feeding rate of adults in each tributary was plotted on growth curve graphs to compare general feeding rates to those simulated

specifically for Steelhead that survived to adulthood based on growth observed in that sample group. A second sensitivity analysis was conducted by increasing the observed composite prey energy density of summer diets to 5000 J/g to evaluate how such an increase might affect the scope of growth during the summer fast growth period at 20%, 25%, and 30% C_{\max} . This analysis provided further insights into which factors, or which combination of factors, most affected growth, and could provide insights into how growth in rearing Steelhead varies in different environments associated with precipitation zones.

Results

Bacon Creek

Annual Growth Between Ages 1–2 and 2–3 Among Life Stage Sample Groups

Bioenergetic simulations for Bacon Creek indicated that approximately 53% of the annual growth of age 1–2 Steelhead, and 56% of the annual growth of age 2–3 Steelhead that survived to adulthood occurred during the summer months (July, August, and September; Figure 2). Although mean annual feeding rate (% C_{\max}) differed by only two-percentage points between ages 1–2 and 2–3 fish sampled as juveniles and adults, this seemingly small difference in feeding rate translated into significant differences in mean annual growth (Table 3).

Increased growth by fish that survived to adulthood (fish sampled as adults) in Bacon Creek resulted from higher feeding rates and total annual consumption during their juvenile stage. Between ages 1 and 2, fish sampled as juveniles grew an average of 11 g per year, fed at an annual mean rate of 23% C_{\max} , and consumed a total of 126 g of invertebrates to achieve the estimated growth. To successfully reach the smolt stage by age 2, Steelhead had to grow an average 14 g while feeding at 24% C_{\max} and consuming 144 g of invertebrates. Fish that

survived to adulthood, however, grew an average of 17 g, fed at an annual mean rate of 25% C_{\max} , and required 154 g of consumption between ages 1 and 2. No age 3 juveniles were captured in Bacon Creek. However, to successfully reach the smolt stage by age 3, Steelhead had to grow an average of 20 g, while feeding at 25% C_{\max} and consuming 274 g of invertebrates. Fish that survived to adulthood, however, grew an average of 32 g, fed at an annual mean rate of 27% C_{\max} , and required 348 g of consumption (Table 3).

Estimated condition factors indicated that W:FL ratios were similar between summer and fall for fish sampled as juveniles at age 1–2, but increased between summer and fall for the age 2–3 group, which corroborated simulated growth during those periods. No juveniles were captured during winter in Bacon Creek, so observed W:FL ratios were not available for comparisons with simulated growth trajectories for each age group between fall and winter (Table 4).

Water Temperature and Composite Prey Energy Density

Moderate year-round water temperatures in Bacon Creek buffered rearing Steelhead from physiological stress that can result from extreme thermal experience. Annual mean daily temperature in Bacon Creek was 6° C (SD: 2° C). Maximum temperature was 11° C, which occurred during only 12 days from late August to mid-September. Temperatures during winter were also relatively moderate, and fell below 3° C only during two days in January (2° C) (Figure 2).

Seasonal composite energy densities of prey were relatively low in Bacon Creek. Macroinvertebrate drift was composed of relatively low-energy items, on average, throughout summer, fall, and winter (three-season mean: 3,647 J/g). Composite prey energy densities were

relatively very low during summer (3,312 J/g) and fall (3,362 J/g), but increased substantially during winter (4,266 J/g). Most of the summer composite energy budget was composed of low-energy aquatic nymphs and larvae (86%), followed by high-energy terrestrial adults (9%), and moderate-energy aquatic adults and terrestrial larvae (5%) (Figure 2).

Growth Sensitivity

Temperature-dependent growth curves for Bacon Creek corroborated modeled growth trajectories, which indicated that growth was greatest during summer months when mean daily water temperatures ranged from 7° C to 11° C (Figure 3). Although the water temperature regime in Bacon Creek appeared to buffer rearing Steelhead from stressful thermal conditions and would have accommodated fast growth given moderate-to-high prey energy densities, the low composite prey energy density during summer and fall lowered the overall scope for growth during these periods. If the summer composite prey energy density was increased from 3,312 J/g to 5,000 J/g, mean summer growth rate for age 1–2 fish feeding at 20% C_{max} increased by 29% from 0.003 g (g/d) to 0.010 g(g/d), but increased by 48% from 0.010 to 0.020 g(g/d) at a feeding rate of 30% C_{max} . This same increase in prey energy density for age 2–3 Steelhead increased the mean summer growth rate by 13% at 20% C_{max} , and by 43% at 30% C_{max} . The increase in prey energy density to 5,000 J/g would have enabled both age groups of fish sampled as juveniles to exceed growth rates observed in fish that survived to adulthood, even at feeding rates of 20% C_{max} and lower.

Illabot Creek

Annual Growth Between Ages 1–2 and 2–3 Among Life Stage Sample Groups

In Illabot Creek, approximately 35% of the annual growth of age 1–2 Steelhead and 73% of the annual growth of age 2–3 Steelhead that survived to adulthood occurred during the summer months (July, August, and September; Figure 4). Mean annual feeding rate (% C_{\max}) at age 1–2 differed only by two-percentage points, but between age 2–3 did not differ between fish sampled as juveniles and those sampled as adults. The relatively small difference in feeding rate at age 1–2 translated into significant differences in mean annual growth during that period. Although feeding rate was identical among life stage sample groups at age 2–3, lower feeding and growth in fish sampled as juveniles during age 1–2 had already set an overall lower growth trajectory for the age 2–3 year of life for that sample group. In other words, juveniles that experienced slower early growth in Illabot Creek were unable to catch up sufficiently at older ages despite the elevated feeding rates at a later age (Table 3).

Increased growth by fish that survived to adulthood in Illabot Creek resulted from higher feeding rates and total annual consumption during their juvenile stage. Between ages 1 and 2, fish sampled as juveniles grew an average of 11 g per year, fed at an annual mean rate of 22% C_{\max} , and consumed a total of 106 g of invertebrates per year to achieve the estimated growth. To successfully reach the smolt stage by age 2, Steelhead had to grow an average of 16 g while feeding at 24% C_{\max} and consuming 131 g of invertebrates. Fish that survived to adulthood, however, grew an average of 17 g, fed at an annual mean rate of 24% C_{\max} , and required 138 g of invertebrates between ages 1 and 2. Between ages 2 and 3, fish sampled as juveniles grew an average of 29 g per year, fed at an annual mean rate of 26% C_{\max} , and consumed a total of 263 g of invertebrates per year to achieve the estimated growth. To successfully reach the smolt stage

by age 3, Steelhead had to grow an average of 26 g, while feeding at 26% C_{max} , and consuming 282 g of invertebrates. Fish that survived to adulthood, however, grew an average of 32 g, fed at an annual mean rate of 26% C_{max} , and required 312 g of invertebrates between ages 2 and 3 (Table 3).

Estimated condition factors indicated that W:FL ratios decreased slightly between summer and fall for fish sampled as juveniles at age 1–2, but decreased significantly between fall and winter for both the age 1–2 and 2–3 groups. Condition factors corroborated the substantial weight loss simulated for both age groups between fall and winter (Table 4).

Water Temperature and Composite Prey Energy Density

Water temperatures in Illabot Creek were moderate-to-low (Figure 4). Rearing Steelhead were buffered from physiological stress that can result from warm thermal experience, but water temperature in mid-to-late fall and early winter contributed to a prolonged period of weight loss during that period. Annual mean daily temperature in Illabot Creek was moderate (6° C), but temperatures were relatively variable (SD: 3° C). Maximum temperature was 11° C, which occurred during only 12 days during late August and mid-September. Temperatures during winter were cold for a prolonged period, falling below 3° C for most of the period between middle-to-late November and the end of January (Figure 4).

Seasonal composite prey energy densities were moderately high in Illabot Creek during summer and fall, but lower in winter (Figure 4). Macroinvertebrate drift was composed of a mixture of low-, medium-, and high-energy content items throughout summer, fall, and winter (three-season mean: 4,015 J/g). The proportion of low-energy prey items (nymphs and larvae) increased from only 14% during summer to 71% during winter. Most of the summer composite

energy budget was composed of moderate-energy aquatic adults and terrestrial larvae (54%), followed by high-energy terrestrial adults (32%), and low-energy aquatic nymphs and larvae (14%) (Figure 4).

Growth Sensitivity

Temperature-dependent growth curves for Illabot Creek during summer corroborated model growth trajectories that indicated growth was greatest during summer months when water temperatures ranged from 7° C to 11° C (Figure 5). Although the water temperature regime in Illabot Creek did not enter stressful thermal ranges during summer, prolonged, very low mid-to-late fall and early winter water temperatures (less than 3° C) combined with low winter composite prey energy density (less than 3,472 J/g), resulting in a substantial period of negative growth for age 1–2 fish during the transition between the fall and winter seasons. Negative growth was also experienced by age 2–3 Steelhead, but weight loss occurred primarily only during middle to late winter as energy reserves became depleted, so overall losses were not as great. If the summer composite prey energy density was increased from 4,281 J/g to 5,000 J/g, mean summer growth rate for age 1–2 fish feeding at 20% C_{max} increased by 70% from 0.007 g (g/d) to 0.010 g(g/d), but increased by 78% from 0.016 g(g/d) to 0.020 g(g/d) if the feeding rate was increased to 30% C_{max} . This same increase in prey energy density for age 2–3 Steelhead increased the mean summer growth rate by 63% at 20% C_{max} , and by 76% at 30% C_{max} . The increase in prey energy density to 5,000 J/g would have enabled juveniles to meet growth rates observed in fish that survived to adulthood at a minimum feeding rate of 21% C_{max} for age 1–2 juveniles, and at a minimum feeding rate of 23% C_{max} for age 2–3 juveniles.

Finney Creek

Annual Growth Between Ages 1–2 and 2–3 Among Life Stage Sample Groups

In Finney Creek, approximately 49% of the annual growth of age 1–2 Steelhead, and 43% of the annual growth of age 2–3 Steelhead that survived to adulthood occurred during the summer months (July, August, and September; Figure 6). Mean annual feeding rate (% C_{max}) for fish sampled as juveniles and those sampled as adults differed by four-percentage points between annuli 1 and 2, and by five-percentage points between annuli 2 and 3. This relatively higher discrepancy in feeding rate between the juvenile and adult samples translated into even greater differences in mean annual growth among life stage sample groups compared to the differences observed between life stage sample groups in Bacon and Illabot creeks (Table 3).

Increased growth by fish that survived to adulthood (fish sampled as adults) in Finney Creek resulted from higher feeding rates and total consumption during their juvenile stage. Between ages 1 and 2, fish sampled as juveniles grew an average of 10 g per year, fed at an annual mean rate of 21% C_{max} , and consumed a total of 140 g of invertebrates per year to achieve the estimated growth. To successfully reach the smolt stage by age 2, Steelhead had to grow an average of 17 g, while feeding at 22% C_{max} , and consuming 217 g of invertebrates. Fish that survived to adulthood, however, grew an average of 26 g, fed at an annual mean rate of 25% C_{max} , and required 257 g of invertebrates between ages 1 and 2. Between ages 2 and 3, fish sampled as juveniles grew an average of 22 g per year, fed at an annual mean rate of 23% C_{max} , and consumed a total of 315 g of invertebrates per year to achieve the estimated growth. To successfully reach the smolt stage by age 3, Steelhead had to grow an average of 29 g, while feeding at 25% C_{max} , and consuming 444 g of invertebrates. Fish that survived to adulthood,

however, grew an average of 54 g, fed at an annual mean rate of 28% C_{max} , and required 659 g of invertebrates between ages 2 and 3 (Table 3).

Estimated condition factors indicated that W:FL ratios increased significantly between summer and fall for fish sampled as juveniles at ages 1–2 and 2–3, but decreased significantly between fall and winter for the age 2–3 group. No age 1–2 juveniles were captured during winter, so estimates of body condition were not available for that age group during that period. Condition factors corroborated simulated increases in weight between summer and fall, and the weight loss simulated for age 2–3 fish between fall and winter. However, only one age 2–3 fish was sampled during winter, and differences in fork lengths within age group 1–2 between summer and fall, and within age group 2–3 between fall and winter may have skewed W:FL ratios during these periods in Finney Creek (Table 4).

Water Temperature and Composite Prey Energy Density

Rearing Steelhead in Finney Creek experienced relatively extreme warm and cold water temperatures (Figure 6). Annual mean daily temperature in Finney Creek was relatively warm (8° C), and daily mean temperatures were highly variable (SD: 5° C). Maximum mean daily temperature was 18° C, but mean daily temperatures greater than 16° C were experienced throughout half of August and September for a combined total of 27 days. Temperatures during winter were cold for a prolonged period, frequently falling below 3° C between late November and the end of January (Figure 6).

Seasonal energy group composition and composite energy density were highly variable among the seasons, and mean seasonal prey energy density for summer, fall, and winter was moderate (4,130 J/g). During summer, drift was composed mainly of high-energy content items

(5,107 J/g), whereas during fall energy densities were relatively very low (3,274 J/g), and in winter were moderate (4,010 J/g). Drift during summer was overwhelmingly composed of high-energy terrestrial adults (92%), followed by medium-energy aquatic adult and terrestrial larvae (7%), and low-energy aquatic nymphs and larvae (1%) prey energy categories (Figure 6).

Growth Sensitivity

Temperature-dependent growth curves for Finney Creek during summer corroborated model growth trajectories that indicated growth was greatest during summer months when water temperatures ranged from 10° C to 18° C (Figure 7). The composite prey energy density for summer was greater than the highest composite energy densities allotted for sensitivity analysis (5,000 J/g). Therefore, the composite energy density was not increased for growth sensitivity analysis in Finney Creek. However, alternate feeding rates were plotted to evaluate how feeding rate affected growth potential during summer for fish that survived to adulthood. For the age 1–2 group, a five-percent decrease in feeding rate from 25% C_{max} to 20% C_{max} resulted in 33% lower growth rate during summer from 0.018 g(g/d) to 0.012 g(g/d), whereas an increase of five-percent resulted in a 33% increase in growth rate during summer (0.025 g[g/d]). For the age 2–3 group, an eight-percent decrease in feeding rate from 28% C_{max} to 20% C_{max} resulted in a 51% lower growth rate during summer from 0.014 g(g/d) to 0.007 g(g/d), whereas an increase of two-percent resulted in a 12% increase in growth rate during summer (0.016 g[g/d]).

Discussion

This study highlighted the sensitivity of growth in juvenile Steelhead to the combined effects of varying thermal regimes, feeding rates, and prey resources under a range of ambient

conditions experienced in the Skagit River basin. Given the evidence that size-selective mortality operates at multiple life stages for these Steelhead (Chapter 2), it becomes important to understand the underlying factors that affect the differences in growth exhibited by the average juvenile compared to those that survived to smolt or adult stages. Environmental conditions vary among the different precipitation zones in the Skagit River basin (Beechie 1992), and differences in thermal regimes and prey resources among tributaries or reaches within the same watershed can heavily influence seasonal growth of juvenile Steelhead (McCarthy et al. 2009). For example, high disparity in growth trajectories among the different life stage sampling groups indicated that size-dependent mortality was relatively high throughout the entire freshwater rearing period for Steelhead in Finney Creek. Conversely, the reduced disparity between age 2–3 growth trajectories for fish sampled as juveniles and adults in Illabot Creek indicated that young Steelhead that survived their first two years in freshwater may have a higher probability of survival to adulthood. However, bioenergetic simulations and seasonal estimates of body condition indicated that all age 1–2 and 2–3 fish in Illabot Creek experienced substantial weight loss during winter, so even very slight differences in annual growth could translate into relatively high overwinter mortality in fish that were unable to reach a minimum weight going into winter (e.g., Biro et al. 2004).

This study revealed biological and physical environmental factors that affected growth of rearing Steelhead in three different tributaries that represent different precipitation zones and thermal regimes. However, while precipitation zones probably explained thermal regimes in rain and snow zones, it might not be as informative at explaining homogeneity in thermal regimes in mixed rain-snow zone tributaries because this zone encompasses increasingly heterogeneous environments (Beechie 1992). For example, tributaries within the snow precipitation zone

exhibited cool and buffered thermal regimes because peak streamflow is dependent on the gradual increase in snowmelt during summer when air temperatures increased at higher elevations. Snow zone tributaries are buffered from increased air temperatures during this period because snowfields or glaciers provided consistent, cool water sources. Conversely, warm mixed rain-snow and rain zone tributaries may exhibit consistent and prolonged periods of warmer water temperatures during warm periods due to ephemeral, rain-dependent water sources that become depleted or stagnant during typical drought summer conditions in the Puget Sound region. Water sources for tributaries in the mixed rain-snow zone encompass a range of environments, from higher-elevation snowfields to moderate-elevation foothills (Beechie 1992).

The sites evaluated in this study encompassed the thermal extremes that can occur among tributaries in the mixed rain-snow zone. On average, water temperatures in Illabot Creek, a mixed zone tributary, were colder than those recorded in Bacon Creek, the snow zone tributary, whereas temperatures in Finney Creek, also a mixed zone tributary, were relatively warm when compared to tributaries in both snow and rain zones. Thus, the summer thermal regime in Finney Creek might be representative of that experienced by Steelhead in warm mixed rain-snow and rain zone tributaries during summer. An improved approach at stratification might incorporate both precipitation zone and water temperature regime because this study showed the high amount of variability in water temperature that can occur within the mixed rain-snow zone.

Precipitation zone may not be the most appropriate level of stratification to evaluate how prey sources influence growth. Prey sources vary substantially based on a number of factors that might co-vary with precipitation zone (Hershey and Lamberti 1998). However, subtle primary factors can affect biological and food web structure, causing high variability in structure of secondary producers among specific streams within precipitation zones. For example, water

chemistry, streamflow regime (not just peak streamflow), riparian vegetation, land use, and lithology all influence water quality production dynamics in streams (Welch et al. 1998, Nakano et al. 1999, Nakano and Murakami 2001), and these factors vary widely among drainages in the Skagit River basin (E. Connor, Seattle City Light, personal communication).

Some assumptions were made in regards to bioenergetics model inputs. First, growth trajectories of fish sampled as juveniles, smolts, and adults were pooled by brood year, and it was assumed that freshwater environmental conditions experienced by adults (brood years 2004–2010) and smolts (brood years 2007–2010) during ages 1–2 and 2–3 were the same as those experienced by juveniles (brood years 2006–2011) for the same age groups. Environmental conditions could have varied markedly among these years; however, size-at-age was normally distributed for age 1–2 Steelhead, so use of pooled-brood years accounted for temporal variability in growth among these years. Secondly, it was assumed that macroinvertebrate drift samples represented actual seasonal diet composition of rearing Steelhead. Johnson (2007) and Johnson et al. 2013 provided some evidence that juvenile Steelhead prey composition varies in relative proportion to prey drift. However, prey items should ideally be collected from a subset of individual fish diets in addition to conducting an evaluation of the quantity and quality of prey items available to Steelhead. Finally, I assumed that mean back-calculated annual growth of each life stage sample group reflected growth that occurred within the tributary under investigation. Although it is possible that fish may have hatched and grown in other tributaries during early stages and then moved into Bacon, Illabot, or Finney creeks during later stages, it is reasonable to assume that most fish sampled as juveniles and smolts originated in streams in which they were captured. Normality tests of size frequencies from within each tributary suggested that fish from each life stage sample group grew at similar rates to each annulus

(Chapter 2). Unfortunately, a lack of site-specific adult samples from Illabot and Bacon creeks necessitated the use of early life growth estimated from adults captured in the upper Skagit River mainstem. Thus, it could not be confirmed that these adults grew as juveniles in Illabot or Bacon creeks. However, use of these samples for comparisons of growth performance and the factors that affect growth was reasonable because Steelhead in the upper Skagit River basin probably experience similar environmental conditions during early stages.

Conclusions

Early life growth influences survival to adulthood in wild Steelhead in the Skagit River (Chapter 2), and the factors that affect growth identified during this study can be monitored and further assessed over time to determine the feasibility and potential effectiveness that system-specific restoration efforts might have on improving survival to adulthood and the production of wild Steelhead. Restoration and recovery efforts often fail to improve population status (or result in unknown effectiveness) because of the focus on physical habitat with little consideration to the measurable factors that actually affect survival (Roni et al. 2002). This study provides an initial framework for identifying the factors that limit growth and bioenergetics in wild Steelhead among three very different environments. A similar framework can be applied in both freshwater and marine environments in the Puget Sound region to identify the relative roles of water temperature, feeding rate, and prey quality on early life growth and survival in wild Steelhead.

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Chapter 3 Figures And Tables

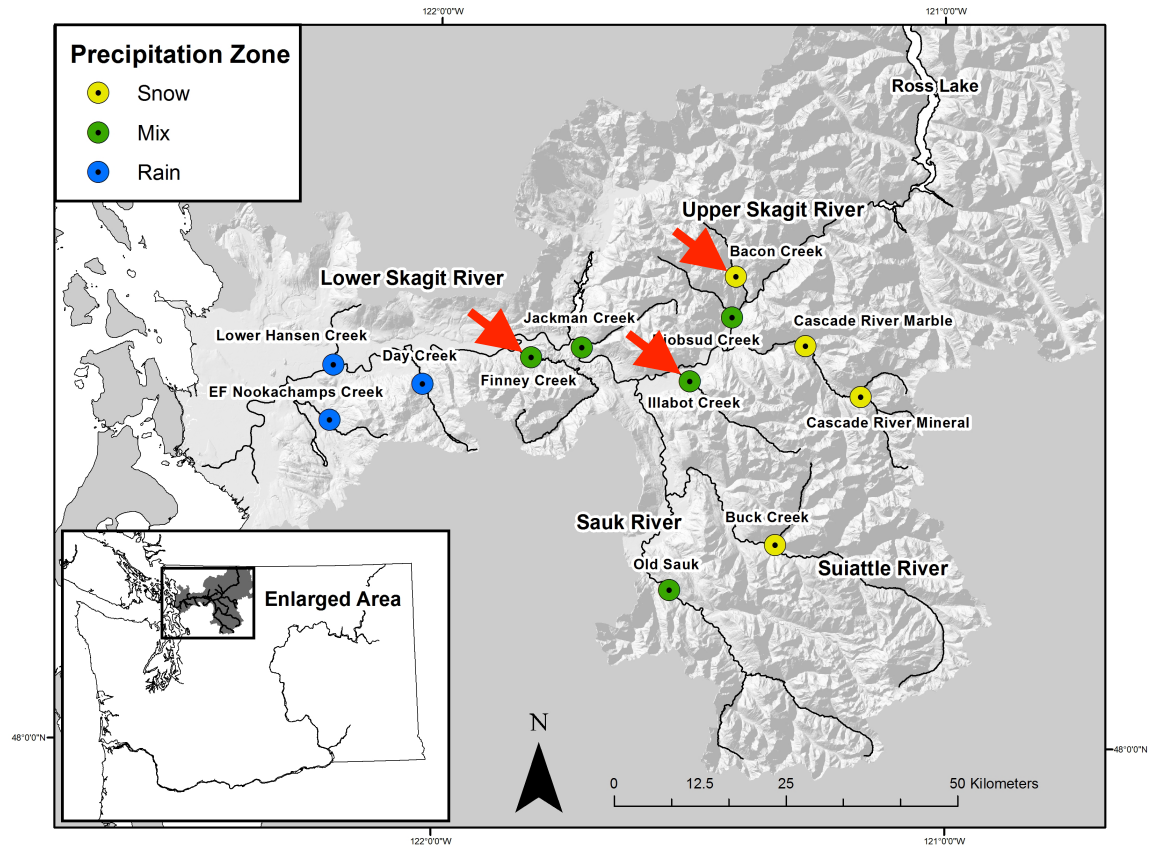


Figure 1. Skagit River basin study area highlighting Bacon, Illabot, and Finney creeks (red arrows), the sites where electrofishing, smolt trapping, and macroinvertebrate drift sampling was conducted. Adult Steelhead were captured in Finney Creek, and those captured in the upper Skagit River basin were used in bioenergetics simulations for Bacon and Illabot creeks. Sites are color-coded to indicate precipitation zone (rain, mixed rain-snow [mix], and snow).

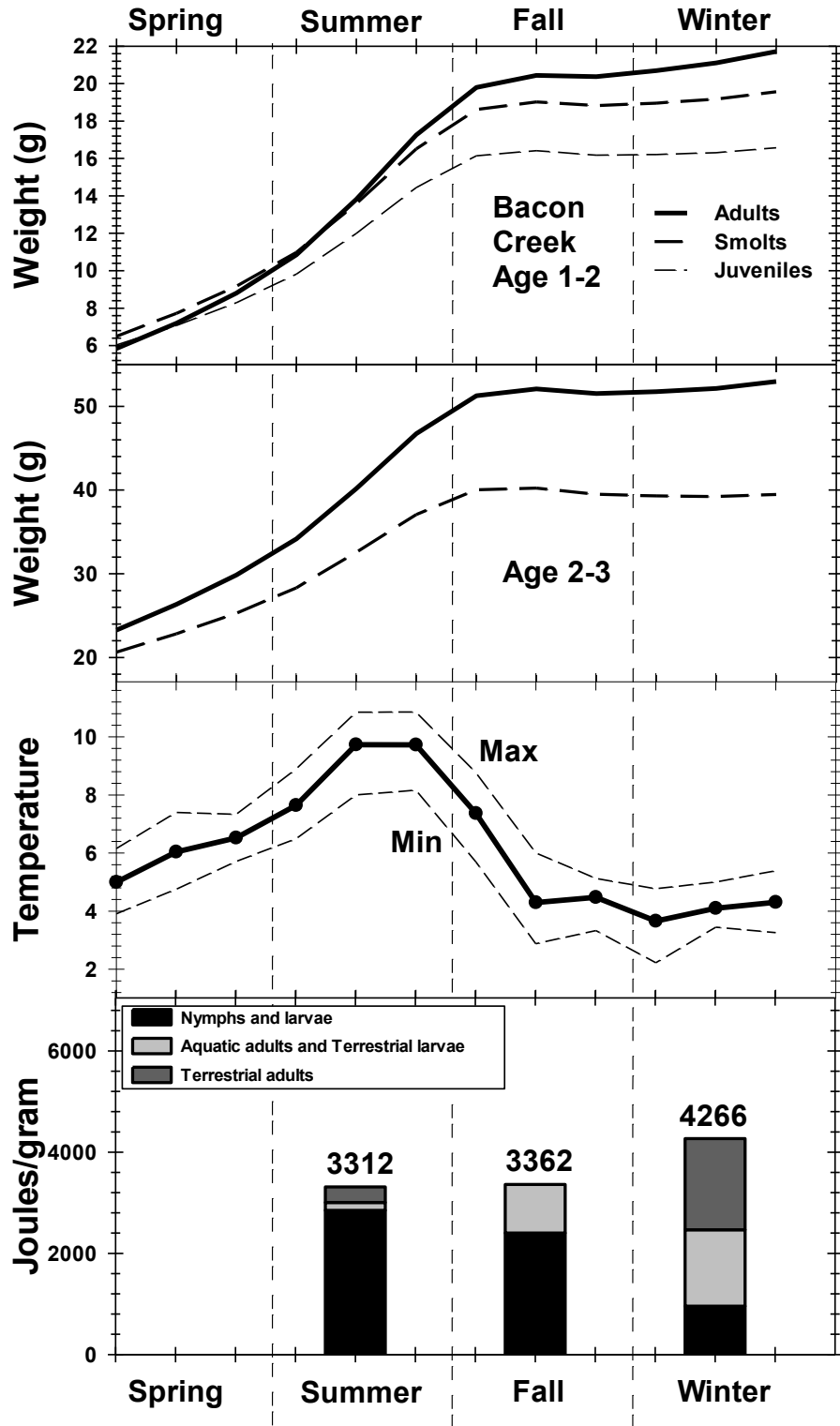


Figure 2. Bioenergetics simulation results of annual growth trajectories for age 1–2 and 2–3 Steelhead sampled as juveniles, smolts, and adults, mean monthly water temperatures (min, max), and seasonal composite prey energy densities for summer, fall, and winter in Bacon Creek.

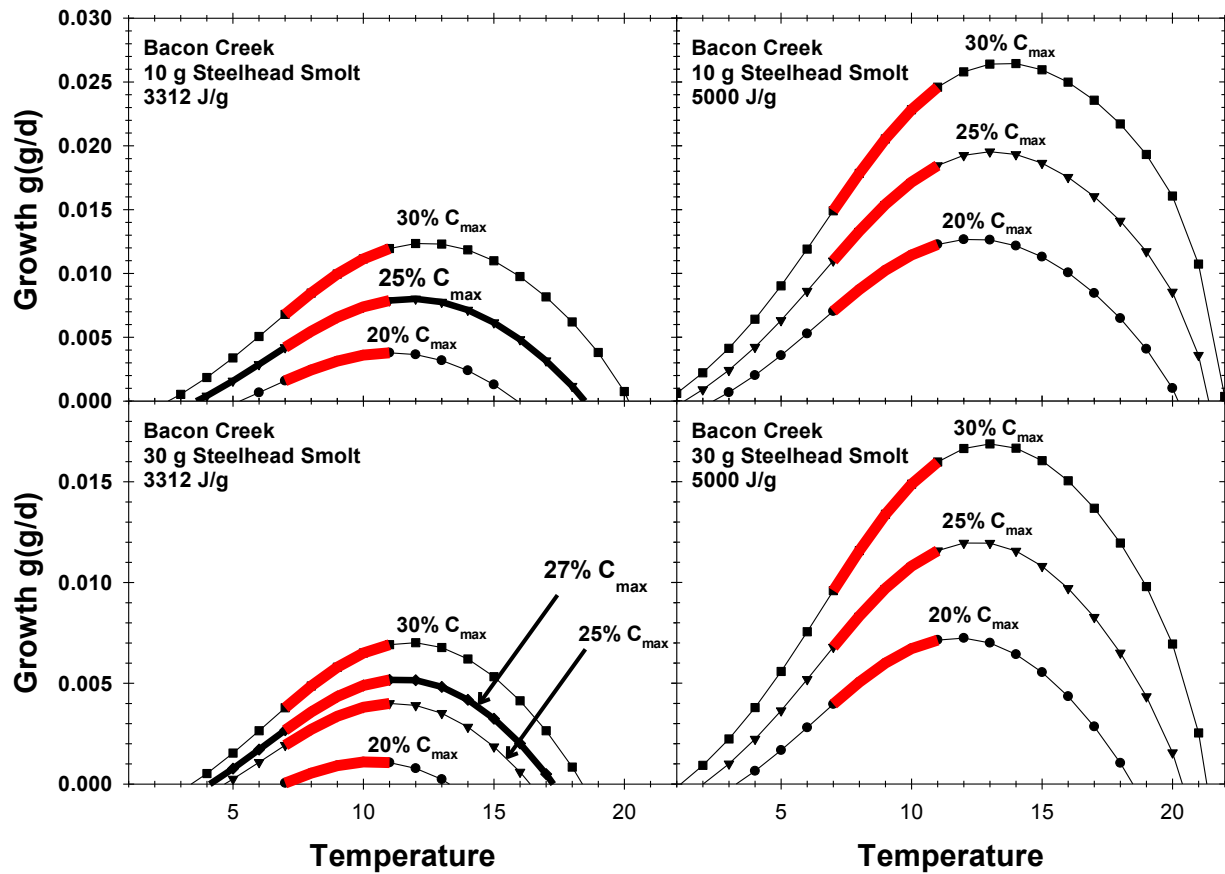


Figure 3. Change in daily growth rate in response to temperature and feeding rate for 10 g (top; age 1–2) and 30 g (bottom; age 2–3) Steelhead feeding on a composite diet with a mean energy density of 3,312 J/g wet weight (left panels) and 5,000 J/g (right panels). The highlighted portion of each curve indicates the thermal experience for Steelhead during the summer fast growth period in Bacon Creek (7° C – 11° C). Bold curves indicate the summer scope of growth for Steelhead that survived to adulthood given estimated summer prey energy density and simulated mean annual feeding rate (larger font).

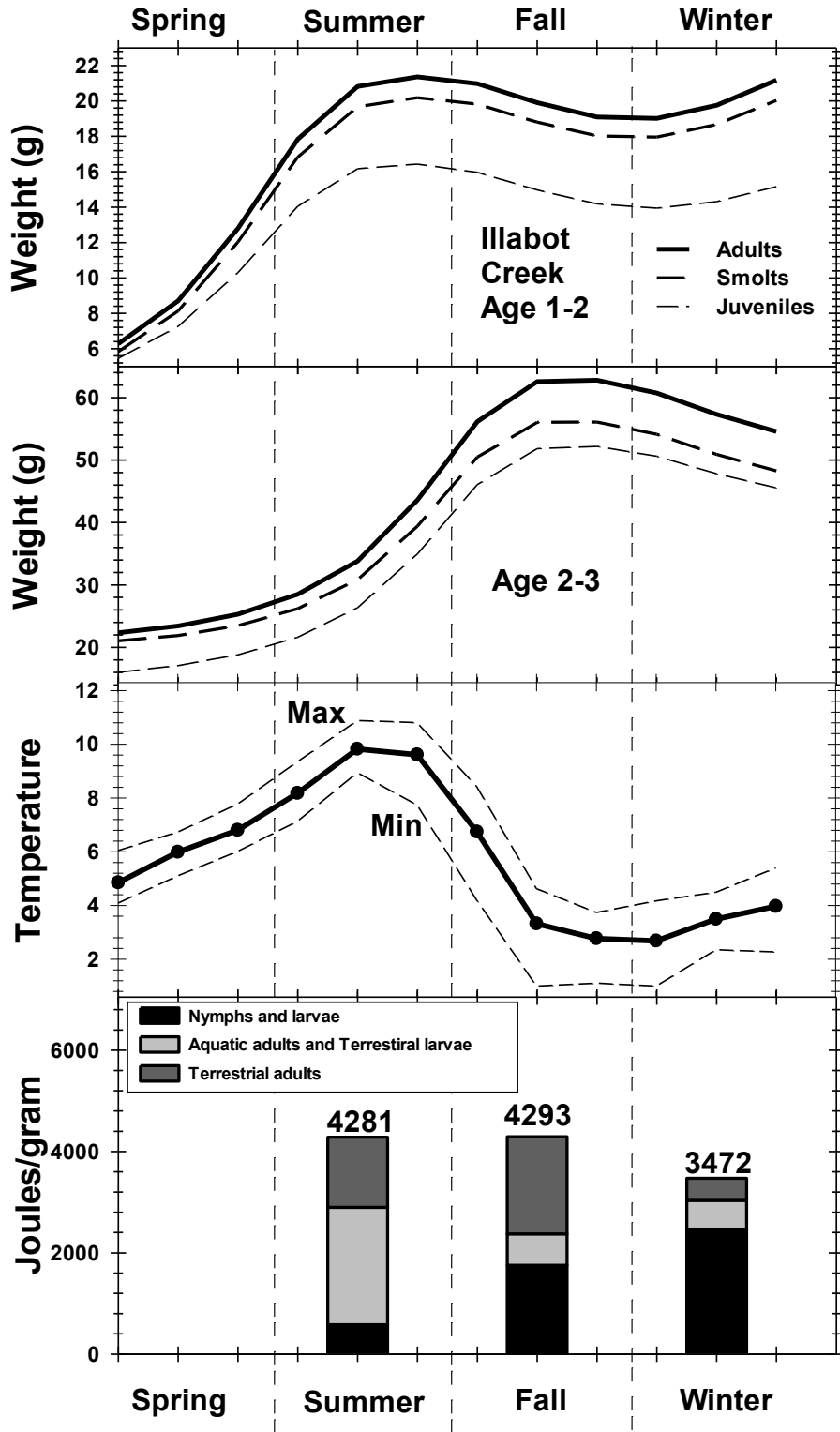


Figure 4. Bioenergetics simulation results of annual growth trajectories for age 1–2 and 2–3 Steelhead sampled as juveniles, smolts, and adults, mean monthly water temperatures (min, max), and seasonal composite prey energy densities for summer, fall, and winter in Illabot Creek.

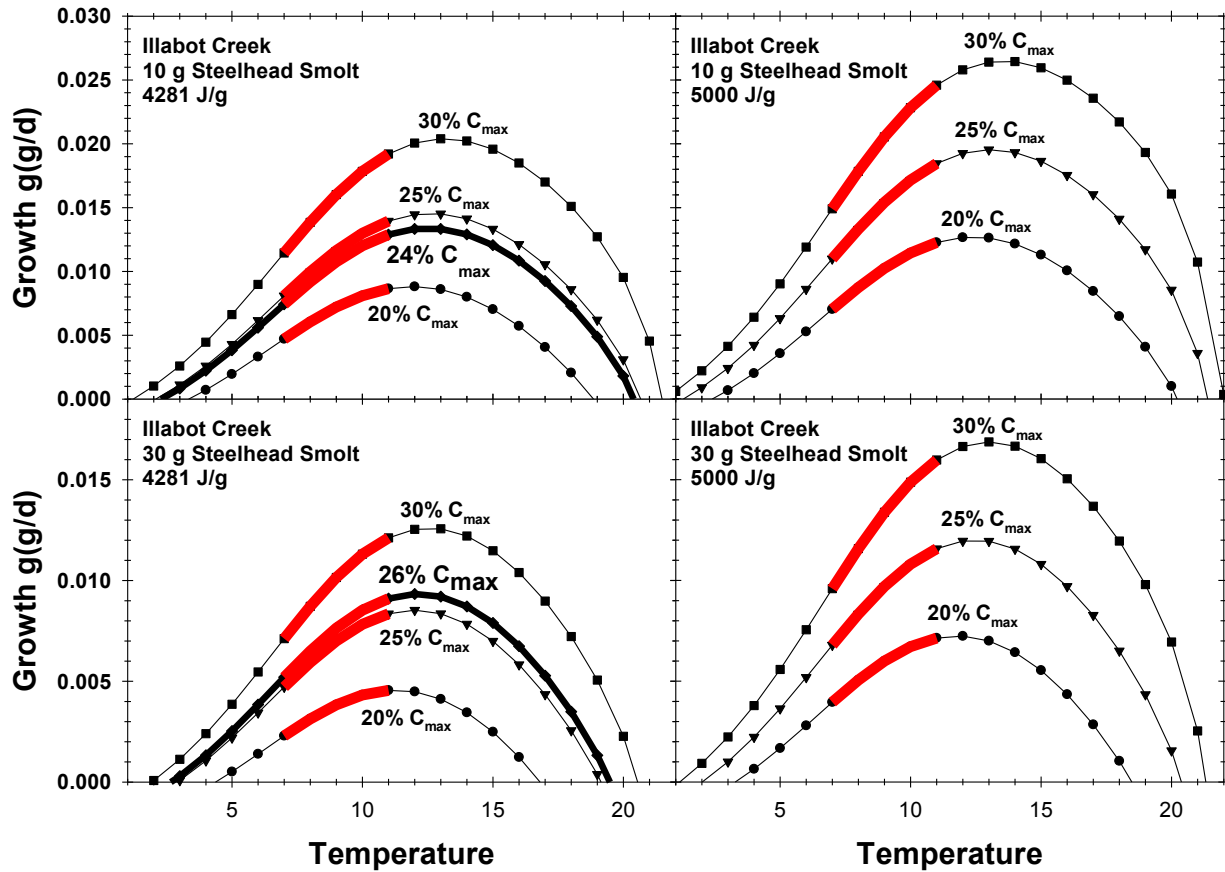


Figure 5. Change in daily growth rate in response to temperature and feeding rate for 10 g (top; age 1–2) and 30 g (bottom; age 2–3) Steelhead feeding on a composite diet with a mean energy density of 4,281 J/g wet weight (left panels) and 5,000 J/g (right panels). The highlighted portion of each curve indicates the thermal experience for Steelhead during the summer fast growth period in Illabot Creek (7° C – 11° C). Bold curves indicate the summer scope of growth for Steelhead that survived to adulthood given estimated summer prey energy density and simulated mean annual feeding rate (larger font).

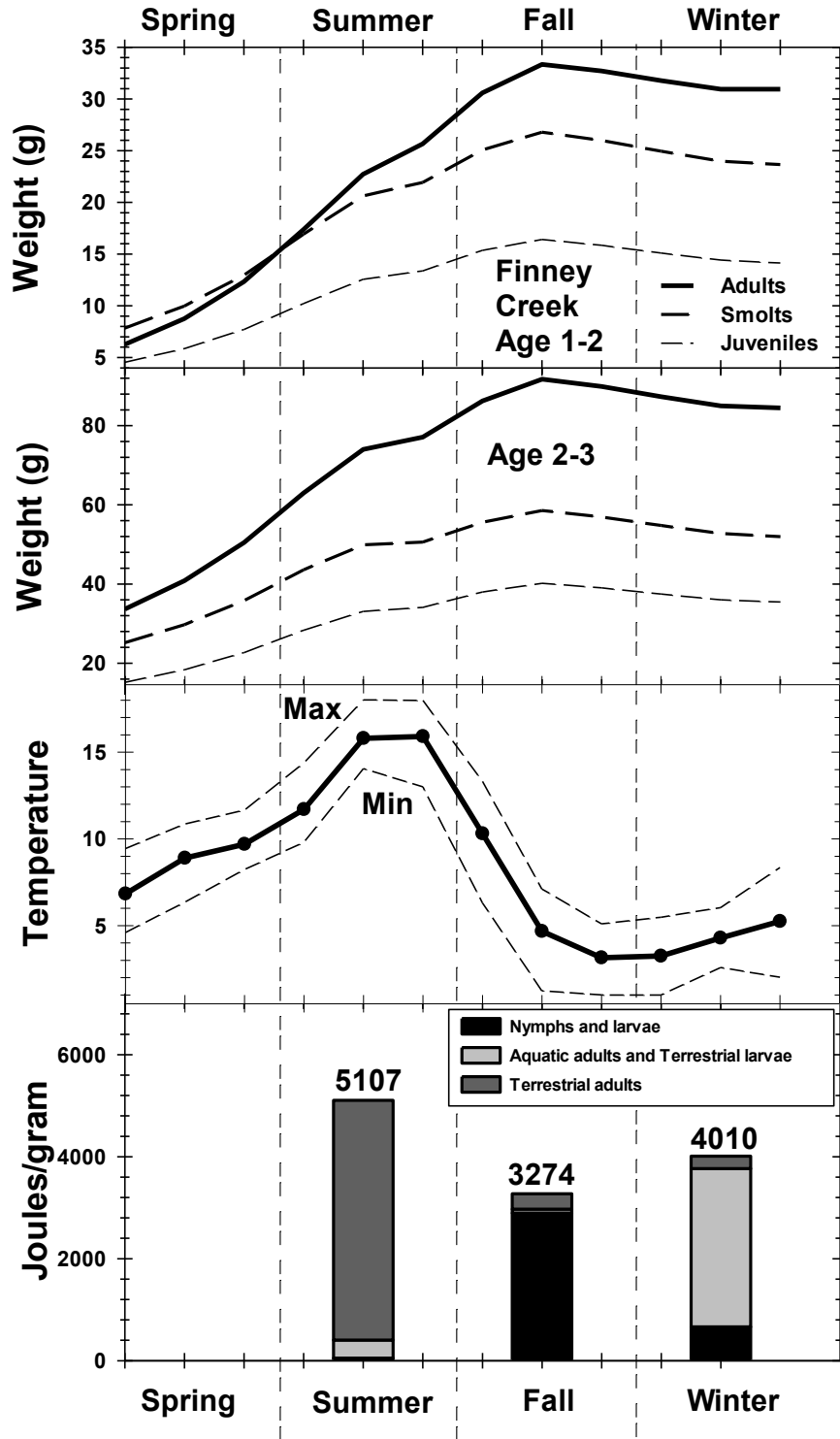


Figure 6. Bioenergetics simulation results of annual growth trajectories for age 1–2 and 2–3 Steelhead sampled as juveniles, smolts, and adults, mean monthly water temperatures (min, max), and seasonal composite prey energy densities for summer, fall, and winter in Finney Creek.

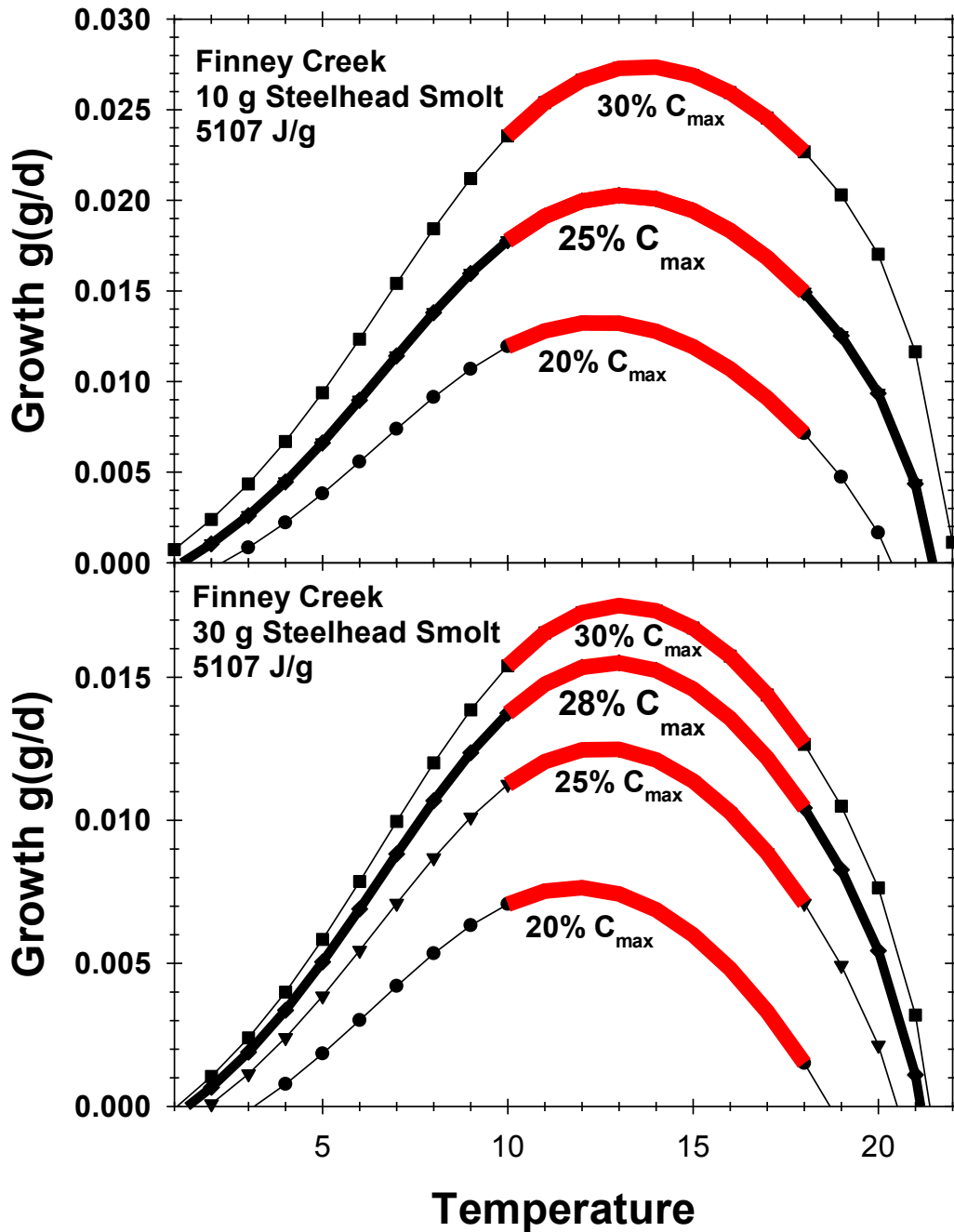


Figure 7. Change in daily growth rate in response to temperature and feeding rate for 10 g (top; age 1–2) and 30 g (bottom; age 2–3) Steelhead feeding on a composite diet with a mean energy density of 5,107 J/g wet weight. The highlighted portion of each curve indicates the thermal experience for Steelhead during the summer fast growth period in Finney Creek (10° C – 18° C). Bold curves indicate the summer scope of growth for Steelhead that survived to adulthood given estimated summer prey energy density and simulated mean annual feeding rate (larger font).

Table 1. Summary statistics for Steelhead captured as juveniles, smolts, and adults in Bacon, Illabot, and Finney creeks. Fork lengths are the mean \pm SE.

| Precipitation Zone | Sample Site (FW Age) | Juvenile | | Smolt | | Adult |
|--------------------|-----------------------------|----------|--------------|----------|--------------|----------|
| | | <i>n</i> | FL (mm) | <i>n</i> | FL (mm) | <i>n</i> |
| Snow | Bacon Creek | | | | | |
| | 1 | 4 | 108 \pm 9 | 1 | 131 | |
| | 2 | 4 | 147 \pm 5 | 16 | 161 \pm 3 | |
| | 3 | | | 11 | 187 \pm 3 | |
| | 4 | | | 3 | 207 \pm 5 | |
| Mix-Cool | Illabot Creek | | | | | |
| | 0 | 54 | 54 \pm 1 | | | |
| | 1 | 18 | 98 \pm 4 | | | |
| | 2 | 5 | 138 \pm 10 | 69 | 174 \pm 2 | |
| | 3 | 3 | 176 \pm 20 | 41 | 192 \pm 2 | |
| | 4 | | | 2 | 196 \pm 25 | |
| Snow/Mix-Cool | Upper Skagit River mainstem | | | | | |
| | 2 | | | | | 12 |
| | 3 | | | | | 17 |
| | 4 | | | | | 2 |
| | 5 | | | | | 1 |
| Mix-Warm | Finney Creek | | | | | |
| | 0 | 113 | 51 \pm 1 | | | |
| | 1 | 14 | 90 \pm 5 | 3 | 139 \pm 10 | 1 |
| | 2 | 16 | 130 \pm 3 | 15 | 162 \pm 4 | 18 |
| | 3 | 10 | 168 \pm 10 | 9 | 183 \pm 5 | 8 |
| | 4 | | | 1 | 213 | 4 |

Table 2. Prey energy densities by taxa and by energy groups used in energy delivery analysis and bioenergetics model simulations (McCarthy et al. 2009). Fifteen-percent of each energy group was considered indigestible in bioenergetics model simulations.

| Energy density category | Taxa | Energy density (J/g) | Energy Group | Mean Energy Density (J/g) |
|-------------------------|-------------------------|----------------------|--------------------------------------|---------------------------|
| Low-energy | *Diptera Larvae/Nymph | 2,911 | Aquatic Nymph and Larvae | 3,072 |
| | **Trichoptera Larvae | 3,509 | | |
| | Ephemeroptera Nymph | 3,076 | | |
| | Plecoptera Nymph | 3,076 | | |
| | Annelida | 2,789 | | |
| Medium-energy | Winged Insect | 4,225 | Aquatic Adult and Terrestrial Larvae | 4,249 |
| | Terrestrial Larvae | 4,272 | | |
| High-energy | Coleoptera Adult | 6,387 | Terrestrial Adult | 5,761 |
| | Other Terrestrial Adult | 5,134 | | |

*Mean of larval and nymph stages

**Mean of soft and rigid body forms

Table 3. Bioenergetics simulation inputs (growth [G]: $W_f - W_i$) and outputs (feeding rate [%Cmax], and consumption [C]) for simulations conducted on fish captured at different life stages for growth estimated between ages 1 and 2, and 2 and 3. Sites were stratified by precipitation zone (snow or mix), and relative water temperature regime (cool or warm).

| Precipitation Zone | Sample Site | Life Stage Sample Group | Age | n | W _i | W _f | % Cmax | G | C |
|---------------------|--------------------|-------------------------------|------------|---------|----------------|----------------|--------------|--------------|----------------|
| Snow | Bacon Creek | Juveniles | 1-2 | 4 | 5.7 | 16.9 | 0.23 | 11.2 | 126.0 |
| | | Smolts | 1-2 | 30 | 6.1 | 20.0 | 0.24 | 13.9 | 143.9 |
| | | Juveniles Smolts | 2-3 2-3 | 0 14 | N/A 20.0 | N/A 40.0 | N/A 0.25 | N/A 20.0 | N/A 274.0 |
| | Upper Skagit River | Adults | 1-2 | 31 | 5.4 | 22.3 | 0.25 | 16.9 | 154.2 |
| | | | 2-3 | 19 | 22.3 | 53.9 | 0.27 | 31.6 | 347.8 |
| | Mix-Cool | Illabot Creek | Juveniles | 1-2 | 8 | 4.8 | 15.8 | 0.22 | 11.0 |
| Smolts | | | 1-2 | 112 | 5.0 | 21.0 | 0.24 | 16.0 | 131.2 |
| Juveniles Smolts | | | 2-3 2-3 | 3 43 | 15.8 21.0 | 44.9 47.4 | 0.26 0.26 | 29.1 26.4 | 262.7 281.5 |
| Upper Skagit River | | Adults | 1-2 | 32 | 5.4 | 22.2 | 0.24 | 16.8 | 137.9 |
| | | | 2-3 | 20 | 22.2 | 53.7 | 0.26 | 31.5 | 311.5 |
| Mix-Warm | | Finney Creek | Juveniles | 1-2 | 25 | 4.2 | 14.4 | 0.21 | 10.2 |
| | Smolts | | 1-2 | 25 | 7.3 | 24.1 | 0.22 | 16.8 | 216.5 |
| | Adults | | 1-2 | 30 | 5.6 | 31.8 | 0.25 | 26.2 | 257.3 |
| | | Juveniles Smolts Adults | 2-3 | 10 | 14.4 | 36.0 | 0.23 | 21.6 | 315.3 |
| | | | 2-3 | 10 | 24.1 | 52.7 | 0.25 | 28.6 | 443.9 |
| | | | 2-3 | 12 | 31.8 | 86.1 | 0.28 | 54.3 | 659.4 |

Table 4. Seasonal sample size, FL (\pm SD), and condition factor K (\pm SD) for fish sampled as juveniles at freshwater ages 1 (age group 1–2) and 2 (age group 2–3) in each sample site.

| Sample Site | Freshwater | | <i>n</i> | FL (mm) | <i>K</i> |
|---------------|------------|--------|----------|--------------|-----------------|
| | Age | Season | | | |
| Bacon Creek | 1 | Summer | 2 | 104 \pm 25 | 1.38 \pm 0.02 |
| | | Fall | 2 | 113 \pm 18 | 1.37 \pm 0.10 |
| | 2 | Summer | 2 | 144 \pm 9 | 1.26 \pm 0.04 |
| | | Fall | 2 | 150 \pm 13 | 1.35 \pm 0.10 |
| Illabot Creek | 1 | Summer | 5 | 83 \pm 12 | 1.27 \pm 0.16 |
| | | Fall | 13 | 95 \pm 14 | 1.24 \pm 0.13 |
| | | Winter | 5 | 113 \pm 10 | 0.99 \pm 0.07 |
| | 2 | Fall | 4 | 132 \pm 9 | 1.16 \pm 0.06 |
| | | Winter | 2 | 149 \pm 35 | 1.01 \pm 0.04 |
| Finney Creek | 1 | Summer | 12 | 100 \pm 7 | 1.08 \pm 0.08 |
| | | Fall | 7 | 79 \pm 14 | 1.22 \pm 0.14 |
| | 2 | Summer | 6 | 133 \pm 14 | 1.10 \pm 0.08 |
| | | Fall | 7 | 134 \pm 12 | 1.25 \pm 0.07 |
| | | Winter | 1 | 100 N/A | 1.18 N/A |