

**Steelhead Recycling in the Willamette River and the Influence of
Freshwater and Ocean Growth on Age at Maturity of Steelhead**

A Thesis

Presented in Partial Fulfillment of the Requirements for the

Degree of Master of Science

with a

Major in Natural Resources

in the

College of Graduate Studies

University of Idaho

by

Charles S. Erdman

Major Professor: Christopher C. Caudill, Ph.D.

Committee Members: Michael C. Quist, Ph.D.; Timothy R. Johnson, Ph.D.

Department Administrator: Lisette P. Waits, Ph.D.

December 2016

Authorization to Submit Thesis

This thesis of Charles S. Erdman, submitted for the degree of Master of Science with a Major in Natural Resources and titled “Steelhead Recycling in the Willamette River and the Influence of Freshwater and Ocean Growth on Age at Maturity of Steelhead,” has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor: _____ Date: _____

Christopher C. Caudill, Ph.D.

_____ Date: _____

Michael C. Quist, Ph.D.

_____ Date: _____

Timothy R. Johnson, Ph.D.

Department Administrator: _____ Date: _____

Lisette P. Waits, Ph.D.

Abstract

Rainbow Trout *Oncorhynchus mykiss* are of conservation and management interest because of their genetic diversity, facultatively anadromous life histories, and importance to recreational fisheries. Summer steelhead, the anadromous form of Rainbow Trout, have been introduced to novel basins to increase recreational fishing opportunities. However, these introductions can pose threats to endemic populations of steelhead; thus, these programs must be evaluated to determine if releases lead to potential impacts on endemic populations. Steelhead also display greater life history diversity compared to most anadromous salmonids, and understanding the mechanisms that produce life history variability is important. This thesis sought to characterize the movement and fate of adult non-local hatchery-produced summer steelhead released back to tributaries of the Willamette River, Oregon. I also examined the importance of freshwater and ocean growth in producing life history variability in steelhead. Jointly, the objectives contribute to refining the management and conservation of steelhead.

Acknowledgements

First, I thank my advisor, Christopher C. Caudill. Chris' enthusiastic nature in thinking about interesting and difficult management and ecological questions was valuable in defining my thinking. I thank him for his patience, guidance, and unwavering support. I appreciate his attention to the scientific process and teaching me the finer details of how to use this process to answer important management and ecological questions.

I also thank my committee members Michael C. Quist and Timothy Johnson for their assistance and guidance.

I owe a great deal to the professionals of the Fish Ecology Research Laboratory and the University of Idaho. Without their support this research would not have been possible. Specifically, I would like to thank Grant Brink, Tim Blubaugh, Matt Knoff, and Mark Morasch for their assistance in tagging summer steelhead and maintaining radiotelemetry arrays. I thank George Naughton for his supervision and humor and Mike Jepson for answering all of my questions about coding, grilling, and life. Tami Clabough helped in database maintenance and upkeep, for which I am thankful. Finally, I thank Matt Keefer and Tracy Bowerman for providing analytical guidance.

I thank the United States Army Corps of Engineers for funding the work in the Willamette River basin and numerous Oregon Department of Fish and Wildlife personnel who assisted in summer steelhead tagging.

Many thanks go to Dean Peard, British Columbia Ministry of the Environment, for providing Nass River and Skeena River steelhead data. I appreciate your willingness to collaborate with me.

I thank Heather Hendrixson with The Nature Conservancy for developing my interest in fisheries work and for being a wonderful mentor.

Thank you to Lee Spencer for his appreciation of the wildness of natural-origin steelhead and his protection of this wildness.

Finally, thanks to Elizabeth Ng for encouraging me to pursue my passion and curiosity of steelhead.

Dedication

This work is dedicated to my parents, sisters, and grandparents.

Table of Contents

Authorization to Submit Thesis	ii
Abstract	iii
Acknowledgements	iv
Dedication	vi
Table of Contents	vii
List of Tables	ix
List of Figures	xi
Chapter 1: General Introduction	1
Thesis Structure	5
References	5
Chapter 2: Release of Hatchery-origin Adult Steelhead for Angler Opportunity Increases	
Potential for Interactions with Endemic Steelhead	13
Summary	13
Introduction	14
Methods	18
Results	23
Discussion	26
Acknowledgements	34
Author Contributions	35

References.....	35
Chapter 3: Length at Ocean Entry and First Ocean Winter Growth Influence Age at Maturity in Populations of Steelhead (<i>Oncorhynchus mykiss</i>).....	60
Abstract.....	60
Introduction.....	61
Methods.....	65
Results.....	73
Discussion.....	75
Acknowledgements.....	87
References.....	87
Chapter 4: General Conclusions	119

List of Tables

Table 2.1. The number, fate, and straying rate of non-local male and female radio-tagged recycled summer-run steelhead in the (A) Middle Fork Willamette River and (B) South Santiam River, Oregon, 2012-2014. Sex was not estimated in 2012 (i.e., unknown). Sex assignment was conducted during tagging.	52
Table 2.2. Parameter estimates and 95% confidence intervals for the logistic regression model that predicted the fate of non-local summer-run steelhead recycled below Dexter Dam in the Middle Fork Willamette River, Oregon. Odds expressed as odds of being harvested compared to remaining in a river. Parameter estimates shown in bold have 95% confidence intervals that do not include 1.	53
Table 2.3. Estimated odds ratios and 95% confidence intervals for the multinomial logistic regression model of fate (angled, recaptured at hatchery, remained in river) including sex, release location (release rkm), year, and release day covariates for non-local summer-run steelhead recycled below Foster Dam in the South Santiam River, Oregon. Parameter estimates shown in bold have 95% confidence intervals that do not include 1.	54
Table 2.4. Annual estimates of the number of recycled non-local summer-run steelhead harvested and remaining in a river based on the fates of radio-tagged steelhead recycled below Foster Dam, South Santiam River, Oregon and annual estimated escapement of winter steelhead to the South Santiam River. Winter steelhead escapement from Jepson et al. 2013, 2014, and 2015. 95% confidence interval in parentheses. Estimates are not corrected for reporting biases, tag retention rate, or tag-related mortality.	55
Table 3.1. Number of summer and winter steelhead from the Skeena, Nass, and Willamette River used to analyze the influence of ocean growth on age at maturity. Life history type	

refers to the number of years spent in freshwater (left of period) and the ocean (right on period) before returning to freshwater to spawn. 106

Table 3.2. Candidate logistic regression models fit to age at maturity for Skeena, Nass, and Willamette River summer and winter steelhead. Loe = length at ocean entry. Gs1 = first ocean summer growth. Gw1 = first ocean winter growth. Gs2 = second ocean summer growth. L2 = length at the end of the second ocean summer. POP = population. Rel = relative growth increment. BIC = Bayesian information criterion. 107

Table 3.3. Summary of results from a logistic regression model predicting the age at maturity of summer and winter steelhead from the Skeena, Nass, and Willamette rivers. The explanatory variables included in the model were length at ocean entry (Loe), first ocean winter growth (Gw1), and population (POP). Coefficients expressed as odds of maturing after two ocean years versus three ocean years. Parameter estimates shown in bold have 95% confidence intervals that do not include 1. 109

List of Figures

Figure 2.1. Map of Willamette River basin, Oregon showing release sites (stars) and locations of fixed radiotelemetry receivers (circles).....	56
Figure 2.2. Fate of non-local radio-tagged summer-run steelhead recycled in the Middle Fork Willamette River (left) and South Santiam River (right), Oregon 2012-2014. Sample size of each fate category is above each bar.....	57
Figure 2.3. Locations of last detections for 108 and 154 non-local radio-tagged summer-run steelhead recycled in the Middle Fork Willamette River (left) and South Santiam River (right), Oregon, respectively, that were assigned a fate of remaining in a river. Sample sizes for individual locations are above the bars.	58
Figure 2.4. Diagram illustrating acceptable harvest levels of non-local animals intentionally released and the associated ecological and social costs and benefits. Thicker boxes indicate scenario in Willamette River basin, Oregon where non-local summer-run steelhead are released and recycled to increase harvest opportunities.	59
Figure 3.1. Map of Skeena, Nass, and Willamette River basins. Black triangles indicate capture locations of summer and winter steelhead used in the study.	110
Figure 3.2. Scale of a mature 4.2 summer steelhead from the Skeena River, British Columbia. Loe = length at ocean entry. Gs1 = first ocean summer growth. Gw1 = first ocean winter growth. Gs2 = second ocean summer growth. L2 = length at the end of the second ocean summer.....	111
Figure 3.3. Estimated length at ocean entry for steelhead from four populations. Sample size is located above each box.	112

- Figure 3.4. Estimated ocean growth for steelhead from four populations. Sample size is located above each box. 113
- Figure 3.5. Relationship between estimated length at ocean entry (mm) and estimated first ocean winter growth (mm) for four populations of steelhead. Points = observed data. Lines = fitted linear regression for each population. Shaded areas represent 95% confidence intervals. 114
- Figure 3.6. The probabilities of maturing after two ocean years for Skeena River summer steelhead, Nass River summer steelhead, Willamette River winter steelhead, and Willamette River summer steelhead across the observed range of estimated length at ocean entry. Estimated growth during the first ocean winter is held at the mean observed value (88.89 mm) while estimated length at ocean entry varies. Shaded areas represent 95% confidence intervals. Vertical line represents mean observed length at ocean entry (188.00 mm). 115
- Figure 3.7. The probabilities of maturing after two ocean years for Skeena River summer steelhead, Nass River summer steelhead, Willamette River winter steelhead, and Willamette River summer steelhead across the observed range of estimated first ocean winter growth. Estimated length at ocean entry is held at the mean observed value (188.00 mm) while estimated first ocean winter growth varies. Shaded areas represent 95% confidence intervals. Vertical line represents mean observed length at ocean entry (88.89 mm). 116
- Figure 3.8. First ocean winter growth when the probability of maturing equals 50% for four winter and summer steelhead populations. 95% confidence intervals calculated using a nonparametric bootstrap percentile method, with 1,000 replications. 117
- Figure 3.9. Summary of habitat characteristics and steelhead age, weight, and feeding rate differences in the Gulf of Alaska and the central North Pacific Ocean. We hypothesize that

differences could lead to faster winter growth for steelhead in the central North Pacific
Ocean, which, given the observed results, could lead to younger age at maturity. 118

Chapter 1: General Introduction

North American Pacific salmon and trout *Oncorhynchus* spp. serve important ecological, economic, and social roles throughout their range (Behnke 2002; Quinn 2005). However, many populations have experienced substantial declines in abundance and reductions in their distributions due habitat degradation and fragmentation, introductions of nonnative species, and factors related to climate change (Slaney et al. 1996; Thurow et al. 2007; Wegner et al. 2011; Penaluna et al. 2016). As a result, many species and subspecies are of conservation concern (ICUN 2016) and are protected by state, federal, or provincial laws (U.S. Endangered Species Act; Canada Species at Risk Act). Therefore, addressing both management- and ecological-related questions is critical for the effective management and conservation of imperiled Pacific salmon and trout populations.

Rainbow Trout *O. mykiss* are of particular conservation and management interest because of their genetic diversity (Currens et al. 2009), facultatively anadromous life histories (Kendall et al. 2015), and importance to recreational fisheries (Brown et al. 1965; Gordon et al. 1973; Donnelly et al. 1985). Rainbow Trout are native to western North America and are now ubiquitous throughout cold-water habitats due mainly to introductions for recreational purposes (Behnke 2002). Persistence in highly dynamic landscapes has resulted in substantial diversity within the species (Minckley et al. 1986; Currens et al. 2009). Glacial, volcanic, and tectonic forces produced geological and hydrological fluctuations throughout the Pacific Rim (McKee 1972; Orr and Orr 2006) that have shaped the evolutionary ecology of Rainbow Trout in their native range (Currens et al. 2009; Blankenship et al. 2011). Genetic differences exist between coastal and inland groups west and east of the Cascade Mountains (Allendorf 1975; Busby et al. 1996), and inland groups

also display different genetic patterns (Currens et al. 2009; Blankenship et al. 2011).

Although major evolutionary groups warrant subspecies recognition (Behnke 2002; Currens et al. 2009), the exact taxonomic classification remains unsettled. Currently, native Rainbow Trout occurring to the west of Cascade and Sierra Nevada mountain ranges are classified as coastal Rainbow Trout *O. mykiss irideus* and those occurring to the east are classified as Redband Trout. Subspecies of Redband Trout were classified by Behnke (2002), have been widely recognized and applied to the management of Redband Trout, and consist of populations from the Columbia and Fraser rivers *O. mykiss gairdneri*, the northern Great Basin and Upper Klamath Lake drainages *O. mykiss newberrii*, and the Pit and McCloud River basins *O. mykiss stonei*.

Rainbow Trout exhibit both anadromous and resident life histories. Individuals that adopt an anadromous life history are known as steelhead. Both coastal Rainbow Trout and Redband Trout have sea-going life histories (Behnke 2002). Juveniles can spend 1-7 years in freshwater before adopting an anadromous or resident life history pathway (Pevan et al. 1994). Variability in the length of ocean residency also exists for steelhead (Moore et al. 2014; Hodge et al. 2016). The extraordinary life history diversity compared to most anadromous salmonids reflects fitness tradeoffs. For example, delayed smoltification increases size at ocean entry and the probability of survival (Ward and Slaney 1988; Henderson and Cass 1991), but postpones the growth and fecundity benefits of ocean productivity. Delayed maturation increases body size, which may improve migratory capacity, spawning ability, and fecundity (Gross 1985; Fleming and Gross 1994; Quinn 2005), but decreases the probability of survival to reproduction. The frequency of studies investigating the mechanisms that influence life history diversity in *O. mykiss* has increased

substantially over the last ten years (reviewed by Kendall et al. 2015). A complex combination of genetics, condition, and environmental factors affect life history diversity in *O. mykiss* (Kendall et al. 2015). Life history diversity influences demographic stability and resiliency and can dampen the effects of poor year classes (Green et al. 2010; Schindler et al. 2010; Moore et al. 2014; Schroeder et al. 2016). The timing of life history transitions among individuals within and among populations is important for understanding population demographics and can provide insight on the mechanisms associated with the decision to undergo these transitions (Policansky 1983).

Two different run types of steelhead exist: summer-run and winter-run (hereafter, summer and winter steelhead). The fundamental difference between summer and winter steelhead is the state of sexual maturity of the fish upon freshwater entry (Burgner et al. 1992). The gonads of summer steelhead are only slightly developed upon freshwater entry and winter steelhead enter with well-developed gonads. Summer steelhead generally return to freshwater from May—October, winter steelhead return from November—April, and both run types generally spawn in the spring. Therefore, summer steelhead generally reside in freshwater for months prior to spawning while winter steelhead spawn shortly after entering freshwater (Shapovalov and Taft 1954). Migration behavior among steelhead populations has likely evolved to provide optimal fitness for specific habitats, and migration timing (i.e., winter or summer return) is at least partially controlled by genetic heterogeneity (Hess et al. 2016).

Popular recreational fisheries exist for steelhead throughout their range (Hooton 2011). However, many populations throughout the historic range of steelhead have experienced significant declines over the last century, and in the U.S. alone, 11 of 15 Distinct

Population Segments are listed as either threatened or endangered under the Endangered Species Act (NOAA 2015). Due to population declines and the importance of recreational fisheries for steelhead, artificial propagation (i.e., hatchery production) of steelhead for both harvest and conservation purposes has been widespread. Furthermore, populations have undergone extensive human-induced transfers to novel basins, often to fulfill harvest objectives. For example, summer steelhead artificially cultivated from the Washougal River (enters the Columbia River at river kilometer [rkm] 195) and Klickitat River (enters the Columbia River at rkm 290) beginning in 1956 at the Skamania Hatchery, Washington (Crawford 1979) were subsequently released in novel tributaries throughout Oregon, Washington, and California to provide recreational opportunities (Howell et al. 1985). These transfers included introductions to areas previously lacking summer-run steelhead and also areas with indigenous summer-run populations. The release of non-local, hatchery-produced genotypes can be detrimental to endemic populations (Araki et al. 2007). Therefore, segregation between populations of the two run types is required where the endemic populations are listed under the Endangered Species Act (ESA; NMFS 2008). Management strategies associated with the artificial propagation of steelhead need to be assessed to determine potential impacts to endemic populations.

Given the ecological and management importance of steelhead life history diversity and the concern that hatchery programs may increase interactions between non-local and endemic populations, this thesis had two main objects. The first objective was to document and characterize the post-release movement and fate of non-local hatchery-origin adult steelhead released to tributaries of the Willamette River, Oregon. The second objective was

to examine the influence of freshwater and seasonal ocean growth in age at maturity for four steelhead populations.

Thesis Structure

This thesis includes four chapters. The second chapter assesses the effectiveness of a hatchery-related program in the Willamette River whereby adult steelhead are collected at acclimation sites and then released back to ongoing fisheries. Chapter two will be submitted to the *North American Journal of Fisheries Management*. The third chapter investigates the relationship between freshwater and ocean growth in predicting age at maturity for steelhead and explores two different conceptual models for describing age at maturity: a carryover effect model versus a conditional strategy model. Chapter three will be submitted to the *Canadian Journal of Aquatic and Fisheries Science*. The final chapter is a general conclusion that summarizes the chapters as they relate to the ecology and management of steelhead.

References

- Allendorf, F. W. 1975. Genetic variability in a species possessing extensive gene duplication: genetic interpretation of duplicate loci and examination of genetic variation in populations of rainbow trout. Doctoral dissertation. University of Washington, Seattle.
- Behnke, R. J. 2002. Trout and salmon of North America. The Free Press, New York.
- Blankenship, S. M., M. R. Campbell, J. E. Hess, M. A. Hess, T. W. Kassler, C. C. Kozfkay, A. P. Matala, S. R. Narum, M. M. Paquin, M. P. Small, J. J. Stephenson, K. I. Warheit,

- and P. Moran. 2011. Major lineages and metapopulations in Columbia River *Oncorhynchus mykiss* are structured by dynamic landscape features and environments. *Transactions of the American Fisheries Society* 140:665–684.
- Brown, W. G., A. K. Singh, and E. N. Castle. 1965. An economic evaluation of the Oregon salmon and steelhead sport fishery. *Journal of Wildlife Management* 22(9), 266-279.
- Burgner, R. L., J. T. Light, L. Margolis, T. Okazaki, A. Tautz, and S. Ito. 1992. Distribution and origins of steelhead trout (*Oncorhynchus mykiss*) in offshore waters of the North Pacific Ocean. *International North Pacific Fisheries Commission Bulletin* 51.
- Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of West Coast steelhead from Washington, Idaho, Oregon, and California. National Oceanic and Atmospheric Administration Technical Memorandum NMFS-NWFSC-27.
- Crawford, B. A. 1979. The origin and history of the trout brood stocks of the Washington Department of Game. Washington State Game Dep., Fishery Research Report, 76 p. (Available from Washington Department of Fish and Wildlife, 600 Capital Way N., Olympia, WA 98501.)
- Currens, K. P., C. B. Schreck, and H. W. Li. 2007. Evolutionary diversity in Redband Trout. Pages 10–11 *in* R. K. Schroeder and J. D. Hall, editors. *Redband Trout: resilience and*

challenge in a changing landscape. American Fisheries Society, Oregon Chapter, Corvallis.

Currens, K. P., C. B. Schreck, and H. W. Li. 2009. Evolutionary ecology of Redband Trout. *Transactions of the American Fisheries Society* 138:797–817.

Donnelly, D. M., J. B. Loomis, C. F. Sorg, and L. J. Nelson. 1985. Net economic value of recreational steelhead fishing in Idaho. USDA Forest Service. Rocky Mountain Forest and Range Experiment Station. Fort Collins, CO. Resource Bulletin RM-9. April 1985.

Flemming, I.A. and M. R. Gross. 1994. Breeding competition in a Pacific salmon (Coho: *Oncorhynchus kisutch*) Measures of natural and sexual selection. *Evolution* 48:637–657.

Gordon, D., D. W. Chapman, and T. C. Bjornn. 1973. Economic evaluation of sport fisheries- What they mean. *Transactions of the American Fisheries Society* 2:293–311.

Greene C. M., J. E. Hall, K. R. Guilbault, T. P. Quinn, and R. Guilbault. 2010. Improved viability of populations with diverse life-history portfolios. *Biology Letters* 6:382–386.

Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. *Nature* 313:47–48.

- Henderson, M. A. and A. J. Cass. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 48:988–994.
- Hess, J. E., J. S. Zendt, A. R. Matala, and S. R. Narum. 2016. Genetic basis of adult migration timing in anadromous steelhead discovered through multivariate association testing. *Proceedings of the Royal Society B Biological Sciences* 283: 20153064.
- Hodge, B. W., M. A. Wilzbach, W. G. Duffy, R. M. Quiñones, and J. A. Hobbs. 2016. Life History Diversity in Klamath River Steelhead. *Transactions of the American Fisheries Society* 145:227–238.
- Hooton, R. S. 2011. *Skeena Steelhead: Unknown Past, Uncertain Future*. Frank Amato Publications, Portland, Oregon.
- Howell, P., K. Jones, D. Scarnecchia, L. LaVoy, W. Kendra, and D. Ortmann. 1985. Stock assessment of Columbia River anadromous salmonids Volume II: Steelhead stock summaries stock transfer guidelines—information needs. Final Report to Bonneville Power Administration, Contract DE-AI79-84BP12737, Project 83-335, 1032 p. (Available from Bonneville Power Administration, P.O. Box 3621, Portland, OR 97208.)
- IUCN (International Union for the Conservation of Nature). 2016. IUCN Red List of Threatened Species. Version 2016-1. Available: www.iucnredlist.org. (July 2016).

- Kendall, N. W., J. R. McMillan, M. R. Sloat, T. W. Buehrens, T. P. Quinn, G. R. Pess, K. V. Kuzishchin, M. M. McClure, and R. W. Zabel. 2015. Anadromy and residency in steelhead and rainbow trout *Oncorhynchus mykiss*: a review of the processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 72:319–342.
- McKee, B. 1972. *Cascadia—the geological evolution of the Pacific Northwest*. McGraw-Hill, New York.
- Minckley, W. L., D. A. Hendrickson, and C. E. Bond. 1986. Geography of western North American freshwater fishes: description and relationships to intracontinental tectonism. Pages 519–614 *in* C. H. Hocutt and E. O. Wiley, editors. *The zoogeography of North American freshwater fishes*. Wiley, New York.
- Moore, J. W., J. D. Yeakel, D. Peard, J. Lough, and M. Beere. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. *Journal of Animal Ecology* 83:1035–1046.
- NOAA (National Oceanic and Atmospheric Administration). 2015. Status review update for Pacific salmon and steelhead listed under the Endangered Species Act: Pacific Northwest. Northwest Fisheries Science Center.
- Orr, W. N., and E. L. Orr. 2006. *Geology of the Pacific Northwest*. Waveland Press, Long Grove, Illinois.

- Penaluna, B. E., A. Abadía-Cardoso, J. B. Dunham, F. J. García-Dé León, R. E. Gresswell, A. R. Luna, E. B. Taylor, B. B. Shepard, R. Al-Chokhachy, C. C. Muhlfeld, K. R. Bestgen, K. Rogers, M. A. Escalante, E. R. Keeley, G. M. Temple, J. E. Williams, K. R. Matthews, R. Pierce, R. L. Mayden, R. P. Kovach, J. C. Garza, and K. D. Fausch. 2016. Conservation of Native Pacific Trout Diversity in Western North America. *Fisheries* 41:286–300.
- Pevan, C. M., R. R. Whitney, and K. R. Williams. 1994. Age and length of steelhead smolts from the Mid-Columbia River Basin, Washington. *North American Journal of Fisheries Management* 14:77–86.
- Policansky, D. 1983. Size, age and demography of metamorphosis and sexual maturation in fishes. *American Zoologist* 23:57–63.
- Quinn, T. P. 2005. *The Behavior and Ecology of Pacific Salmon and Trout*. American Fisheries Society, Bethesda, Maryland.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465:609–612.
- Schroeder, R. K., L. D. Whitman, B. Cannon, and P. Olmsted. 2016. Juvenile life-history diversity and population stability of spring Chinook salmon in the Willamette River

Basin, Oregon. Canadian Journal of Aquatic and Fisheries Science doi:10.1139/cjfas-2015-0314

Shapovalov, L. and A. C. Taft. 1954. Life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. California Department of Fish and Game Fisheries Bulletin 98.

Slaney, T. L., K. D. Hyatt, T. G. Northcote, and R. J. Fielden. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries 21(10):20–35.

Thurrow, R. F., B. Rieman, D. C. Lee, P. J. Howell, and R. D. Perkinson. 2007. Distribution and status of Redband Trout in the interior Columbia basin and portions of the Klamath River and Great basins. Pages 28–46 in R. K. Schroeder and J. D. Hall, editors. Redband Trout: resilience and change in a changing landscape. American Fisheries Society, Oregon Chapter, Corvallis.

Ward, B. R. and P. A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. Canadian Journal of Fisheries and Aquatic Sciences 45:1110–1122.

Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, and A. F. Hamlet. 2011. Flow

regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences* 108:14175-14180.

Chapter 2: Release of Hatchery-origin Adult Steelhead for Angler Opportunity Increases Potential for Interactions with Endemic Steelhead

Summary

1. Translocation is often used to increase local abundance of fish and wildlife populations for conservation or harvest purposes, and effects of releases on recipient populations are context dependent. Release of non-local animals intended for harvest can have negative demographic, genetic, and ecological risks to endemic populations when not harvested.
2. In 2012-2014, we used radiotelemetry to monitor the fate and potential for interactions between non-local hatchery-origin adult summer-run steelhead *Oncorhynchus mykiss* ($n = 423$) and Endangered Species Act-listed native winter-run steelhead in two tributaries of the Willamette River, Oregon, USA. Summer steelhead were ‘recycled’—collected, translocated downstream, and released—to provide additional angler opportunity as a part of a regional mitigation program.
3. Overall, reported harvest rate of recycled steelhead was low (15%) and a majority of individuals (62%) were last recorded in the release tributary. Further, 14% of radio-tagged recycled steelhead were last detected outside the release tributary (i.e., strayed after release). Expanded estimates indicate the number of recycled summer-run steelhead remaining in the South Santiam River exceeded the winter-run steelhead spawning population size.
4. *Synthesis and applications.* Low reported harvest and straying and demographic estimates indicate the recycling program may have negative effects on endemic

winter-run steelhead. Translocation and hatchery supplementation are likely to remain important conservation and mitigation tools in the future, though these results highlight the importance of monitoring the fates of releases and considering the risks and benefits of translocations to endemic populations and communities.

Key words: endemic, harvest, hatchery, non-local, recycling, steelhead, translocation

Introduction

The intentional release of animals (i.e., translocation) to increase abundance for conservation or harvest is a widely applied management strategy for fish and wildlife populations.

Releases can buffer imperiled populations from extinction by creating self-sustaining populations (Griffith et al. 1989), reducing the effects of climate change through assisted colonization (Hoegh-Guldberg et al. 2008), and increasing genetic heterogeneity (Deredec & Courchamp 2007; DeMay et al. 2016). Programs may also be production-focused and enhance socially- and economically-important harvest opportunities (Allen 1956), which can both increase and decrease the risk of mortality to native populations. The release of animals outside their historic native range (i.e., introduction) or restocking of non-local conspecifics (i.e., genetically exotic populations; Armstrong & Seddon 2008; Champagnon et al. 2012) can have direct and indirect adverse effects on endemic biodiversity (Allendorf & Waples 1996; Gebhardt 1996; Westemeier et al. 1998; Christian & Wilson 1999; Sih 2010). Given the potential consequences associated with the release of non-local animals, the risk to locally-adapted populations can be substantial. Therefore, it is critical to understand the movement and fate of animals after intentional release.

Harvest of some managed species relies on augmentation through the continued intentional release of alien or non-local animals including birds, mammals, and fishes (Laikre et al. 2010) and often these animals are captive-bred or artificially propagated (hereafter hatchery-produced; Champagnon et al. 2012). A central implicit or explicit tenet is that the majority of released individuals are harvested, perish due to unsuitable environmental conditions or maladaptation due to domestication (Bereijikian & Ford 2004), or otherwise have minimum effects on recipient systems. In some cases, deliberate segregation from endemic populations is desired or required when non-local conspecifics are introduced (Mobernd et al. 2005; Naish et al. 2008) because individuals that escape harvest are expected to negatively affect local adaptations and population structure (Utter 2004). For example, Iberian populations of the red-legged partridge *Alectoris rufa* experience widespread hybridization with captive-reared birds released to increase hunting activity (Blanco-Aguilar et al. 2008) and segregation between wild and farm-raised individuals is necessary to minimize admixing and protect the genetic integrity of endemic partridge populations. Thus, the relative benefits of augmentation with artificially produced fish and wildlife versus risks posed by intentionally-released animals that avoid harvest depend on the ecological, conservation, and social context.

Salmon *Oncorhynchus* ssp. and steelhead *O. mykiss* have been artificially propagated to enhance harvest since the 1870s and propagation programs have frequently transferred broodstock across basins (Naish et al. 2008). Because salmon and steelhead populations display extensive life history diversity (Moore et al. 2014), adaptations to local freshwater

environments (Taylor 1991), and genetic structuring at small spatial scales (Waples et al. 2001), the release of non-local, hatchery-produced genotypes can be detrimental to endemic populations (Araki et al. 2007). Hatchery-produced summer-run steelhead (anadromous form of Rainbow Trout; SRS) have been widely stocked to non-native watersheds with endemic ecotypes. Beginning in 1956, hatchery SRS derived from two lower Columbia populations (Washougal and Klickitat rivers) were artificially cultivated at the Skamania Hatchery, Washington and released throughout Oregon, Washington, and California to provide recreational opportunity (Crawford 1979). Introductions occurred into areas with native winter-run steelhead (WRS), areas previously lacking SRS, and areas with indigenous summer-run populations. Segregation is often a requirement since listing of endemic populations under the U.S. Endangered Species Act (ESA; NMFS 2008) and because of potential negative effects to endemic populations (Chilcote et al. 1986; Leider et al. 1990; Kostow 2003). Thus, there is considerable interest in determining to what degree SRS management actions result in increased mixing between endemic and propagated non-local SRS populations.

Anadromous salmonid hatchery programs rely on the homing mechanism of salmon and steelhead (Hendry et al. 2004; Quinn 2005) whereby adults return to their hatchery of origin or a juvenile release site (i.e., acclimation site). Returns can exceed broodstock requirements, allowing managers to allocate surplus fish to other goals. One management action is recycling, where collected adults are released back to fisheries for additional angling opportunity (Lindsay et al. 2001; Kock et al. 2016). The implicit or explicit assumption is adults will home again and be recollected at a hatchery if not harvested. However, any SRS

not harvested or recaptured could increase competition for mates on spawning grounds, spawn with other hatchery-produced fish, or hybridize with endemic conspecifics locally or after straying to other basins (Araki et al. 2007; Berntson et al. 2011). The net effects of a recycling program could be detrimental in basins with endemic populations, depending on the degree to which recycled SRS avoid harvest and their distribution and behavior during spawning. Recycling protocols may influence the fate and distribution of recycled fish. For example, we expected earlier release and release further downstream from the collection site would result in higher harvest rates through greater additional exposure to fisheries.

Therefore, some recycling protocols could increase the harvested proportion of recycled and decrease potential interactions with endemic conspecifics. Finally, comparison of the relative size of recycled and endemic populations during the spawning period is important because the potential effects on recipient populations is expected to increase as the ratio of released animals to endemics increases.

In this study, we: (i) used radiotelemetry to evaluate post-release fates of non-local SRS recycled in the Willamette River, Oregon, USA, (ii) altered the timing, location, and sex ratios of releases to explore whether varying these might be used to increase harvest of recycled SRS, and (iii) evaluated the potential demographic effects of recycling on endemic populations downstream of the collection site. Analyses were used to test two specific hypotheses. First, we tested the assumption that recycled steelhead return to their acclimation site a second time if not harvested. Second, we hypothesized that increasing the distance of releases from an acclimation site and earlier releases would result in increased exposure to harvest and higher capture rates. Finally, we compared expanded estimates of recycled

steelhead that avoid harvest to the estimated spawning population size of endemic steelhead populations.

Methods

Study Area.— Historically, late-run WRS were the only ecotype of steelhead present in the Willamette River upstream of Willamette Falls (205 river kilometers [rkm] from the Pacific Ocean; Fig. 2.1; Myers et al. 2006; Van Doornik et al. 2015) because the Falls restricted passage except during winter and spring high flows (Clemens 2015). Construction of a fish ladder at the falls in 1885 (Kostow 1995) later allowed for the introduction and subsequent colonization of SRS in the upper Willamette River (UWR; Keefer & Caudill 2010; ODFW & NMFS 2011). Summer steelhead were introduced to the UWR in 1966 by the Oregon Department of Fish and Wildlife (ODFW) to mitigate loss of WRS spawning and rearing habitat after construction of Willamette Valley Project dams (ODFW 2004). Released SRS smolts (approximately 570,000 annually) are adipose clipped and are assumed to migrate rapidly through their release rivers (ODFW 2004). Since 1990, the average annual count of SRS passing Willamette Falls has been four times higher than WRS (ODFW 2015a). The UWR WRS distinct population segment was listed as threatened under the ESA in 1999 (NMFS 1999) and minimizing interactions between WRS and SRS has been identified as a conservation and management priority (NMFS 2008; ODFW & NMFS 2011). In the Willamette River basin, recycling has occurred in South Santiam River (SSR) since at least 1974 (ODFW 1975) and continues today in the North Santiam, SSR, and Middle Fork Willamette (MFW) rivers (Fig. 2.1).

Fish tagging.—SRS were trapped at Dexter Fish Collection Facility (Dexter; rkm 491.2) on the MFW and Foster Fish Collection Facility (Foster; rkm 418.2) on the SSR during June-August in 2012-2014 (Fig. 2.1). Adult fish traps at both collection facilities were operated by ODFW personnel and all trapped SRS were initially anesthetized (CO₂: Dexter and Foster 2012, 2013; AQUI-S 20E [active ingredient: 10% eugenol; AquaTactics Fish Health and Vaccines, Kirkland, Washington]: Foster 2014) and tagged dorsally with colored T-bar tags (Floy Tag Inc., Seattle) to indicate that they were to be recycled. A subsample was randomly selected, immediately placed in a 90- or 265-L plastic holding tank containing hatchery water and 5-10 mg/L AQUI-S 20E. University of Idaho personnel recorded sex based on morphology (only in 2013 and 2014) and fork length (FL; cm), and intragastrically inserted a uniquely-coded radio transmitter (model MCFT-3A; Lotek Wireless, Newmarket, Ontario; 6-s burst rate; 16 × 46 mm; 16 g in air; 455 day battery; Keefer et al. 2004). A 1-cm diameter ring of silicone tubing was used to increase transmitter retention (Keefer et al. 2004). Immediately after tagging, individual fish were either placed in a recovery tank for a minimum of 5 min (Dexter), loaded into ODFW hatchery trucks (Foster 2012, 2013) or sent down sorting pipes to holding ponds (Foster 2014) prior to release.

A US\$25 reward was offered in exchange for return of the radio tag and the corresponding harvest information (e.g., date and location of capture) in 2013 and 2014. Reward tags were not used in 2012 due to concerns rewards would increase angling pressure (Pollock et al. 2001; Pine et al. 2003; Kerns et al. 2016). All fish handling methods were approved by the University of Idaho Institutional Animal Care and Use Committee and permitted by the State of Oregon and the U.S. National Marine Fisheries Service.

Fish releases.—Releases generally occurred immediately after tagging. In the MFW, 140 steelhead were radio tagged over three years and released to the Dexter Dam tailrace. At Foster Dam, 283 fish were radio tagged and recycled to one of four sites in the SSR over three years. Fish collected at Foster were released at the Waterloo County Park in Waterloo, Oregon (Waterloo; rkm 395.6) and the Pleasant Valley Boat Ramp in Sweet Home, Oregon (Pleasant Valley; rkm 411.7) in all three study years. In 2013, SRS were also released to Wiley Creek (rkm 417). In 2014, fish were also released to the Foster Dam tailrace (rkm 418.1). Releases in MFW and SSR occurred in June, July, and August. The total radio-tagged samples in the SSR were 2.7% of all SRS recycled by ODFW below Foster across the three years. After 2012, ODFW restricted releases to only June and July in the SSR.

Monitoring movement.—Steelhead movements were monitored using a combination of fixed receiver sites and mobile tracking, as detailed in Keefer et al. (2015). Briefly, a minimum of 44 fixed-site radio receivers were distributed throughout the Willamette River basin each year (Fig. 2.1; Keefer et al. 2015). Receivers provided time-stamped detections that were assembled into a telemetry database each year. Fixed-site detections were supplemented with mobile tracking data collected by UI and ODFW crews using antennas mounted to vehicles. Mobile tracking occurred in the MFW from Dexter Dam to the confluence of the upper Willamette River (rkm 465.2) and in the SSR from Foster Dam to Waterloo, Oregon (rkm 395.6). Tracking occurred weekly during the summer when steelhead were released and the following late-winter/spring during spawning periods. Transmitter returns from fisheries, hatcheries, and traps were used to refine fish distribution and fate.

Fate assignments.—Fate classes differed between releases in the SSR and MFW basins due to differences in SRS management between the basins. Adults were classified to three fates in the SSR: (a) reported as harvested, (b) remained in a river, or (c) recaptured and removed at Foster. In the MFW classes (a) and (b) were used; (c) did not occur at Dexter Dam because all recaptured SRS were rereleased the tailrace. We assumed that individuals last detected by a fixed-site or during mobile tracking had remained in the river. Thus, this category included fish that remained in the river and spawned, died prior to spawning, were unreported harvest by anglers, or moved to another river without detection. Consequently, reported estimates may slightly underestimate harvest and straying. Twelve (4.5%) individuals tagged at Foster and 9 (6.0%) at Dexter were assigned an unknown fate and censored from all analyses because these individuals had no detections after release, their tag was recovered on the riverbank without the fish, or recapture data were not consistent with fixed-site detection data (e.g., no fixed-site detections in tributary where recapture was reported).

Straying behavior is defined as adult migration to and attempted reproduction at non-natal sites (Quinn 1993; Keefer and Caudill 2014). Because we were unable to directly quantify reproduction, a radio-tagged recycled steelhead was classified as a stray if it was last detected in-river but outside of the release tributary. Estimates of straying behavior of radio-tagged recycled steelhead were not corrected for detection efficiencies at the furthest-downstream telemetry receiver sites in the SSR and the MFW. Therefore, straying estimates are likely conservative.

Analyses.—The association between fate class and recycling-related management actions (e.g., release location) in each basin was evaluated using logistic regression (Hosmer et al. 2013). A logistic regression model for the MFW included covariates for sex, release day, and year. We used a multinomial logistic regression model of fate in the SSR in relation to sex, release day and location, and year. Release day was measured as days since 1 June, the typical start of recycling each year. Logistic regression analyses only included data from releases in 2013 and 2014 because sex was not estimated and reward tags were not used in 2012. Males were significantly larger than females (Dexter: $t = 4.67$, $df = 92.84$, $P < 0.001$; Foster: $t = 5.74$, $df = 92.35$, $P < 0.001$); therefore, FL was not included in the models. Likelihood-ratio tests were used to assess the significance of model covariates in influencing the fate of SRS recycled in each basin. We used chi-square tests of independence to evaluate whether straying rates were higher for males than females.

We compared estimates of population size for recycled SRS remaining in the SSR below Foster Dam to estimates of WRS population size for the same river reach (confluence of South and main Santiam rivers to Foster Dam). Annual numbers of recycled SRS by fate class were estimated by expanding observed proportions for each fate class in the radio-tagged samples by the total number recycled by ODFW. The total number of fish recycled annually by ODFW was corrected to account for double counting of SRS recycled more than one time (17.7%). To assess the 95% confidence limits for the estimates, a non-parametric bootstrap percentile method (Efron 1987) was used after the data were re-sampled 1,000 times. Annual values for WRS escapement were provided by a larger radio-telemetry study of WRS migration in the Willamette River during the same study period (Jepson et al. 2015).

The population size comparison was conducted only for the SSR basin because the MFW is outside the ESA-listed range of WRS, though recent evidence suggests WRS also spawn there (Jepson et al. 2015). All analyses were conducted using the R statistical computing language (R Development Core Team 2009).

Results

MFW.—The majority (77.1%; $n = 108$) of radio-tagged SRS recycled below Dexter Dam in the MFW remained in a river and proportions did not differ among years ($\chi^2 = 1.7$, $df = 2$, $P = 0.44$; Fig. 2.2). Approximately one in five adults strayed from the MFW into the main stem Willamette River or tributary outside the MFW ($n = 31$; 22.1% of all Dexter-released radio-tagged fish; Fig. 2.3). Approximately half of the fish that remained in the MFW were concentrated in the 5 km below Dexter Dam, and a third were last detected in the Dexter Dam tailrace. Females tended to stray more frequently than males, though this trend was not significant ($\chi^2 = 2.55$, $df = 1$, $P = 0.11$; Table 2.1). Only one (0.7%) individual displayed behavior consistent with post-spawn downstream movement (i.e., kelt behavior).

Reported harvest rates were similar to straying rates, with slightly more than one in five radio-tagged steelhead recycled in the MFW reported as harvested during the study ($n = 32$; 22.9%). Annual harvest varied from 19.2% in 2013 to 29.2% in 2014, and reported harvest rate did not increase with the addition of tag rewards beginning in 2013 ($\chi^2 = 1.02$, $df = 2$, $P = 0.60$). The spatial distribution of reported harvest was concentrated in the Dexter Dam tailrace ($n = 21$; 65.7% of reported harvest). Five steelhead (15.6% of reported harvest) were captured in the main stem Willamette River between the confluence of the Santiam River

(rkm 338.7) upstream to the MFW, and one fish (3.1% of reported harvest) was harvested in the Willamette River downstream of the confluence with the Santiam River. Males were harvested more frequently (Table 2.1) and the odds of being reported as harvested compared to remaining in a river was 2.72 times higher for males recycled below Dexter Dam than females ($\chi^2 = 3.95$, $P = 0.047$; Table 2.2). Neither release day nor year were significantly associated with fate (release day: $\chi^2 = 1.80$, $P = 0.18$; year: $\chi^2 = 0.25$, $P = 0.62$; Table 2.2), although there was an expected negative relationship between the probability of being harvested and release date.

SSR.—Overall patterns in fate of recycled steelhead were similar to the MFW, but harvest and straying rates were lower in the SSR, perhaps because steelhead were also removed at the hatchery (Fig. 2.2). Most were last detected in a river during our study ($n = 153$; 54.4%; Fig. 2.2), followed by recaptured and removed at Foster Dam ($n = 97$; 34.3%) and reported as harvested ($n = 32$; 11.3%). Reported harvest rate was not associated with the addition of tag rewards beginning in 2013 ($\chi^2 = 0.89$, $df = 2$, $P = 0.64$), though harvest was lowest in 2012 (8.8%) when reward tags were not used. Individuals last detected in a river were generally concentrated in the SSR ($n = 127$; 82.5%; Fig. 2.3). Approximately 10% of all recycled steelhead strayed outside the SSR ($N = 27$; 9.5%; Fig. 2.3). Two (0.7%) fish were last detected in Wiley Creek, a spawning tributary for upper Willamette River WRS emptying to the Foster Dam tailrace. The point estimate of straying rate for steelhead released at Wiley Creek (15.0%) was higher than rates for the other three release sites, but differences were not significant ($\chi^2 = 3.63$, $df = 3$, $P = 0.30$).

Fate of steelhead released to the SSR differed between males and females in a complex manner (Table 2.1). Overall, sex was associated with fate ($\chi^2 = 6.78$, $df = 2$, $P = 0.03$; Table 2.3). Males ($n = 16$, 25.8%) were recaptured and removed less frequently than females ($n = 59$; 45.4%), most likely reflecting broodstock collection practices. The model illustrated that the odds of removal at Foster compared to remaining in a river was 60% lower for males (Table 2.3). Reported harvest of males (16.1%) was not significantly higher than females (10.8%; $\chi^2 = 0.48$, $df = 1$, $P = 0.49$). Point estimates of straying were higher in males than females, though this difference was not significant ($\chi^2 = 3.42$, $df = 1$, $P = 0.06$; Table 2.1). Other management actions were not associated with the fate of steelhead recycled in the SSR. Specifically, neither release timing ($\chi^2 = 0.0003$, $df = 2$, $P = 0.99$; Table 2.3) nor release distance from Foster Dam ($\chi^2 = 7.15$, $df = 6$, $P = 0.31$; Table 2.3) were associated with fate or harvest rate.

Recycled SRS remaining at large.—The number of SRS recycled annually by ODFW in the SSR varied based upon annual hatchery returns to Foster. Oregon Department of Fish and Wildlife recycled $3,901 \pm 2,651$ (mean \pm SD) SRS annually during the study. Annual population estimates of fish recycled in the SSR that remained at large were greater than WRS escapement point estimates during 2012 and 2013 and similar in 2014 (Table 2.4). The greatest difference occurred in 2012 when the estimated population of SRS remaining in a river (4,647 [3,961 – 5,256; 95% CI]) was approximately six times higher than the estimated WRS escapement (811 [579 – 1,119; 95% CI]; Table 2.4).

Discussion

Our findings have direct application to managing programs that release animals to increase harvest opportunities in systems with species of conservation concern. We observed that most recycled SRS in the MFW and SSR avoided angler harvest and removal at Foster and remained in the release tributary or main stem Willamette River. Substantial numbers also moved out of the recipient streams prior to spawning. Reported harvest rates were generally low. Contrary to expectations, the effects of release day and location on fate were weak or not significant, but sex was important in predicting fate in both basins. Expansion of radio-tagged recycled SRS fates suggests the number remaining in a river after recycling by ODFW was greater than the number of adult endemic WRS returning to spawn in the SSR. In the sections that follow we interpret our results with respect to potential bias in our fate estimates, address the effects of management actions, discuss potential demographic and genetic effects on WRS populations, and present a conceptual framework for assessing the potential costs and benefits of non-local translocations with respect to the donor population and recipient community.

Potential Biases:

The exploitation of wild animals and plants often relies on releases of translocated individuals, and accurately quantifying harvest is therefore important. Harvest estimates in this study were almost certainly biased low because harvest rates are commonly underreported in many salmonid studies (Meyer et al. 2012a). Self-reported harvest data can be sensitive to self-reporting bias, including deliberate misreporting bias and nonresponse

(Pollock et al. 1994; McCormick et al. 2015). Anglers could misreport harvest as an attempt to influence season length (McCormick et al. 2013); however, this is unlikely in the UWR because the SRS angling season is long (ODFW 2015b). Reward tags can be used to reduce bias associated with self-reporting and Nichols et al. (1991) found that approximately US\$100 was needed to generate reporting rates approaching 100%. Thus our reward rate (\$25) may have contributed to underreporting. However, the absence of an observable change in reported harvest rate between 2012 (no reward tags) and later years implies that self-reporting bias was relatively small. Application of corrections based on other studies may inform how a bias might impact our study conclusions. Specifically, weighted mean reporting rates were 69.7% for \$10 tags and 91.7% for \$50 tags in a reward-recovery study in Idaho (Meyer et al. 2012a). Extrapolating to an expected reporting rate of 78% for the \$25 rewards used in this study, an adjusted harvest rate of recycled steelhead increases from 22.9% to 33.6% in the MFW and from 11.3% to 16.3% in the SSR. Finally, the observed harvest estimates were similar to the minimum estimate of recycled steelhead harvest in the Clackamas River (10.3%; Schemmel et al. 2011) and the Cowlitz River (19.2%; Kock et al. 2016) and to estimated harvest of Atlantic salmon *Salmo salar* and upper Columbia River steelhead radio tagged with tags of similar reward value (Smith et al. 1998; Keefer et al. 2005). However, estimates of harvest in the SSR were over 50% lower than an initial estimate of recycled steelhead harvest in the same basin from 2003 creel data (39.2%; confidence interval not reported; ODFW 2004). Collectively, our data and rates reported from other systems suggest that the degree of non-reporting was likely not more than ~20-25% and true harvest rates were 40% or less. Therefore, adjustment for bias would not likely

alter the conclusion that a minority of recycled steelhead are harvested and most remain in a river.

Tag retention and tag-related mortality are concerns for any tagging study (Ramstad & Woody 2003). Our results rely on the assumptions that tag retention and tag-related mortality were sufficiently high and low, respectively, to meet the study objectives (Pine et al. 2012). While we were unable to directly evaluate these assumptions, past studies on tag regurgitation rates for steelhead radio tagged in the Columbia River using similar tags and methods (6.7%; Keefer et al. 2004) and tag-related mortality among adult sockeye salmon *Oncorhynchus nerka* (2.0%; Ramstad & Woody 2003) suggest these potential biases were also unlikely to alter the qualitative conclusions of the study.

Management Actions:

Translocation supplementation protocols are expected to affect the fate of released animals depending on the timing, location, and habitat conditions upon release. Contrary to our expectations for SRS, additional exposure to fisheries from greater release distance and earlier release date did not measurably increase the probability of harvest. In fact, although it was not statistically significant, point estimates of harvest rates were higher for adults released within ~1 km of Foster Dam and were similar to harvest rates in the MFW where all fish were recycled into the dam tailrace. The higher harvest rates near juvenile release sites (i.e., the dam tailraces in these basins where philopatric adults return) were associated with a concentration of anglers who perceive higher potential catch rates at juvenile release sites

(Wagner 1969; Slaney et al. 1993; Quinn 2005). A single tailrace release site could increase the removal of steelhead recycled in SSR, but multiple release sites decreases angler density and could increase the quality of the fishing experience. The trade-off between harvest probability and quality of experience, both metrics of the quality of a fishery, are important for managers to consider (McCormick et al. 2014). Although reported harvest was low, recreational anglers could be releasing a large proportion of recycled fish, indicating that the program may be successful at providing a robust fishery with suitable catch rates. Mandatory removal of all captured animals could be implemented to further improve segregation between released animals and endemic populations. Sex, and therefore length, was important in predicting fate probabilities for recycled steelhead in both basins. Limiting recycling in the MFW to only male steelhead (i.e., longer fish) would potentially increase harvest and therefore decrease the proportion that remains at large, but could also affect interactions on the spawning ground by, for example, biasing sex ratios. Historically, releases of genetically distinct populations of species that already exist naturally in the release area were rarely monitored for possible effects on endemic populations (Laikre et al. 2010). Specific release strategies can increase survival of released animals to improve harvest opportunities or to aid in the conservation of imperiled populations (Brennan et al. 2006; Burner et al. 2011), generally demonstrating the importance of understanding how release strategies interact with spatial patterns of harvest to influence the fate of released animals. These results highlight that intuitive assumptions about the effects of management protocols may not manifest as expected.

Potential Demographic and Genetic Effects:

The release of non-local animals that remain at-large can affect animals in recipient systems through behavioral, demographic, or genetic effects. Quantifying these effects was beyond the scope of the study, but effects were likely given that the estimate of recycled SRS remaining in-river in the SSR in all study years exceeded the number of WRS. Evidence for spatial and, to a lesser degree, temporal overlap in spawning exists between the two ecotypes in the Willamette River basin (Jepson et al. 2015). Releases of non-local organisms can negatively affect locally adapted populations through decreased effective population size (Wang & Ryman 2001; Chilcote 2003; Chilcote et al. 2011), decreased fitness (McGinnity et al. 2003; Araki et al. 2007), changes in life history traits (Fast et al. 2015) and gene expression (Christie et al. 2016), and reduced survival (Peterson et al. 2004). Offspring of SRS generally emerge earlier than WRS potentially placing WRS at a disadvantage for occupying prime juvenile rearing habitats (Kostow et al. 2003). Large numbers of SRS spawners could decrease spawning success of WRS through demographic processes such as density-dependent feedback (Stewart et al. 2005; Putaala & Hissa 1998). Hybridization can cause direct and indirect genetic effects, including introgression, outbreeding depression, or altered selection regimes (Waples 1991; Araki et al. 2008), and studies have documented gene flow from genetically alien populations released into native, conspecific populations (Mamuris et al. 2001; Barilani et al. 2005). The continued outnumbering of WRS in the SSR by SRS could lead to a hybrid sink effect (Allendorf et al. 2013). Although recent genetic analyses by Van Doornik et al. (2015) showed low effective rates of introgression into adult populations, higher rates of introgression were observed in preliminary samples of naturally

produced juveniles collected at Willamette Falls (Johnson et al. 2014). Regardless, under the ESA, the SRS hatchery program must be monitored and managed to maximize segregation and minimize genetic and fitness-related effects of SRS on WRS populations (NMFS 2008). Releases of non-local animals can provide important harvest opportunities, but consequences of such releases are expected if released animals avoid harvest, indicating that future research should focus on quantifying the ecological and genetic effects of such releases.

Movement by translocated individuals outside of target management areas after release may have important ecological and socioeconomic implications that are challenging to quantify. Straying of recycled fish to WRS spawning tributaries is a concern because WRS populations are depressed and strays can have considerable effects when the recipient population is small (Keefer & Caudill 2014). Keefer & Caudill (2014) reported typical straying rates of 3-10% for SRS, suggesting that straying rates of steelhead recycled in the MFW were high, though we note that straying rate depends in-part on the scale of observation and most estimates in Keefer & Caudill (2014) were at larger scales. Minimizing the movement of animals outside the release area is critical because release strategies that promote widespread straying can result in homogenized populations (Lindley et al. 2009). If the specific goal of a release program is to increase abundance in the release area, then dispersal of introduced organisms outside the release area is problematic, both ecologically and socioeconomically (Skjelseth et al. 2007). For example, straying of recycled fish reduces angling opportunities in the targeted release rivers. However, dispersal of released organisms to habitats outside the release area may be necessary in order to find suitable mates, favorable foraging opportunities, or distribute novel alleles, which could be beneficial for rescuing populations or species

suffering from lower population sizes (Ebenhard 1995). The probability of released animals moving into adjacent habitats depends on the behavioral, physiological, and ecological characteristics of the released species (Westley et al. 2013) and the habitat to which animals are released. These results demonstrate released animals can frequently move out of the respective release area.

Harvest and Non-local Translocation:

Intentional releases of non-local animals are generally used to increase population abundance for either conservation or harvest purposes. The management strategies for release should explicitly consider the origin of released animals and the goals of the program (Fig. 2.4). For example, if releases are intended to buffer the recipient population from extinction, then integration between the non-local and endemic animals is expected and desired (Griffith et al. 1989; DeMay et al. 2016), and therefore, harvest of the non-local animals would be detrimental to management objectives. However, if releases are for harvest enhancement, either segregation- or integration-based management strategies could be warranted. If segregation is required by the ESA, for example, harvest or removal of all released non-local animals is essential because individuals that avoid harvest conflict with conservation goals mandated by the ESA. In the Willamette River basin, harvest or removal of all released SRS fulfills ESA requirements to minimize opportunities that lead to interactions. Recycling of anadromous fishes remains a practical method to increase angling opportunity by using a surplus of hatchery-produced fish that have returned to a hatchery. However, recycling of non-local genotypes could increase risk to endemic populations and actions should be taken

to minimize this risk. Continued separation between these populations will help ensure that vulnerable endemic populations are better able to persist in the face of future environmental and anthropogenic challenges. This case study highlights the multiple, frequently conflicting, management goals for populations affected by translocation or augmentation. Similar frameworks should assist in structuring risk-to-benefit analyses considering ecological and genetic effects.

Whether the objective of intentionally releasing non-local organisms is to conserve imperiled populations or improve harvest opportunities, identifying post-release fates are important. Post-release fate may affect native conspecifics, similar species within the same guild or assemblage (i.e., other cold-water fishes), community dynamics via food web effects, or energy and nutrient flows within the recipient ecosystem. To assess how programs balance providing harvest options of non-local animals through intentional releases, such as put-and-take fisheries (Johnson et al. 1995; Meyer et al. 2012b), big game hunting preserves (Adams et al. 2016), and upland bird introductions (Blanco-Aguiar et al. 2008), with conservation of endemic populations, quantification of the proportion of released individuals that avoid harvest or removal is the first step to quantifying these potential effects. Quantifying post-release fate provides insight on how to carry out releases in a way that does not unnecessarily reduce biological diversity.

Post-release fitness is also important to consider because a naturalized population of translocated animals has more potential long-term impact compared to true put-and-take animals. There could be cause for ecological and genetic concern if the population size of

non-local releases is greater than the endemic recipient population (e.g., demographic or genetic swamping). The necessity of understanding demographic effects of translocations, regardless of the specific objectives, becomes even more critical in the face of climate change, as many populations will not be able to migrate sufficiently (Loarie et al. 2009), anthropogenic pressures on endemic populations may become more intense, and assisted migration is considered as a management strategy. There is also a need to address issues in a more interdisciplinary action (Champagnon et al. 2012). Hunting and angling are important components of natural resource management and strategies for increasing interest in these resources and opportunities should be provided; however, it is critical to test assumptions about programs where releases are used to increase harvest in systems with native populations of conservation concern.

Acknowledgements

Many people contributed to the success of this project. Tim Blubaugh, Grant Brink, Matt Knoff, Mark Morasch, and Eric Powell assisted with tagging and maintenance of fixed receiver sites. Tami Clabough assisted with database management, Karen Johnson and Cheryl Chambers provided administrative support, and Cameron Sharpe provided assistance in study design and logistical support. We thank ODFW hatchery personnel, especially Dan Peck, Tim Wright, Brett Boyd, Reed Fischer, and Naomi Halpern, for their assistance in tagging. We appreciate reviews by Tim Johnson and Mike Quist. This project was funded by the U.S. Army Corps of Engineers' Portland District with the assistance of Robert Wertheimer, David Griffith, Glenn Rhett, and Deberay Carmichael.

Author Contributions

CE, CC, GN, and MJ conceived the idea and designed methodology; CE and GN collected the data; MJ and CE coded the data; CE analyzed the data; CE and CC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

References

- Adams, K.P., Murphy, B.P. & Ross, M.D. (2016) Captive white-tailed deer industry— Current status and growing threat. *Wildlife Society Bulletin*, 40, 14–19.
- Allendorf, F.W., Luikart, G. & Aitken, S.N. (2013) Conservation and the genetics of populations. John Wiley and Sons, United Kingdom.
- Allendorf, F.W. & Waples, R.S. (1996) Conservation and genetics of salmonid fishes. *Conservation Genetics: Case Histories from Nature* (eds J.C. Avise & J.L. Hamrick), pp. 238-239. Chapman and Hall, New York, New York, USA.
- Allen, D.L (1956) Pheasants in North America. Stackpole Company, Harrisburg, PA, and Wildlife Management Institution, Washington, DC, USA.
- Anderson, L.E., & Lee, T.S. (2013) Untangling the recreation value of wild and hatchery salmon. *Marine Resource Economics*, 28, 175–197.

Araki, H., Ardren, W.R., Olsen, E., Cooper, B., & Blouin, M.S. (2007) Reproductive success of captive-bred steelhead trout in the wild: evaluation of three hatchery programs in the Hood River. *Conservation Biology*, **21**, 181–190.

Araki, H., Berejikian, B.A., Ford, M.J. & Blouin, M.S. (2008) Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications*, **1**, 342–355.

Armstrong, D.P., & Seddon, P.J. (2008) Directions in reintroduction biology. *Trends in Ecology & Evolution*, **23**, 20–25.

Barilani, M., Deregnacourt, S., Gallego, S., Galli, L., Mucci, N., Piombo, R., Puigcerver, M., Rimondi, S., Rodríguez-Teijeiro, J.D., Spanò, S., & Randi, E. (2005) Detecting hybridization in wild (*Coturnix c. coturnix*) and domesticated (*Coturnix c. japonica*) quail populations. *Biological Conservation*, **126**, 445–455.

Berntson, E.A., Carmichael, R.W., Flesher, M.W., Ward, E.J., & Moran, P. (2011) Diminished reproductive success of steelhead from a hatchery supplementation program (Little Sheep Creek, Imnaha Basin, Oregon). *Transactions of the American Fisheries Society*, **140**, 685–698.

Blanco-Aguilar, J., González-Jara, P., Ferrero, M., Sánchez-Barbudo, I., Virgó, E., & Villafuerte, R. (2008) Assessment of restocking contributions to anthropogenic

hybridization: The case of the Iberian red-legged partridge. *Animal Conservation*, **11**, 535–545.

Brennan, N.P., Darcy, M.C., & Leber, K.M. (2006) Predator-free enclosures improve post-release survival of stocked common snook. *Journal of Experimental Marine Biology and Ecology*, **335**, 302–311.

Burner, F.D., Brownie, S.J., & Aebischer, N.J. (2011) Experimental assessment of release methods for the re-establishment of a red-listed galliform, the grey partridge (*Perdix perdix*). *Biological Conservation*, **144**, 593–601.

Champagnon, J., Elmberg, J., Guillemain, M. Cauthier-Clerc, M., & Lebreton, J.D. (2012) Conspecifics can be aliens too: A review of effects of restocking practices in vertebrates. *Journal for Nature Conservation*, **20**, 231–241.

Chilcote, M.W. (2003) Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 1057–1067.

Chilcote, M.W., Goodson, K.W., & Falcy, M.R. (2011) Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**, 511–522.

- Chilcote, M.W., Leider, S.A., & Loch, J.J. (1986) Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. *Transactions of the American Fisheries Society*, **115**, 726–735.
- Christian, J.M., & Wilson, S.D. (1999) Long-term ecosystem impacts of an introduced grass in the Northern Great Plains. *Ecology*, **80**, 2397–2407.
- Christie, M.R., Marine, M.L., Fox, S.E., French, R.A., & Blouin, M.S. (2016) A single generation of domestication heritably alters the expression of hundreds of genes. *Nature Communications*, **7**, 10676.
- Clemens, B.J. (2015) A survey of steelhead age and iteroparity rates from a volunteer angler program in the Willamette River basin, Oregon. *North American Journal of Fisheries Management*, **35**, 1046–1054.
- Crawford, B.A. (1979) The origin and history of the trout brood stocks of the Washington Department of Game. Washington State Game Dep., Fishery Research Report, 76 p. (Available from Washington Department of Fish and Wildlife, 600 Capital Way N., Olympia, WA 98501.)
- DeMay, S.M., Becker, P.A., Waits, L.P., Johnson, T.R., & Rachlow, J.L. (2016) Consequences for conservation: population density and genetic effects on reproduction of an endangered lagomorph. *Ecological Applications*, **26**, 784–795.

Deredec, A., & Courchamp, F. (2007) Importance of the Allee effect for reintroductions.

Ecoscience, **14**, 440–451.

Ebenhard, T. (1995) Conservation breeding as a tool for saving animal species from

extinction. *Trends in Ecology and Evolution*, **10**, 438–443.

Efron, B. (1987) Better bootstrap confidence intervals. *Journal of the American Statistical*

Association, **82**, 171–185.

Evenson, M.D., & Cramer, S.P. (1984) An evaluation of recycling hatchery spring chinook

salmon through the sport fishery in the upper Rogue River. Report Series 84–10, Oregon

Department of Fish and Wildlife, Corvallis, Oregon, USA.

Fast, D.E., Bosch, W.J., Johnston, W.V., Strom, C.R., Knudsen, C.M., Fritts, A.L., Temple,

G.M., Pearsons, T.N., Larsen, D.A., Dittman, A.H., & May, D. (2015) A synthesis of

findings from an integrated hatchery program after three generations of spawning in the

natural environment. *North American Journal of Aquaculture*, **77**, 377–395.

Ford, M.J., Murdoch, A. & Hughes, M. (2015) Using parentage analysis to estimate rates of

straying and homing in Chinook salmon (*Oncorhynchus tshawytscha*). *Molecular*

Ecology, **24**, 1109–1121.

- Fraser, D.J. (2008) How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications*, **1**, 535–586.
- Gebhardt, H. (1996) Ecological and economic consequences of introductions of exotic wildlife (birds and mammals) in Germany. *Wildlife Biology*, **2**, 205–211.
- Griffith, B., Scott, J.M., Carpenter, J.W., & Reed, C. (1989). Translocation as a species conservation tool: status and strategy. *Science*, **245**, 477–480.
- Hendry, A.P., Castric, V., Kinnison, M.T., & Quinn, T.P. (2004) The evolution of philopatry and dispersal. *Evolution illuminated: Salmon and Their Relatives* (eds A.P. Hendry & S.C. Stearns), pp. 52–91. Oxford University Press, United Kingdom.
- Hilborn, R. (1992) Hatcheries and the future of salmon in the Northwest. *Fisheries*, **17**, 1–8.
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P., & Thomas, C.D. (2008) Assisted colonization and rapid climate change. *Science*, **321**, 345–346.
- Hosmer Jr, D.W., Lemeshow, S., & Sturdivant, R.X. (2013) Applied logistic regression. John Wiley & Sons, Hoboken, New Jersey, USA.

Jepson, M.A., Keefer, M.L., Caudill, C.C., Clabough, T.S., Erdman, C.S., Blubaugh, T., & Sharpe, C.S. (2015) Migratory behavior, run timing, and distribution of radio-tagged adult winter steelhead, summer steelhead, spring Chinook salmon, and coho salmon in the Willamette River: 2011-2014. UI FERL for U.S. Army Corp of Engineers Portland District, Technical Report 2015-1, Portland, Oregon, USA.

Johnson, D.M., Behnke, R.J., Harpman, D.A., & Walsh, R.G. (1995) Economic benefits and costs of stocking catchable rainbow trout: a synthesis of economic analysis in Colorado. *North American Journal of Fisheries Management*, 15, 26–32.

Johnson, M.A., Friesen, T.A., Teel, D.J., & Van Doornik, D.M. (2013) Genetic stock identification and relative natural production of Willamette River steelhead. ODFW and NOAA Fisheries for U.S. Army Corps of Engineers Portland District, Portland, Oregon, USA.

Keefer, M.L., & Caudill, C.C. (2010) A review of adult salmon and steelhead life history and behavior in the Willamette River basin: identification of knowledge gaps and research needs. UI FERL for U.S. Army Corps of Engineers Portland District, Technical Report 2010-8, Portland, Oregon, USA.

Keefer, M.L., & Caudill, C.C. (2014) Homing and straying by anadromous salmonids: a review of mechanisms and rates. *Reviews in Fish Biology and Fisheries*, 24, 333–368.

Keefer, M.L., Clabough, T.S., Jepson, M.A., Naughton, G.P., Blubaugh, T.J., Joosten, D.C., & Caudill, C.C. (2015) Thermal exposure of adult Chinook salmon in the Willamette River basin. *Journal of Thermal Biology*, **48**, 11–20.

Keefer, M.L., Peery, C.A., Ringe, R.R., & Bjornn, T.C. (2004) Regurgitation rates of intragastric radio transmitters by adult Chinook salmon and steelhead during upstream migration in the Columbia and Snake rivers. *North American Journal of Fisheries Management*, **24**, 47–54.

Keefer, M.L., Peery, C.A., Daigle, W.R., Jepson, M.A., Lee, S.R., Boggs, C.T., Tolotti, K.R., & Burke, B.J. (2005) Escapement, harvest, and unknown loss of radio-tagged adult salmonids in the Columbia River Snake River hydrosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 930–949.

Kock, T.J., Perry, R.W., Gleizes, C., Dammers, W., & Liedtke, T.L. (2016). Angler harvest, hatchery returns, and tributary stray rates of recycled adult summer steelhead *Oncorhynchus mykiss* in the Cowlitz River, Washington. *River Research and Applications*, doi:10.1002/rra.3023.

Kostow, K.E. (1995) Biennial report on the status of wild fish in Oregon. Oregon Department of Fish and Wildlife, Salem, Oregon, USA.

Kostow, K.E., Marshall, A.R., & Phelps, S.R. (2003) Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. *Transactions of the American Fisheries Society*, **132**, 780-790.

Kerns, J.A., Allen, M.S., & Hightower, J.E. (2016) Components of mortality within a black bass high-release recreational fishery. *Transactions of the American Fisheries Society*, **145**, 578–588.

Laikre, L., Schwartz, M.K., Waples, R.S., Ryman, N., & The GeM Working Group. (2010) Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals. *Trends in Ecology and Evolution*, **25**, 520–529.

Leider, S.A., Hulett, P.L., Loch, J.J., & Chilcote, M.W. (1990) Electrophoretic comparison of the reproductive success of naturally spawning transplanted and wild steelhead trout through the returning adult stage. *Aquaculture*, **88**, 239–252.

Lindley, S.T., Grimes, C.B., Mohr, M.S., Peterson, W., Stein, J., Anderson, J.T., Botsford, L.W., Bottom, D.L., Busack, C.A., Collier, T.K., Ferguson, J., Garza, J.C., Grover, A.M., Hankin, D.G., Kope, R.G., Lawson, P.W., Low, A., MacFarlane, R.B., Moore, K., Palmer-Zwahlen, M., Schwing, F.B., Smith, J., Tracy, C., Webb, R., Wells, B.K., & Williams, T.H. (2009) What caused the Sacramento River fall Chinook stock collapse? NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-447.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052–1055.

Lindsay, R.B., Kenaston, K.R., & Schroeder, R.K. (2001) Reducing impacts of hatchery steelhead programs. Oregon Department of Fish and Wildlife, Portland, Oregon, USA.

Mamuris, Z., Sfougaris, A.I., & Stamatis, C. (2001) Genetic structure of Greek brown hare (*Lepus europaeus*) populations as revealed by mtDNA RFLP-PCR analysis: implications for conserving genetic diversity. *Biological Conservation*, **101**, 187–196.

McCormick, J.L., Quist, M.C., & Schill, D.J. (2013) Self-reporting bias in Chinook salmon sport fisheries in Idaho: implications for roving creel surveys. *North American Journal of Fisheries Management*, **33**, 723–731.

McCormick, J.L., & Porter, T.K. (2014) Effect of fishing success on angler satisfaction on a central Oregon rainbow trout fishery: Implications for establishing management objectives. *North American Journal of Fisheries Management*, **34**, 938–944.

McCormick, J.L., Whitney, D., Schill, D.J., & Quist, M.C. (2015) Evaluation of angler reporting accuracy in an off-site survey to estimate statewide steelhead harvest. *Fisheries Management and Ecology*, **22**, 134–142.

- McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., ó Maoiléidigh, N., Baker, N., Cotter, D., O’Hea, B., Cooke, D., Rogan, G., Taggart, J., & Cross, T. (2003) Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proceedings of the Royal Society of London: Biological Sciences*, **270**, 2443–2450.
- Meyer, K.A., Elle, F.S., Lamansky Jr, J.A., Mamer, E.R., & Butts, A.E. (2012a) A reward-recovery study to estimate tagged-fish reporting rates by Idaho anglers. *North American Journal of Fisheries Management*, **32**, 696–703.
- Meyer, K.A., High, B., & Elle, F.S. (2012b) Effects of stocking catchable-sized hatchery rainbow trout on wild rainbow trout abundance, survival, growth, and recruitment. *Transactions of the American Fisheries Society*, **141**, 224–237.
- Meyer, K.A., & Schill, D.J. (2014) Use of statewide angler tag reporting system to estimate rates of exploitation and total mortality for Idaho sport fisheries. *North American Journal of Fisheries Management*, **34**, 1145–1158.
- Mobrand, L.E., Barr, J., Blankenship, L., Campton, D.E., Evelyn, T.T.P., Flagg, T.A., Mahnken, C.V.W., Seeb, L.W., Seidel, P.R., & Smoker, W.W. (2005) Hatchery reform in Washington state: Principles and emerging issues. *Fisheries*, **30**, 11–23.

- Myers, J., Busack, C., Rawding, D., Marshall, A., Teel, D., Van Doornik, D.M., & Maher, M.T. (2006) Historical population structure of Pacific salmonids in the Willamette River and lower Columbia River basins. NOAA Technical Memorandum NMFS-NWFSC-73.
- Naish, K.A., Taylor, J.E., Levin, P.S., Quinn, T.P., Winton, J.R., Huppert, J., & Hilborn, R. (2008) An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology*, **53**, 61–194.
- Nichols, J.D., Blohm, R.J., Reynolds, R.E., Trost, R.E., Hines, J.E., & Bladen, J.P. (1991) Band reporting rates for mallards with reward bands of different dollar values. *Journal of Wildlife Management*, **55**, 119–126.
- NMFS (National Marine Fisheries Service). (1999) Endangered and threatened species: threatened status for two ESUs of steelhead in Washington and Oregon. Federal Register 64:57(25 March 1999):14517–14528.
- NMFS (National Marine Fisheries Service). (2008) 2008–2023 Willamette River basin project biological opinion. NMFS, Northwest Region, Seattle.
- ODFW (Oregon Department of Fish and Wildlife). (1975) Willamette River Steelhead Federal Aid Progress Reports. ODFW, Portland.

ODFW (Oregon Department of Fish and Wildlife). (2004) Upper Willamette Steelhead HGMP 2004. Upper Willamette Summer Steelhead (Stock 24). ODFW, Salem.

ODFW (Oregon Department of Fish and Wildlife). (2015a) Lower Willamette fisheries and Willamette Falls fish counts. Available:
www.dfw.state.or.us/fish/fish_counts/willamette%20falls.asp. (accessed November 2015).

ODFW (Oregon Department of Fish and Wildlife). (2015b) Oregon sport fishing regulations. Available:
http://www.dfw.state.or.us/fish/docs/2015/2015%20Oregon%20Sport%20Fishing%20Regs_r12-11-14.pdf. (accessed November 2015).

ODFW (Oregon Department of Fish and Wildlife) & NMFS (National Marine Fisheries Service). (2011) Upper Willamette River conservation and recovery plan for Chinook Salmon and steelhead. Report prepared for the ODFW, Salem and NMFS, Northwest Region, Portland, Oregon.

Pine, W.E., Pollock, K.H., Hightower, J.E., Kwak, T.J., & Rice, J.A. (2003) A review of tagging methods for estimating fish population size and components of mortality. *Fisheries*, **28**, 10–23.

- Pine, W.E., Hightower, J.E., Coggins, L.G., Laretta, M.V., & Pollock, K.H. (2012). Design and analysis of tagging studies. *Fisheries Techniques* (eds A.V. Zale, D.L. Parrish, & T.M. Sutton), pp. 521–572. American Fisheries Society Bethesda, Maryland, USA.
- Pollock, K.H., Jones, C.M., & Brown, T.L. (1994) Angler survey methods and their applications in fisheries management. American Fisheries Society Bethesda, Maryland, USA.
- Pollock, K.H., Hoenig, J.M., Hearn, W.S., & Calingaert, B. (2001) Tag reporting rate estimation I: an evaluation of the high-reward tagging method. *North American Journal of Fisheries Management*, **21**, 521–532.
- Putala, A., & Hissa, R. (1998) Breeding dispersal and demography of wild and hand reared grey partridges *Perdix perdix* in Finland, *Wildlife Biology*, **4**, 137–145.
- Quinn, T.P. (1993) A review of homing and straying of wild and hatchery-produced salmon. *Fisheries Research*, **18**, 29–44.
- Quinn, T.P. (2005) The behavior and ecology of Pacific salmon and trout. UBC Press, Vancouver, British Columbia, Canada.
- R Development Core Team. (2009) R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna.

- Ramstad, K M., & Woody, C.A. (2003) Radio Tag Retention and Tag-Related Mortality among Adult Sockeye Salmon. *North American Journal of Fisheries Management*, **23**, 978–982.
- Schemmel, E., Clements, S., Schreck, C., & Noakes, D. (2011) Using radio-telemetry to evaluate the success of a hatchery steelhead recycling program. *Advances in Fish Tagging and Marking Technology* (eds J. McKenzie, B. Parsons, A. Seitz, R.K. Kopf, M. Mesa, & Q. Phelps), pp. 371–378. American Fisheries Society Symposium No. 76. Bethesda, Maryland, USA.
- Sih, A., Bolnick, D.I., Luttbeg, B., Orrock, J.L., Peacor, S.D., Pintor, L.M., Preisser, E., Rehage, J.S., & Vonesh, J.R. (2010) Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos*, **119**, 610–621.
- Skjelseth, S., Ringsby, T.H., Tufto, J., Jensen, H., & Saether, B. (2007) Dispersal of introduced house sparrows *Passer domesticus*: an experiment. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1763–1771.
- Slaney, P.A., Berg, L., & Tautz, A.F. (1993) Returns of hatchery steelhead relative to site of release below an upper-river hatchery. *North American Journal of Fisheries Management*, **13**, 558–566.

Smith, G.W., Campbell, R.N.B., & MacLaine, J.S. (1998) Regurgitation rates of intragastric transmitters by adult Atlantic salmon (*Salmo salar* L.) during riverine migration.

Hydrobiologia, **371**, 117–121.

Stewart, K., Bowyer, R., Dick, B. Johnson, B., & J. Kie. (2005) Density-dependent effects on physical condition and reproduction in North American elk: An experimental test.

Oecologia, **143**, 85–93.

Taylor, E.B. (1991) A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture*, **98**, 185–207.

Utter, F. (2004) Population genetics, conservation and evolution in salmonids and other widely cultured fishes: Some perspectives over six decades. *Reviews in Fish Biology and Fisheries*, **14**, 125–144.

Van Doornik, D.M., Hess, M. A., Johnson, M.A., Teel, D.J., Friesen, T.A., & Myers, J.M. (2015) Genetic population structure of Willamette River steelhead and the influence of introduced stocks. *Transactions of the American Fisheries Society*, **144**, 150–162.

Wagner, H.H. (1969) Effect of stocking location of juvenile steelhead, *Salmo gairdneri* on adult catch. *Transactions of the American Fisheries Society*, **98**, 27–34.

- Wang, J., & Ryman, N. (2001) Genetic effects of multiple generations of supportive breeding. *Conservation Biology*, **15**, 1619–1631.
- Waples, R.S. (1991) Genetic interactions between hatchery and wild salmonids: lessons learned from the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 124–133.
- Waples, R.S., Gustafson, R.G., Weitkamp, L.A., Myers, J.M., Johnson, O.W., Busby, P.J., Hard, J.J., Bryant, G.J., Waknitz, F.W., Neely, K., Teel, D., Grant, W.S., Winans, G.A., Phelps, S., Marshall, A., & Baker, B.M. (2001) Characterizing diversity in salmon from the Pacific Northwest. *Journal of Fish Biology*, **59**, 1–41
- Wen-Hwa, K., & Lawrie, A.H. (1981) Pink Salmon in the Great Lakes. *Fisheries*, **6**, 2–6.
- Westemeier, R.L., Buhnerkempe, J.E., Edwards, W.R., Brawn, J.D., & Simpson, S.A. (1998) Parasitism of greater prairie-chicken nest by ring-necked pheasants. *Journal of Wildlife Management*, **62**, 854–863.
- Westley, P.A., Quinn, T.P., & Dittman, A.H. (2013) Rates of straying by hatchery-produced Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) differ among species, life history types, and populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **70**, 735–746.

Table 2.1. The number, fate, and straying rate of non-local male and female radio-tagged recycled summer-run steelhead in the (A) Middle Fork Willamette River and (B) South Santiam River, Oregon, 2012-2014. Sex was not estimated in 2012 (i.e., unknown). Sex assignment was conducted during tagging.

(A)

Sex	Radio-tagged	Reported as harvested		Remained in river		Remained in river: outside release tributary	
	N	N	%	N	%	N	%
2012							
Unknown	45	9	20.0	36	80.0	12	26.7
2013							
Male	25	5	20.0	20	80.0	4	16.0
Female	22	4	18.2	18	81.8	8	36.4
2014							
Male	22	10	45.5	12	54.5	1	4.5
Female	26	4	15.4	22	84.6	6	23.1

(B)

Sex	Radio-tagged	Reported as harvested		Remained in river		Removed at Foster		Remained in river: outside release tributary	
	N	N	%	N	%	N	%	N	%
2012									
Unknown	91	8	8.8	61	67.0	22	24.2	13	14.3
2013									
Male	39	8	20.5	22	56.4	9	23.1	6	15.4
Female	56	5	8.9	20	35.7	31	55.4	3	5.4
2014									
Male	23	2	8.7	14	60.9	7	30.4	2	8.7
Female	74	9	12.2	37	50.0	28	37.8	2	2.7

Table 2.2. Parameter estimates and 95% confidence intervals for the logistic regression model that predicted the fate of non-local summer-run steelhead recycled below Dexter Dam in the Middle Fork Willamette River, Oregon. Odds expressed as odds of being harvested compared to remaining in a river. Parameter estimates shown in bold have 95% confidence intervals that do not include 1.

Variable	Estimate	Confidence interval	
		Lower	Upper
Intercept	1.17	0.04	31.86
Sex (male)	2.77	1.01	7.85
Release day	0.97	0.92	1.02
Year (2014)	0.61	0.08	4.20

Coefficients are expressed as odds ratios.

Table 2.3. Estimated odds ratios and 95% confidence intervals for the multinomial logistic regression model of fate (angled, recaptured at hatchery, remained in river) including sex, release location (release rkm), year, and release day covariates for non-local summer-run steelhead recycled below Foster Dam in the South Santiam River, Oregon. Parameter estimates shown in bold have 95% confidence intervals that do not include 1.

Variable	Estimate	Confidence interval	
		Lower	Upper
Reported as harvested			
Intercept	0.68	0.12	3.87
Sex (male)	0.94	0.36	2.44
Release site (PLV)	0.68	0.16	2.92
Release site (WLC)	0.54	0.05	5.90
Release site (WTL)	0.23	0.04	1.24
Year (2014)	0.49	0.12	2.01
Release day	1.00	0.96	1.05
Removed at hatchery			
Intercept	1.28	0.39	4.21
Sex (male)	0.40	0.20	0.83
Release site (PLV)	1.31	0.45	3.78
Release site (WLC)	0.56	0.10	3.27
Release site (WTL)	1.16	0.40	3.35
Year (2014)	0.56	0.24	1.32
Release day	1.00	0.97	1.03

Coefficients are expressed as odds ratios relative to fate probability of remaining in a river (i.e., remaining in a river was the reference category).

Table 2.4. Annual estimates of the number of recycled non-local summer-run steelhead harvested and remaining in a river based on the fates of radio-tagged steelhead recycled below Foster Dam, South Santiam River, Oregon and annual estimated escapement of winter steelhead to the South Santiam River. Winter steelhead escapement from Jepson et al. 2013, 2014, and 2015. 95% confidence interval in parentheses. Estimates are not corrected for reporting biases, tag retention rate, or tag-related mortality.

Year	Number of fish recycled by ODFW	Percent radio-tagged	Estimate of fish recycled once by ODFW	Percent radio-tagged reported as harvested	Percent radio-tagged remaining in river	Harvest estimate of recycled fish	Estimate of recycled fish remaining in river	Estimated winter steelhead escapement
2012	8423	1.08	6932	8.79	67.03	609 (229 – 1067)	4647 (3961 – 5256)	811 (579 – 1119)
2013	3355	2.83	2761	13.38	44.21	369 (203 – 581)	1227 (959 – 1511)	833 (627 – 1083)
2014	2444	3.97	2011	11.34	52.58	228 (104 – 352)	1057 (850 – 1265)	1085 (848 – 1364)

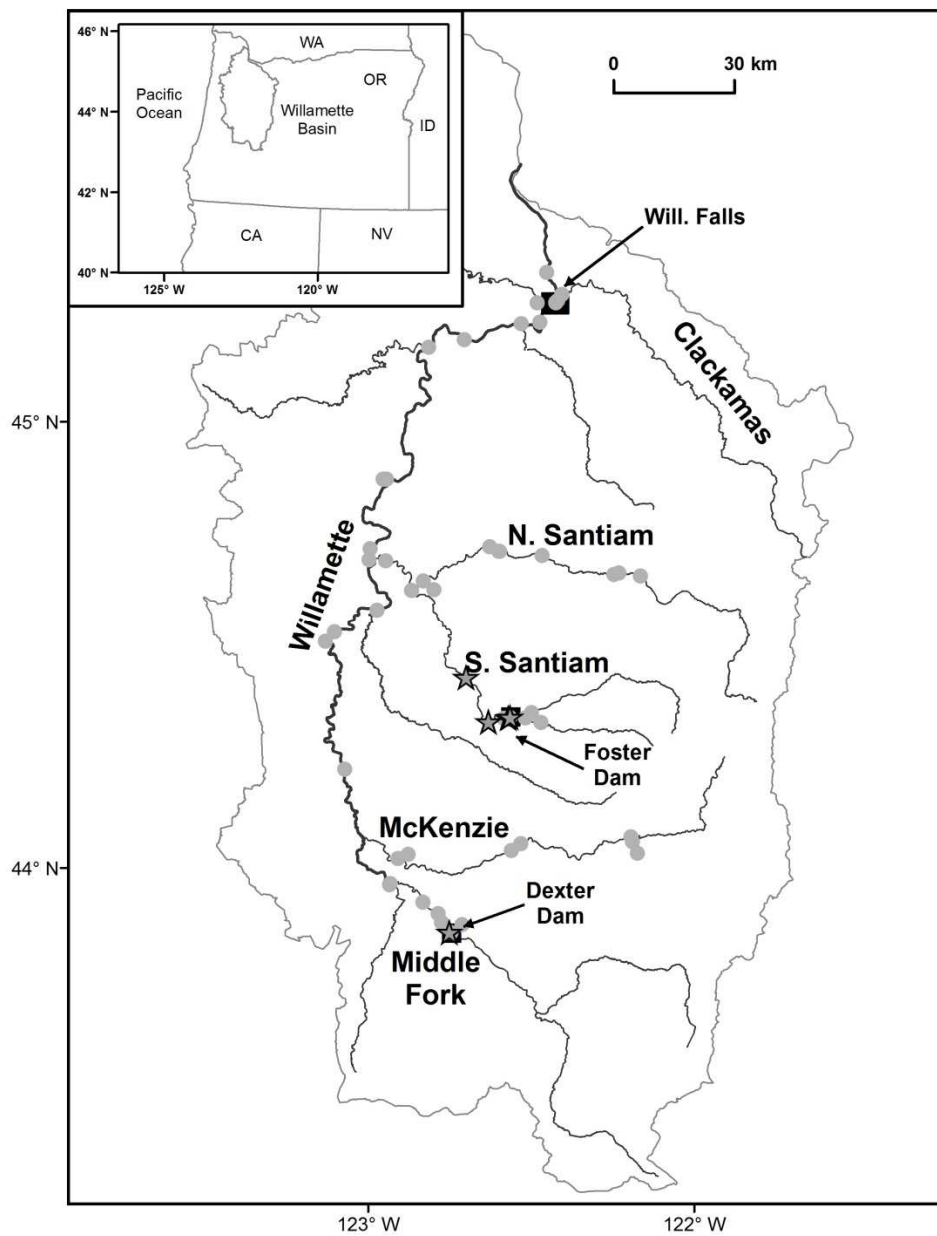


Figure 2.1. Map of Willamette River basin, Oregon showing release sites (stars) and locations of fixed radiotelemetry receivers (circles).

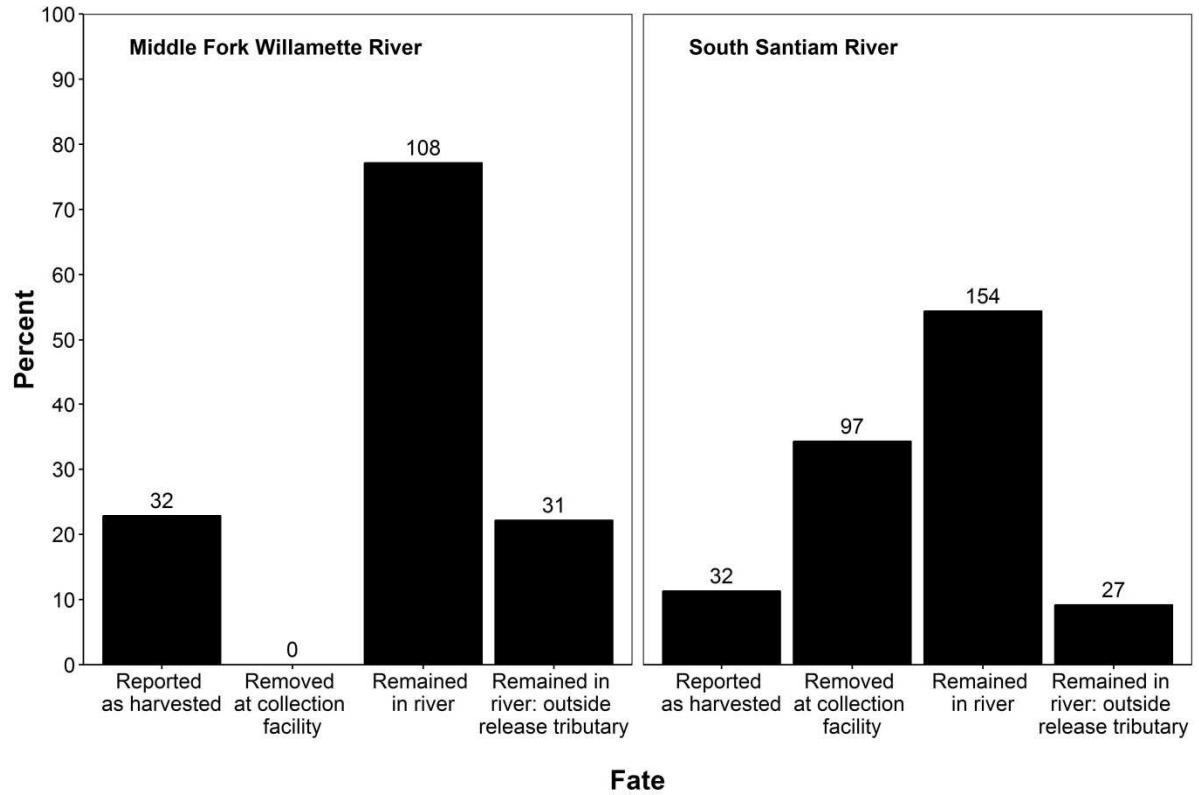


Figure 2.2. Fate of non-local radio-tagged summer-run steelhead recycled in the Middle Fork Willamette River (left) and South Santiam River (right), Oregon 2012-2014. Sample size of each fate category is above each bar.

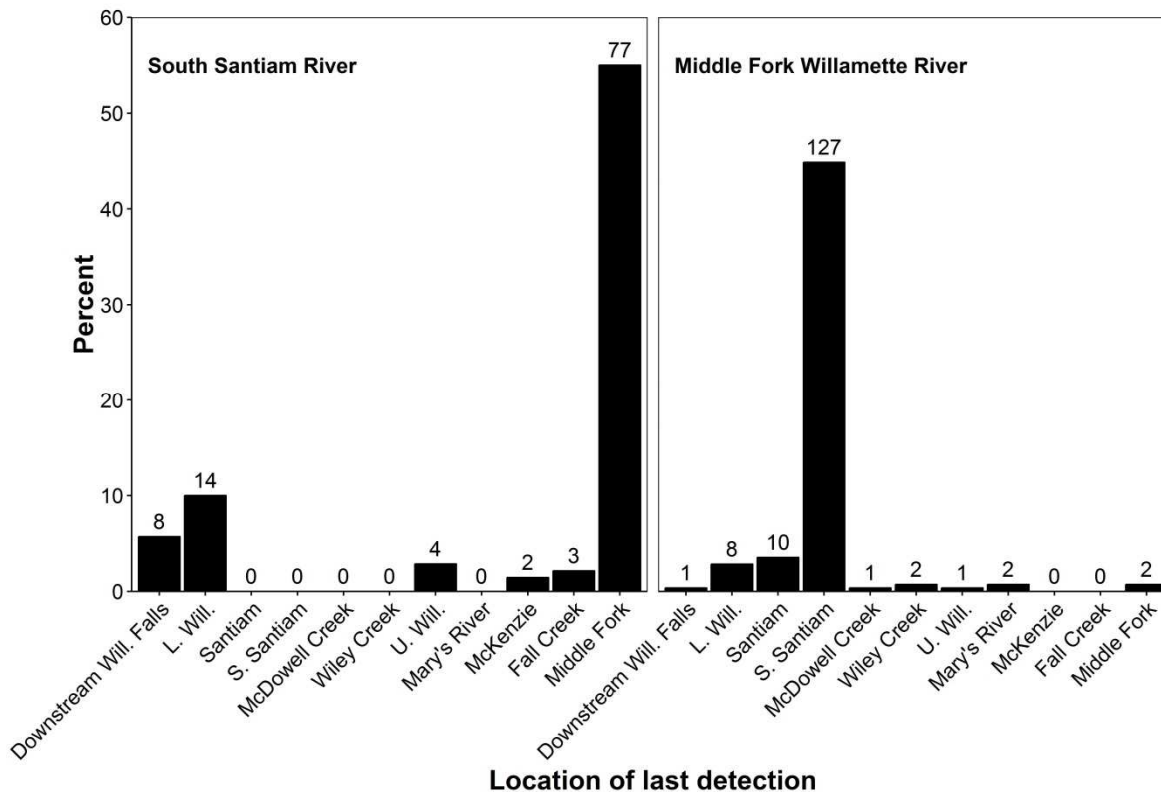


Figure 2.3. Locations of last detections for 108 and 154 non-local radio-tagged summer-run steelhead recycled in the Middle Fork Willamette River (left) and South Santiam River (right), Oregon, respectively, that were assigned a fate of remaining in a river. Sample sizes for individual locations are above the bars.

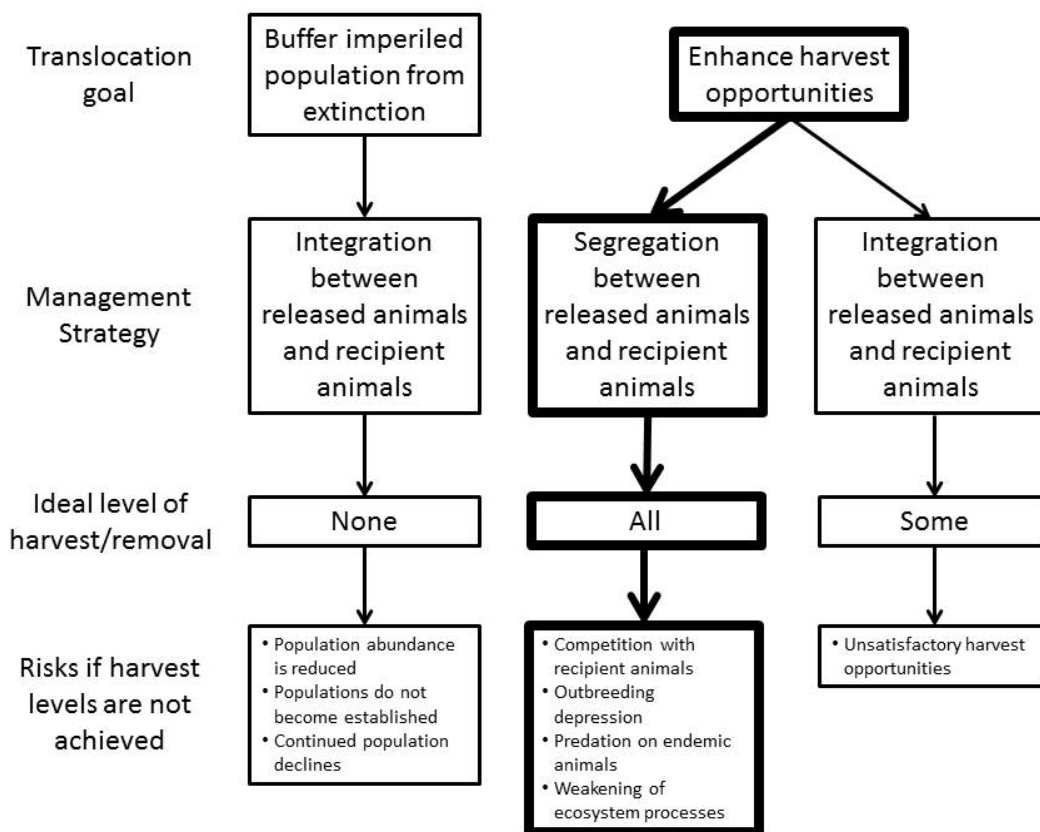


Figure 2.4. Diagram illustrating acceptable harvest levels of non-local animals intentionally released and the associated ecological and social costs and benefits. Thicker boxes indicate scenario in Willamette River basin, Oregon where non-local summer-run steelhead are released and recycled to increase harvest opportunities.

Chapter 3: Length at Ocean Entry and First Ocean Winter Growth Influence Age at Maturity in Populations of Steelhead (*Oncorhynchus mykiss*)

Abstract

Variation in age at both smoltification and maturation produces life history diversity in salmon *Oncorhynchus* ssp. and steelhead *O. mykiss*. Variation in timing of the two life history transitions can provide conservation benefit by providing resiliency and stability to populations in the face of environmental change. Growth trajectories in both freshwater and the ocean can influence transition timing. Additionally, freshwater growth can influence age at maturity for steelhead through carryover effects. Conversely, ocean growth during key stage(s) could act as a threshold trait and therefore dampen or amplify the influence of freshwater growth on age at maturity. We estimated length at ocean entry and seasonal ocean growth of 841 steelhead from four populations in the Nass, Skeena, and Columbia River basins. We used logistic regression and multimodel selection to determine the associations between growth history and age-at-maturation and evaluate hypotheses about underlying mechanisms. Length at ocean entry and growth during the first ocean winter were significantly and positively associated with the probability of maturing after two versus three years of ocean growth and the relative importance of first ocean winter growth suggests that a threshold trait model best explains steelhead maturation. A review of the literature on ocean residence of steelhead suggests that distributional differences in the North Pacific Ocean could produce the variable growth trajectories that were observed. Our results offer insight into the maturation schedules of steelhead and provide evidence that age at maturity is, in part, a conditional trait responsive to resource availability during ocean growth.

Introduction

Life history theory provides an essential perspective on the evolutionary forces that shape differences in behavior among individuals and can also provide important insight for the conservation and management of sensitive species (Roff 1992). Life history transitions involve fitness-related tradeoffs (Stearns 1992) and physiological, morphological, or behavioral changes from one state or stage to another (e.g., juvenile to adult). Intrapopulation variability in transition timing can result from habitat heterogeneity, environmental variance, and different genotypes. Increased variability leads to demographic stability and resiliency, decreases variance in population size through time (Green et al. 2010; Schindler et al. 2010; Moore et al. 2014; Schroeder et al. 2016) and thus improves food security for indigenous people (Nesbitt and Moore 2016). Therefore, a mechanistic understanding of the forces creating and maintaining life history diversity is important and should be incorporated into management frameworks.

Two critical life history transitions exist for anadromous species such as salmon *Oncorhynchus* spp. and steelhead *O. mykiss*: 1) smoltification, where juveniles transition from a freshwater environment to a marine environment; and 2) maturation, where adults subsequently return to a freshwater environment to spawn (Quinn 2005). Delayed smoltification increases size at ocean entry and the probability of survival upon ocean entry (Ward and Slaney 1988; Henderson and Cass 1991), but postpones the growth benefits of ocean productivity. Delayed maturation increases body size, which may improve migratory capacity, spawning ability, and fecundity (Gross 1985; Fleming and Gross 1994; Quinn 2005), but decreases the probability of survival to reproduction and increases generation time. Life history theory predicts that past selection will produce an allocation of energy to

reproduction versus growth or condition prior to maturing that maximizes long-term average fitness (Roff 1992; Stearns 1992). Selection should act to optimize fitness by altering the timing of life history transitions and the proximate mechanisms can include both direct selection on genotypic traits and selection on reaction norms affecting decision thresholds in phenotypically plastic traits.

Age and size at maturity affect an individual's reproductive success, and are therefore some of the most important life history traits affecting fitness (Roff 1992; Stearns 1992). Growth rate determines size-at-age. Thus, the relationship between individual growth rate, a partial proxy for environmental conditions, and the timing of age at maturity is often examined to understand life history diversity in fishes (Hutchings 2004). Maturation and reproductive tactics are also coupled with migration timing and duration because growth rates differ between habitats, e.g., freshwater and marine (Sloat et al. 2014). Age at maturity can be influenced by both freshwater and ocean growth, and differences in the effects of ocean growth on age at maturity have been reported among populations of anadromous salmonids (Nicieza and Braña 1993; Vøllestad et al. 2004; Quinn et al. 2011b; Tattam et al. 2015). For anadromous salmonids, a genetically-fixed maturation schedule could exist, whereby an individual must mature at given time, regardless of growth history. Conversely, recent growth history (i.e., ocean growth) could directly affect the maturation decision via conditional developmental switches during critical periods (i.e., "decision windows"; Satterthwaite et al. 2009), or prior growth experience (i.e., freshwater growth) could influence maturation through carryover effects (Harrison et al. 2011; O'Connor et al. 2014). Determining the relative importance of freshwater versus ocean growth history is useful for

understanding how freshwater conditions interact with ocean conditions to influence age at return.

Steelhead generally reside in freshwater longer than other anadromous salmonids in the North Pacific region (Quinn 2005) and serve as an ideal organism to investigate which elements of growth history (i.e., freshwater versus ocean growth) are associated with maturation. The effects of genetic, environmental, and individual condition on age at maturity have been well documented in *O. mykiss*; however, the majority of this work has investigated processes and patterns shaping partial migration (reviewed in Kendall et al. 2015). *O. mykiss* is facultatively anadromous, where the anadromous form is known as steelhead and the resident form is known as Rainbow Trout (Quinn 2005), and the species displays extraordinary life history diversity compared to most anadromous salmonids (Behnke 2002). Juveniles can spend 1-7 years in freshwater before adopting an anadromous or resident life history pathway (Pevan et al. 1994). Variability in the length of ocean residency also exists for steelhead. For example, steelhead in the Skeena and Nass rivers in British Columbia spend 1-4 years in the ocean before returning to freshwater to spawn (Moore et al. 2014). The exact relationship between historical (i.e., smoltification) and contemporary (i.e., ocean) condition in steelhead and age at maturity is unclear (Ward and Slaney 1988; Quinn et al. 2011b), and thus, further investigation is warranted.

In this study we explored the relative influence of stage-specific (i.e., freshwater and ocean) and season-specific ocean growth on maturation of natural- and hatchery-origin summer- and winter-run steelhead (hereafter winter and summer steelhead, respectively) from four populations in British Columbia and Oregon. The objectives of our study were to: (1) identify periods of growth that influence age at maturity in steelhead; (2) investigate

whether ecological carryover or threshold trait models best explain steelhead maturation; 3) determine the timing of the maturation decision window for these steelhead populations; and (4) review literature on steelhead ocean residence to develop hypotheses regarding conditions that could influence different ocean growth profiles. If freshwater growth directly predicts age at maturity, we hypothesized that slow freshwater growth would result in delayed maturation, regardless of the ocean growth experienced. However, if steelhead maturation is determined by ocean growth, we hypothesized that: (1) slow freshwater growth and fast ocean growth would result in early maturation and (2) fast freshwater growth and slow ocean growth would lead to delayed maturation. Finally, we hypothesized that homogenous freshwater and ocean growth (i.e., fast or slow growth during both periods) would result in early maturation (fast growth) or delayed maturation (slow growth), and this could result from either an ecological carryover effect or conditional strategy influence on age at maturity depending upon the relative importance of the two growth periods. Both freshwater and ocean growth rate have been previously shown to affect maturation timing. Therefore we also tested for the relative strength of association between stage-specific growth rates and the probability of maturation to determine the relative importance of carryover effects versus recent experience on maturation. A maturation decision window for California steelhead was proposed to occur in April approximately a year prior to spawning (Satterthwaite et al. 2009). Therefore, we hypothesized that if ocean growth influences age at maturity, differences during this time period would produce variable life history trajectories.

Methods

To test hypotheses about the influence of stage-specific growth on steelhead maturation schedules, we used scales from four different steelhead populations to estimate length-at-age and construct estimated growth profiles: (1) summer steelhead from the Skeena River, British Columbia; (2) summer steelhead from Nass River, British Columbia; (3) winter steelhead from the Willamette River, Oregon; and (4) summer steelhead from the Willamette River. Summer steelhead generally return to freshwater from May—October in relatively immature reproductive state and winter steelhead return from November—April in relatively mature reproductive condition (Burgner et al. 1992; Busby et al. 1996). The summer steelhead populations from the Nass and Skeena rivers and the winter steelhead population from the Willamette River were of natural origin, and summer steelhead from the Willamette River were hatchery origin.

Skeena and Nass River Scale Collection and Ageing.—The Skeena and Nass watersheds are located in northwestern British Columbia (Figure 3.1). Summer steelhead populations from these two rivers expressed 36 unique life-history pathways (Moore et al. 2014). Freshwater residency for steelhead varied between 2 and 6 years, whereas ocean residency varied between 1 to 4 years (Moore et al. 2014). Most (92.9%) steelhead from these basins resided in freshwater for three or four years. The majority of Nass River steelhead (60.5%) spent two years in the ocean and Skeena River steelhead stayed at sea for two years (65.5%; Moore et al. 2014). Steelhead populations from major tributaries within these basins are genetically distinct (Beacham et al. 2012).

Scales from Skeena River summer steelhead were collected from 2010-2014 during the Tyee test fishery that occurs at the mouth of the Skeena River using multipanel and

multimesh-sized gillnet (Moore et al. 2014). The Tyee test fishery is used to evaluate and estimate salmon and steelhead returns to the Skeena River and has been conducted since 1955. Scales from Nass River adult summer steelhead were collected from 2009-2014 at fish wheels that operate in lower portions of the river (Moore et al. 2014). All samples were aged by Birkenhead Scale Analysis. Resorption was assumed to be minimal because steelhead were sampled in the lower reaches of both rivers.

Willamette River Scale Collection and Ageing.—The Willamette River is a major tributary to the Columbia River, joining near Portland, Oregon approximately 150 river kilometers (rkm) from the Pacific Ocean. The upper Willamette River winter-run distinct population segment is listed as threatened under the Endangered Species Act (NMFS 1999) and includes all naturally spawned populations in the Willamette River and its tributaries from Willamette Falls upstream to the Calapooia River (ODFW and NMFS 2011). Winter steelhead typically enter the Willamette River in February—May with peak spawning occurring in late April and early May. Winter steelhead in the Willamette River typically spend two years in freshwater before outmigrating and most return to spawn after two or three years in the ocean (Clemens 2015). Summer steelhead are a nonnative run type (Skamania stock) to the Willamette River basin upstream of Willamette Falls (rkm 41) and were introduced in the 1960s to mitigate habitat loss associated with the construction of impassable dams on tributaries (Busby et al. 1996; ODFW 2004; Clemens 2015). Summer steelhead are released as age-1 smolts and generally spend two or three years in the ocean (Clemens 2015).

Scales from winter and summer steelhead were collected as part of a larger movement, migration, and run-timing study conducted by the University of Idaho at

Willamette Falls Dam in 2012-2014 (Jepson et al. 2015). Scales from steelhead collected in 2012 and 2013 were sent to the Oregon Department of Fish and Wildlife (ODFW) Fish Life History Analysis Project (FLHAP) lab for ageing (Borgerson et al. 2014). Assignment of freshwater and saltwater ages for steelhead captured in 2014 was conducted by the first author. A total of 140 summer and winter steelhead captured at Willamette Falls in 2013 was independently aged by the author and ODFW FLHAP personnel to assess variation in age estimates. Average coefficient of variation in age estimates made by the author and ODFW FLHAP readers was 2.3% for this sample; therefore, samples from 2012-2014 were included in analyses. Images of scale impressions were captured using a Leica DFC295 camera attached to a Leica M125 compound microscope. Images were captured at various magnifications using a computerized video digitizing system (Leica Application Suite, version 4.3.0, Leica Camera AG) and a calibrated scale was imprinted on each image that was used for measurements. We assumed resorption to be minimal because steelhead were sampled in the lower Willamette River.

Sample.—A total of 841 fish from the four populations was included in the analysis, including 268 Skeena River summer steelhead, 301 Nass River summer steelhead, 153 Willamette River winter steelhead, and 119 Willamette River summer steelhead (Table 3.1). Scale ages presented here follow the standard of two numerals separated by a decimal point (Koo 1962; Davis and Light 1985), where the first numeral represents the number of full years spent in freshwater and the second numeral represents the number of years spent in the ocean. For example, a fish with a life history 2.1 resided in freshwater for two years and the ocean for 1 year before returning to spawn. No iteroparous individuals were included in the sample.

Samples were selected to achieve reasonable sample sizes and were therefore limited to the most common life histories present within populations. Brood years of steelhead included in the analysis were: 2004-2007 (Skeena River), 2004-2008 (Nass River), 2008 and 2009 (Willamette River winter steelhead), and 2009 and 2010 (Willamette River summer steelhead; Table 3.1). Individuals were randomly selected from the most common age-at-smolt within each population and brood year to control for age at smoltification, in part because there was little overlap in age at smoltification among populations. Therefore, age at smoltification was constant across all individuals within a population. Population-specific paired life histories were selected to maximize sample sizes and included 4.2 and 4.3 summer steelhead from the Skeena River, 3.2 and 3.3 summer steelhead from the Nass River, 2.2 and 2.3 winter steelhead from the Willamette River, and 1.2 and 1.3 summer steelhead from the Willamette River (Table 3.1). In all basins, the majority of steelhead reside in the ocean for two years. Fifty ocean age-2 individuals were randomly sampled from each brood year from Skeena, Nass, and Willamette river summer steelhead populations, and all ocean age-2 Willamette River winter steelhead were included in the analyzed sample. All ocean age-3 individuals were included in the sample unless the condition of the scale made measuring impractical. Scales were not measured if scale condition was poor; therefore, annual sample totals of ocean age-2 from the Skeena, Nass, and Willamette river summer steelhead populations do not always equal 50 (Table 3.1).

Scale Measurements.—ImageJ software version 1.48 with the ObjectJ plug-in (Rasband 2014; Vischer and Nastase 2014) was used for all scale measurements. One scale from each individual was measured along the anterior-posterior axis, often offset about 20°-25° perpendicular, from the focus of the scale to the scale edge (Figure 3.2; Martinson et al.

2000; Quinn et al. 2011b). If scale circuli along this axis was incomplete, a measurement along a vertical axis was used instead.

The spacing of scale circuli generally reflects the rate at which an individual grows. Narrowly spaced circuli are associated with slow periods of growth (i.e., winter growth for anadromous salmonids in the Northern Hemisphere) while widely spaced circuli are linked to periods of fast growth (i.e., summer growth for anadromous salmonids in the Northern Hemisphere; Quinn 2005; Quist et al. 2012). Additionally, for anadromous fishes, the period of freshwater residence can be distinguished from the period of ocean residence by fine, closely spaced circuli near the focus of the scale indicating freshwater residence, and thick, widely spaced circuli indicating ocean growth (Davis and Light 1985). Given these characteristics, we measured five different increments on each scale: (1) scale focus to ocean entry; (2) focus to end of first ocean summer; (3) focus to end of first ocean winter; (4) focus to end of second ocean summer; and (5) focus to the edge of scale (Figure 3.2).

Analyses.—The Fraser-Lee back-calculation method (Fraser 1916; Lee 1920) was used to estimate length for the i th fish from scale radius of the i th fish at the end of each period t :

$$L_{i,t} = \left(\frac{L_{i,c} - a}{S_{i,c}} \right) S_{i,t} + a, \quad (1)$$

where a is the intercept, $L_{i,t}$ is the back-calculated length of the i th fish at the end of period t , $L_{i,c}$ is the length of the i th fish at capture, $S_{i,t}$ is the radius of the scale from the i th fish at the end of period t , and $S_{i,c}$ is the radius of the hard structure from the i th fish at capture (Ricker 1975). The intercept parameter, a , is the length at which an individual exhibits the onset of

scale formation and can vary by species and population. A value of 34 mm was used in this study based on other published values of length at initial scale formation for *O. mykiss* (Snyder 1938; Kesner and Barnhart 1972; Hopelain 1998; Bond et al. 2008). Estimated growth for the i th fish during period t was calculated as:

$$G_{i,t} = L_{i,t} - L_{i,t-1}, \quad (2)$$

where $L_{i,t}$ is the estimated length for the i th fish at end of the period of interest and $L_{i,t-1}$ is the estimated length for the i th fish at the end of the previous period. Therefore, we estimated growth during freshwater residence (i.e., length at ocean entry), the first ocean summer, the first ocean winter, and the second ocean summer for each steelhead. For a given brood year and population, each growth increment for the paired life histories occurred during the same time period. For example, the first ocean summer growth of Nass River steelhead from both life histories (3.2 and 3.3) and the 2006 brood year occurred during the summer of 2009.

Because the dependent variable was binary (mature at ocean age-2 versus mature at ocean age-3), we used logistic regression in program R to evaluate the probability of maturing relatively early after two ocean years (response) versus three ocean years (non-response; Hosmer et al. 2013; R Development Core Team 2009). We constructed 51 candidate models related to hypotheses about the influence of previous growth history on the probability of maturing (Table 3.2). Specifically, three models were constructed to first determine whether absolute length or previous growth history best predicts steelhead maturation schedules. Individuals of similar body length at maturity can have different growth histories (Metcalf and Monaghan 2001; Ali et al. 2003), and the complex interaction

between length and growth history suggests the need to test whether absolute length or growth provides a trigger for maturation in anadromous salmonids. If absolute length influences the probability of maturing after two ocean years, the logistic regression model will depend on length at the end of ocean residence:

$$\text{logit}(p) = \beta_0 + \beta_1 L_2 + \beta_2 POP, \quad (3)$$

where p is the probability of maturing after two ocean years, L_2 is length at the end of the second ocean summer (i.e., last length estimate prior to two-ocean fish returning to spawn), POP is population, and each β is the parameter of the corresponding covariate. If the probability of maturing after two ocean years depends on previous growth history, the logistic regression model will depend on the smolt length and the seasonal growth increments during ocean residency:

$$\text{logit}(p) = \beta_0 + \beta_1 L_{oe} + \beta_2 G_{s1} + \beta_3 G_{w1} + \beta_4 G_{s2} + \beta_5 POP, \quad (4)$$

where p is the probability of maturing after two ocean years, L_{oe} is estimated length at ocean entry, G_{s1} is growth during the first ocean summer, G_{w1} is growth during the first ocean winter, G_{s2} is growth during the second ocean summer, and POP is population. Each β is the parameter of the corresponding covariate. Two models based on Equation 4 were used, one with absolute growth increments and one with relative growth increments. Relative growth was calculated as the growth during the period of interest minus growth during the previous period divided by growth during the previous period. Because brood year was unbalanced

(Table 3.1), we conservatively did not include brood year as a covariate in any of the models in the candidate set. Brood year did not significantly influence the probability of maturing after two ocean years for Nass River summer steelhead ($\chi^2 = 4.5$, $df = 4$; $P = 0.361$). Additionally, while environmental conditions within and between brood years differ and thus could lead to variability in interannual growth experiences for steelhead, we expected the underlying processes describing steelhead maturation schedules to be similar across years (i.e., similar growth patterns would produce similar trends in maturation despite annual differences in environmental conditions).

To evaluate the influence of specific growth increments and whether absolute or relative growth is more important in predicting the probability of maturing after two ocean years, other candidate models were constructed with both absolute and relative estimated growth increments (Table 3.2). We also fitted models that included interactions between the growth predictor variables to investigate whether growth during a particular period influences maturation differently depending on growth during other periods. We used Bayesian information criterion (BIC; Schwarz 1978) selection in program R to rank models. Models with a BIC score within 2.0 of the top model were considered plausible models. To test for an overall effect of population on the probability of maturing after two ocean years, a Wald chi-square test was used. Once the associations between maturation age and specific growth increments were identified by the model selection process, we estimated the growth for each population at which the probability of maturing was 50%. To assess the 95% confidence limits for the population-specific growth estimates associated with a probability of maturing of 50%, a non-parametric bootstrap percentile method (Efron 1987) was used after the data were re-sampled 1,000 times. Finally, three methods were used to determine

relative importance of growth variables in the top model: (1) a Wald chi-square test; (2) general dominance weights (Budescu 1993); and (3) rescaling by subtracting the mean and dividing by two standard deviations (Gelman 2008). All analyses were conducted using the R statistical computing language (R Development Core Team 2009). Model selection was performed with the *MuMIn* package (Barton 2016). The *yhat* package (Nimon et al. 2013) and the *arm* package (Gelman and Su 2015) were used for the dominance analysis and rescaling, respectively.

Results

Steelhead that matured after three ocean years (mean = 822.7 mm; SD = 69.1) were significantly larger than those maturing after two ocean years (mean = 706.3 mm; SD = 46.2; ANOVA: $F_{1,839} = 794.5$, $P < 0.001$). Estimated FL at the end of the second ocean summer significantly influenced the probability of maturing (equation 3; $z = 4.7$; $P < 0.001$), and steelhead maturing after two years in the ocean were larger at the end of the second ocean summer in all populations except for the Nass River summer steelhead. Hatchery-origin summer steelhead from the Willamette River were on average longer upon ocean entry than steelhead from the other three populations (Figure 3.3). However, Willamette River summer steelhead experienced slow ocean growth, and both British Columbia populations experienced faster ocean growth compared to the other populations (Figure 3.4).

The BIC model selection process identified that the model with length at ocean entry, absolute growth during the first ocean winter, and population ($L_{oe} + G_{w1} + POP$) provided the best description of the data (Table 3.2), indicating that stage-specific growth history influences age at maturity for steelhead. There was little evidence of over-dispersion ($\hat{c} =$

1.09). The probability of maturing was best explained by growth increments (eq. 4) instead of length as both growth models (relative and absolute; equation 4) had more support than the length model (equation 3; Table 3.2). Model selection also indicated that absolute growth increments described the data more appropriately than increments of relative growth (Table 3.2). Models with interactions generally had high BIC scores, suggesting that the marginal effect of a specific growth period on the probability of maturing did not vary by growth during a different period, though some support was found for an interaction between $L_{oe} * G_{w1}$ (delta BIC =2.52). Our top model specified that steelhead maturing after two ocean years were significantly larger upon ocean entry ($z = 3.8; P < 0.001$; Table 3.3) and experienced significantly greater growth during the first ocean winter ($z = 6.5; P < 0.001$; Table 3.3). Increasing length at ocean entry and growth during the first ocean winter both increased the odds of maturing after two ocean years compared to maturing after three ocean years (Table 3.3). Estimated length at ocean entry did not influence estimated growth during the first ocean winter (Figure 3.5; $t = 1.9, P = 0.0542$), suggesting a weak or non-existent carryover effect of estimated FL at ocean entry on estimated growth during the first ocean winter. Population was an important covariate in predicting the probability of maturing after two ocean years ($\chi^2 = 17.5, df = 3; P < 0.001$), emphasizing variation across populations in the growth necessary to achieve a probability of maturing greater than 50%. The probability of maturing after two ocean years was higher for Willamette River summer steelhead for a given amount of growth during freshwater residency and the first ocean winter than the other three populations (Figures 3.6 and 3.7). Values of first ocean winter growth necessary for a probability of maturing after two ocean years equal to 50% were highest for Skeena River summer steelhead and Willamette River winter steelhead (Figure 3.8).

Two of three methods to test for relative variable importance indicated that growth during the first ocean winter was more important than length at ocean entry in predicting the probability of maturing after two ocean years. After rescaling each growth variable, the coefficient for first winter ocean growth (1.266) was more than 1.5 times the coefficient for length at ocean entry (0.753). General dominance weights were higher for first winter ocean growth (0.049) than length at ocean entry (0.019), suggesting that first winter ocean growth contributed more unique variance on average across models of all-possible-subset sizes than length at ocean entry. Finally, a statistically significant difference did not exist between the coefficients for length at ocean entry and growth during the first ocean winter ($\chi^2 = 2.8$, $df = 1$; $P = 0.10$).

Discussion

Age at maturity of both winter and summer steelhead was influenced by length at ocean entry and growth during the first ocean winter. Although we observed a positive relationship between body size and the probability of maturing, model selection indicated that previous growth history best described the probability of maturing after two ocean years. Length at ocean entry and first ocean winter growth were both inversely associated with age at maturity. The results indicate that a threshold trait model best describes steelhead maturation due to the relative importance of winter ocean growth in determining age at maturity. Observed results are consistent with a study of winter steelhead that found a weak but nonsignificant inverse relationship between size at smoltification (i.e., FL at ocean entry) and the propensity for early maturation (Quinn et al. 2011b). The authors also found a statistically significant inverse association between early ocean growth (i.e., first year at sea)

and age at first return. The observed results corroborate other studies of both natural- and hatchery-origin anadromous salmonids that found inverse relationships between smolt length and age at return (Vøllestad et al. 2004; Tattam et al. 2015). The influence of ocean growth in the maturation schedules of chum salmon *Oncorhynchus keta* was similar to steelhead in that increased ocean growth increased the probability of maturing (Morita and Fukuwaka 2006). However, Tattam et al. (2015) did not find an influence of ocean productivity on age at maturity and Vøllestad et al. (2004) observed a significant negative relationship between the proportion of jack coho salmon *Oncorhynchus kisutch* and ocean growth, suggesting that some variation exists among anadromous salmonid species in the effect of ocean growth on age at maturity. The results help characterize and identify periods of growth that influence maturation schedules in steelhead and provide the first evidence that ocean growth during a period of reduced resource availability may affect the decision to return. Below we discuss potential genotypic controls on steelhead maturation that could not be accounted for, steelhead maturation strategy, differences in pelagic habitat conditions that potentially influence ocean growth, and fitness-related trade-offs.

Genotypic controls on maturation

Maturation onset in steelhead is controlled through activation of the brain-pituitary-gonad axis and genetic factors, metabolic signals, and environmental inputs are linked to initiation of maturation in teleosts (Taranger et al. 2010). Genetic differences among individuals produce variability in life history expression (Ruzycki et al. 2009; Berejikian et al. 2014), but separating the genotypic and environmental cues that influence maturation

timing remains difficult (Morita et al. 2005; Bourret et al. 2016) and was beyond the scope of this study. We observed similar growth-related trends in maturation schedules across all three natural-origin populations, providing evidence for similar underlying general genetic controls on age at maturity across populations. The population-specific responses to growth that we observed could indicate inter-population variation in the threshold for winter ocean growth, which has a genetic origin (Piché et al. 2008). Studies focusing on patterns of anadromy and residency in *O. mykiss* have found evidence for genetic and maternal controls on the incidence of maturation (McMillan et al. 2012; Doctor et al. 2014; Pearse et al. 2014). Furthermore, research on other anadromous salmonids has found a significant genetic component for the timing of sexual maturation (e.g. Chinook salmon; Hankin et al. 1993; Heath et al. 1994), but many of these have concentrated on jacks and precocious males. However, it is likely that these findings hold true and population-specific genotypic influences exist for steelhead maturation. There could also be genetic effects on growth rates (Gjerde et al. 1994), and this interaction complicates our mechanistic understanding of life history diversity. Heritability estimates for Fulton's condition factor were high and quantitative trait loci have been identified for body mass and condition factor in *O. mykiss* (Martyniuk et al. 2003), further complicating the ability to decipher the proximate cues for maturation. Although our results provide insight into the influence of ocean growth on maturation schedules for steelhead, we cannot determine the extent to which the variation in age maturity is of genotypic or phenotypic origin as acquiring biological data on the proximate mechanisms influencing the expression of a phenotype is difficult (Tomkins and Hazel 2007) and outside the scope of this study.

Steelhead maturation strategy

Conditional strategies and threshold traits clearly contribute to life history diversity in salmonines (Kendall et al. 2015; Sloat et al. 2014) and involve using proximate cues to select a specific life history pathway that will maximize expected fitness given encountered environmental conditions (Roff 1996). Under this model, the current physiological status (i.e., condition) of the fish relative to a genetically-determined threshold predicts the expression of life history pathways (Mangel 1994; Piché et al. 2008; Thorpe et al. 1998). We used growth rate as a proxy for condition because it reflects recent performance in a particular environment (Dodson et al. 2013), can directly influence survival to reproduction and fecundity (Friedland et al. 2000; Peyronnet et al. 2007), and may provide an important cue for individuals to begin reallocating energy from somatic growth to gametogenesis. The model selection process identified that both smolt length and growth during the first ocean winter were important in predicting age at maturity of steelhead. However, general dominance weights and rescaling of model coefficients indicated that growth during the first ocean winter was more influential in the maturation schedules of steelhead. Therefore, the observed results suggest that a conditional strategy model may best explain steelhead maturation.

An individual's reproductive system is generally suppressed until somatic development has reached a sufficient level (Taranger et al. 2010). In steelhead, energetic reserves are not only necessary for reproductive development, but also for migration, stream residence prior to spawning, nest building, and other energetically demanding behaviors associated with spawning (Jonsson et al. 1991). Therefore, the results suggest that fast winter

growth provides a signal that sufficient energetic reserves are available for maturation and the associated behaviors. Recent research has focused on the specific timing of when a threshold is exceeded (i.e., decision windows; Satterthwaite et al. 2009; Beakes et al. 2010). Steelhead maturation must be initiated well in advance of the actual spawning period because migration and gonadal development can take months to complete (Sumpter et al. 1984; Bromage and Cumaranatunga 1988); therefore, the maturation decision window for steelhead must precede spawning. We show that a maturation decision window occurs during the first ocean winter. Although the timing of a first ocean winter decision window is logical for winter steelhead that spawn during the subsequent winter, summer steelhead maturing after two ocean years remain in the ocean for a second winter before returning to freshwater and do not spawn until two years after the first ocean winter. We were unable to estimate growth during the second ocean winter in summer steelhead because some fish returned before a complete winter growth period was laid down on the scale. Photoperiod is an important environmental factor for the initiation of maturation because steelhead reside at moderate to high latitudes (Taranger et al. 2010). Generally, *O. mykiss* maturation is initiated during increasing photoperiod and reproduction is regulated by an endogenous circannual clock that is entrained by the seasonal changes in daylength (Randall et al. 1998). The observed timing of the decision window in winter steelhead appears to coincide with this circannual rhythm and increasing photoperiod.

The distribution of conditional thresholds for maturation varies amongst populations due to local selective pressures (Hazel et al. 1990; Piché et al. 2008). We observed differences among the four steelhead populations in the amount of first ocean winter growth required for an increase in the probability of maturing after two ocean years, suggesting that

selective pressures are acting differently on steelhead from different populations and population-specific growth thresholds for maturation could be genetic based. Population-specific differences in the oceanic migration of Pacific salmon have been reported (Quinn et al. 2011a), which could reflect genetic influence on the distribution of salmon and steelhead in the ocean. Therefore, selective forces based on growth opportunities in different ocean habitats could produce the population-specific growth differences required for a 50% probability of maturing. Importantly, the probability thresholds presented here are not conditional thresholds; instead, the estimates provide a method for conceptualizing threshold differences amongst the populations. A fitness advantage of faster growth due to favorable habitat conditions could result in directional selection for higher first winter ocean growth thresholds for maturation. Populations that reside at lower latitudes in the North Pacific Ocean (NPO) should evolve higher first ocean winter growth thresholds and thus later maturation due to environmental conditions that are favorable for faster growth. The growth required for a 50% probability of maturing after two ocean years was lowest for hatchery-origin summer steelhead from the Willamette River. Positive selection for adaptation to the hatchery environment leads to deleterious consequences in the wild (Ford 2002) and could result in winter growth conditional thresholds for maturation that are lower than those of natural-origin populations. For example, reduced forage capacity of hatchery-origin steelhead could result in directional selection for a lower conditional threshold. Regardless of inter-population differences, the underlying patterns were the same across all three natural-origin populations, indicating a similar maturation mechanism across steelhead populations.

Inconsistencies in the relationship between freshwater and ocean growth and steelhead age at maturity have been reported. Ward and Slaney (1988) did not observe a

relationship between mean smolt size and age at return for Keogh River, British Columbia steelhead, and Quinn et al. (2011b) also did not find significant evidence for early-maturing winter steelhead to be larger as smolts. However, similar to our results, Hooton et al. (1987) detected earlier maturation for larger steelhead smolts. Additionally, Quinn et al. (2011b) observed greater first year ocean growth in steelhead that matured after two ocean years compared to fish that matured a year later. Scales were used to estimate length at ocean entry for steelhead in all of the above studies. Inconsistencies in measurable effects of freshwater growth on age at maturation for steelhead could be caused by population-specific differences in the importance of freshwater growth in age at maturity, variability in the angle of scale measurement, poorly representative scale samples, or incorrect ocean age assignments.

Validation is an important component of an age and growth study and refers to the accuracy of the age or growth estimate (Beamish and McFarlane 1983; Quist et al. 2013). Inaccurate growth estimations could lead to misidentification of specific periods that are important in determining age at maturation; however, we did not conduct validation of our growth estimates. Our estimates of length at ocean entry and growth during the first ocean summer are similar to estimates made by other researchers and similar to the fork length (FL) of fish captured in the wild. Mean estimated length at the end of the first ocean summer for all steelhead included in this study was 361.5 mm, which is similar to mean FL (332 mm; $n = 134$) of juvenile steelhead captured during their first summer at sea from 1993-2000 and mean FL of captured ocean age-0 steelhead from 1955-1985 (FL = 337 mm; $n = 53$; Myers et al. 2001). Our estimates of length at ocean entry (mean = 188.0 mm), were also similar to the FL of steelhead smolts from the Keogh River (FL = 173 mm; Ward and Slaney 1988). Hooton et al. (1987) used scales and back-calculation techniques to estimate the length of

steelhead as they entered the ocean from six populations on Vancouver Island, British Columbia, and the mean back-calculated lengths ranged from 173 to 185 mm.

Pelagic habitat heterogeneity

Variation in the observed growth rates during the first ocean winter could be caused by habitat heterogeneity, manifested as disparities in water temperature and the distribution and abundance of prey and its energetic content. Energy assimilation, and therefore growth and survival, in salmon and steelhead at sea are influenced by pelagic habitat conditions (e.g., Quinn 2005; Beauchamp et al. 2007). Unfortunately, little is known about the winter ecology of steelhead in the NPO because sampling is sporadic (Welch et al. 1998) and catches have been low or nonexistent (Myers et al. in press). Ocean thermal conditions could influence steelhead growth via effects on metabolic processes, the distribution of prey, and migratory behavior (Wells et al. 2007; Wells et al. 2008; Friedland and Todd 2012). Optimal ocean growth in steelhead occurs during a narrow temperature window and steelhead growth was higher in years when the thermal experience was close to optimal (Atcheson et al. 2012a). Winter sea surface temperatures in the central NPO are generally closer to the thermal optima for steelhead than temperatures in the Gulf of Alaska (GOA), which could result in faster growth for fish residing in the central NPO during winter.

The winter distribution and quality of prey in the pelagic environment directly influence steelhead growth. In the context of the observed results, steelhead experiencing greater prey availability and quality may be able to acquire the energy resources required for homeward migration and spawning earlier and therefore return at a younger age. The

consumption of specific prey species varies based on the pelagic distribution and age of steelhead (Light 1985; Kaeriyama et al. 2004; Atcheson et al. 2012a, b). A greater diversity of prey was observed in the stomachs of steelhead captured in the GOA than steelhead captured in the central NPO, where steelhead primarily feed on fish and cephalopods (Atcheson et al. 2012b). Since cephalopods have a higher caloric value than fish, this has consequences for growth (Davis et al. 1998; Davis 2003). Estimates of body weights of ocean age 1 steelhead migrating to the central NPO were significantly larger than steelhead sampled in the GOA (Atcheson et al. 2012a), indicating that steelhead condition parallels spatial distribution. Bioenergetics modeling also showed that feeding rates were lower in the GOA than in the central NPO during the first ocean year (Atcheson et al. 2012a). Quinn et al. (2012) found differences in stable isotope values amongst steelhead populations that reflected differences in trophic ecology or foraging location. Given the known differences in prey quality and consumption patterns, steelhead condition, and sea surface temperatures between the NPO and GOA, it could be hypothesized that steelhead that inhabit the NPO have higher growth and thus different growth trajectories (Figure 3.9). Stable isotope analysis (Quinn et al. 2012) could be used to test this hypothesis.

The importance of winter ocean growth, as opposed to summer growth, is interesting. The winter has been proposed as a critical period for juvenile salmon (Beamish and Mahnken 2001); however, there is no consensus as to whether or not winter is a critical period for salmon or steelhead (SSC and CSRS 2016). A reduction in feeding intensity of salmon and steelhead occurs during the winter and this may be a function of reduced metabolic demand at lower temperatures (Ueno et al. 1997; Nagasawa 2000) rather than a reduction in prey availability (Naydenko and Kuznetsova 2013). Differences in winter ocean growth could be

more important than summer growth in predicting maturation for two reasons: 1) there is not sufficient time after the summer to initiate maturation, develop gonads or ovaries, and undergo homeward migration (Taranger et al. 2010), and 2) given ocean productivity during the summer, there are sufficient foraging opportunities for most fish, regardless of size. Given the known differences in age-specific pelagic distribution of steelhead, prey consumption and quality, steelhead condition, and spatial heterogeneity in sea surface temperatures, it could be hypothesized that steelhead that inhabit the NPO have higher growth and thus different growth trajectories (Figure 3.8). Stable isotope analysis (Quinn et al. 2012) could be used to test this hypothesis. Future research should be aimed at deciphering differences in the winter distribution and winter ecology of steelhead.

Fitness-related considerations

The fitness benefits and costs that drive the tradeoff between allocations of energy to reproduction versus growth produce life history variation in anadromous salmonids. Age at first reproduction influences fitness through generation time, social status, and the size dependency of fecundity (Stearns and Koella 1986). Because there are significant positive relationships between body length, egg mass, and fecundity (Quinn et al. 2011b), natural selection should favor steelhead that continue to allocate energy to somatic growth and mature at a larger size. However, delaying maturation reduces the probability of successfully reproducing, thus leading to the life history trade-off shaping the decision to mature. Quinn et al. (2011b) did not observe an effect of ocean growth on egg mass or egg number, and suggested that the processes controlling the egg size–fecundity trade-off were unclear. It has

been hypothesized that individuals develop an optimum number and size of eggs depending on their growth and food supply during maturation (Hays and Brett 1988). Given the uncertainties in how ocean growth affects egg mass and fecundity, we can only hypothesize about the fitness effects of variability in ocean growth and the evolution of adaptive phenotypic plasticity. The implicit assumption within life history theory that natural selection will favor schedules of survival and fecundity that generate the highest per capita rate of fitness (Roff 1992; Stearns 1992) suggests that steelhead are selecting their respective life history trajectories based on freshwater and first ocean winter growth to maximize fitness. Nonetheless, because overall recruitment variations appear to be related primarily to variation in ocean, not freshwater, survival (Ward 2000), understanding the fitness implications of different ocean growth trajectories is critical and should be a focus of future research.

The age composition and size of anadromous salmonids at maturity and the mechanisms that influence variability in these life history characteristics are of evolutionary, ecological, and management interest and present insight into the population dynamics of Pacific salmon and steelhead. From an evolutionary viewpoint, thresholds for life history expression can evolve rapidly due to anthropogenic alterations (Phillis et al. 2016) and we therefore need to understand how shifts in these thresholds influence population dynamics. From an ecological perspective, understanding how both freshwater and ocean growth affect maturation schedules provides insight into how stage- or age-specific expenditures of reproductive effort respond to factors that influence survival and fecundity (Schaffer 2004), which results in the evolution of different life history strategies (Winemiller and Rose 1992). Changes in life history expression can have effects on population dynamics through

influences on resiliency and the ability to respond to environmental change (Hutchings 2003; Schindler et al. 2010; Moore et al. 2014). Therefore, understanding how proximate and ultimate cues alter life history expression is important for predicting the response of populations to future anthropogenic disturbances and natural changes in the environment (Healy 1991; Scheuerell and Williams 2005).

From a management perspective, maintaining late-maturing salmon and steelhead is important to the quality of commercial, tribal, and recreational fisheries, as larger fish are generally desired. Variability in age at maturity, leading to differences in individual size, may affect the total biomass of catch (Bilton et al. 1982). Additionally, declines in age or size have been observed in many populations of salmon and steelhead (Bigler et al. 1996; Quinn 2005), and fishery-induced selection has been a hypothesized source of this decline (Kendall et al. 2009; Kuparinen et al. 2009). Because increases in adult mortality are expected to decrease plasticity (Hutchings 2004), the decrease in age at maturity of salmon and steelhead and convergence of life history expression in anadromous salmonids could result from increased mortality pressures associated with fishing. Understanding maturation schedules is critical before conclusions can be drawn about potential evolutionary and ecological effects of fishery selection on populations of Pacific salmon. Maintaining life history diversity is important for ecosystem stability (Schindler et al. 2010; Moore et al. 2014) and the stability of indigenous fisheries (Nesbitt and Moore 2016); therefore, incorporating life history knowledge into the management of salmon and steelhead should be emphasized. Energetic modeling showed that under future climate-induced sea surface temperature scenarios, steelhead growth would be reduced because temperatures warm beyond the optimum growth temperature (Atcheson et al. 2012a). If this is the case, achieving a particular threshold for

maturing could be delayed and therefore, fish would return at an older age. Conversely, reduced growth could lead to lower thresholds for maturation via selective forces and the size at return would continue to decline. Our results help clarify steelhead maturation schedules and illustrate that growth trajectories during both freshwater and ocean residence can lead to variability in age at maturity.

Acknowledgements

This project would not have been successful without the willingness of Dean Peard to share data and scale images for Nass and Skeena River steelhead. We are extremely thankful for and appreciate his generosity and collaboration. Kanani Bowden and the ODFW FLHAP provided valuable insight and support, and we thank them for their continued collaboration. We appreciate reviews from Elizabeth Ng, Tim Johnson, and Mike Quist on an earlier version of the manuscript.

References

- Ali, M., Nieceza, A. and Wootton, R.J. 2003. Compensatory growth in fishes: a response to growth depression. *Fish Fish.* **4**: 147–190.
- Atcheson, M.E., Myers, K.W., Beauchamp, D.A. and Mantua, N.J., 2012a. Bioenergetic response by steelhead to variation in diet, thermal habitat, and climate in the North Pacific Ocean. *T. Am. Fish. Soc.* **141**: 1081–1096.

- Atcheson, M.E., Myers, K.W., Davis, N.D. and Mantua, N.J., 2012b. Potential trophodynamic and environmental drivers of steelhead (*Oncorhynchus mykiss*) productivity in the North Pacific Ocean. *Fish. Oceanogr.* **21**: 321–335.
- Barton, K. 2016. MuMIn: Multi-Model Inference. R package version 1.15.6.
- Beacham, T.D., Wallace, C.G., Le, K.D. and Beere, M. 2012. Population structure and run timing of steelhead in the Skeena River, British Columbia. *N. Am. J. Fish. Manage.* **32**: 262–275.
- Beakes, M.P., Satterthwaite, W.H., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M., and Mangel, M. 2010. Smolt transformation in two California steelhead populations: effects of temporal variability in growth. *Transactions of the American Fisheries Society* **139**: 1263–1275.
- Beamish, R.J and McFarlane, G.A. 1983. The forgotten requirement for age validation in fisheries biology. *T. Am. Fish. Soc.* **112**: 735–743.
- Beamish, R.J., and Mahnken, C. 2001. A critical size and period hypotheses to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Prog. Oceanogr.* **49**: 423–437.

- Beauchamp, D.A., Cross, A.D., Armstrong, J.L., Myers, K.W., Moss, J.H., Boldt, J.L. and Haldorson, L.J. 2007. Bioenergetic responses by Pacific salmon to climate and ecosystem variation. *Nor. Pac. Anadr. Fish Comm. Bull.* **4**: 257–269.
- Behnke, R.J. 2002. Trout and salmon of North America. The Free Press, New York.
- Berejikian, B.A., Bush, R.A., and Campbell, L.A. 2014. Maternal control over offspring life history in a partially anadromous species, *Oncorhynchus mykiss*. *T. Am. Fish. Soc.* **143**: 369–379.
- Bilton, H.T., Alderdice, D.F., and Schnute, J.T. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. *Can. J. Fish. Aquat. Sci.* **39**: 426–447.
- Bond, M.H., Hayes, S.A., Hanson, C.V., and MacFarlane, R.B. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. *Can. J. Fish. Aquat. Sci.* **65**: 2242–2252.
- Borgerson, L., Clemens, B., Bowden, K., and Gunckel, S. 2014. Fish life history analysis project: methods for scale analysis. Oregon Department of Fish and Wildlife, Information Report 2014-10, Corvallis.

- Bourret, S.L., Caudill, C.C. and Keefer, M.L. 2016. Diversity of juvenile Chinook salmon life history pathways. *Rev. Fish. Biol. Fisheries* **26**: 375–403.
- Bromage, N. and Cumaranatunga, R. 1988. Egg production in the rainbow trout. *In* Recent advances in aquaculture. *Edited* by J.F. Muir and R.J. Roberts. Springer, Netherlands pp. 63–138.
- Budescu, D.V. 1993. Dominance analysis: A new approach to the problem of relative importance of predictors in multiple regression. *Psychol. Bull.* **114**: 542–551.
- Burgner, R.L., Light, J.T., Margolis, L., Okazaki, T., Tautz, A., and Ito, S. 1992. Distribution and origins of steelhead trout (*Oncorhynchus mykiss*) in offshore waters of the North Pacific Ocean. *Int. N. Pac. Fish. Comm. Bull.* 51.
- Busby, P.J., Wainwright, T.C., Bryant, G.J., Lierheimer, L.J., Waples, R.S., Waknitz, F.W. and Lagomarsino, I.V. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon, and California. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.
- Clemens, B.J. 2015. A survey of steelhead age and iteroparity rates from a volunteer angler program in the Willamette River basin, Oregon. *N. Am. J. Fish. Manage.* **35**: 1046–1054.

Davis, N.D. 2003. Feeding ecology of Pacific salmon (*Oncorhynchus* spp.) in the central North Pacific and central Bering Sea 1991–2000. Doctoral dissertation, Hokkaido University, Hakodate, Japan.

Davis, N.D., and Light, J.T. 1985. Steelhead age determination techniques. International North Pacific Fisheries Commission. FRI-UW–8506. Fisheries Research Institute, University of Washington, Seattle, Wash.

Davis, N.D., Myers, K.W. and Ishida, Y. 1998. Caloric values of high-seas salmon prey organisms and simulated salmon ocean growth and prey consumption. Nor. Pac. Anadr. Fish Comm. Bull. **1**: 146–162.

Doctor, K., Berejikian, B., Hard, J.J., and Van Doornik, D. 2014. Growth-mediated life history traits of steelhead reveal phenotypic divergence and plastic response to temperature. T. Am. Fish. Soc. **143**: 317–333.

Efron, B. 1987. Better bootstrap confidence intervals. J. Am. Stat. Assoc. **82**: 171–185.

Falconer, D.S. 1989. Introduction to Quantitative Genetics. Longmans, N.Y.

Flemming, I.A., and Gross, M.R. 1994. Breeding competition in a Pacific salmon (Coho: *Oncorhynchus kisutch*) Measures of natural and sexual selection. Evol. **48**: 637-657.

Ford, M.J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. *Conserv. Biol.* **16**: 815–825.

Fraser, C.M. 1916. Growth of the spring salmon. *Trans. Pac. Fish. Soc.* **7**: 5–8.

Friedland, K.D., Hansen, L.P., Dunkley, D.A., and MacLean, J. C. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES. J. Mar. Sci.* **57**: 419–429.

Friedland, K.D. and Todd, C.D. 2012. Changes in Northwest Atlantic Arctic and Subarctic conditions and the growth response of Atlantic salmon. *Polar Biol.* **35**: 593–609.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Statist. Med.* **27**: 2865–2873.

Gelman, A., and Su, Y. 2015. *arm: Data Analysis Using Regression and Multilevel/Hierarchical Models*. R package version 1.8-6.

Gjerde, B., Simianer, H., and Refstie, T. 1994. Estimates of genetic and phenotypic parameters for body weight, growth rate and sexual maturity in Atlantic salmon. *Livestock Prod. Sci.* **38**: 133–143.

- Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. *Nature* **313**: 47–48.
- Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* **11**: 92–98.
- Hankin, D.G., Nicholas, W., Downey, T.W. 1993. Evidence for inheritance of age of maturity in Chinook salmon *Oncorhynchus tshawytscha*. *Can. J. Fish. Aquat. Sci.* **50**: 347–358.
- Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. and Bearhop, S. 2011. Carry-over effects as drivers of fitness differences in animals. *J. Anim. Ecol.* **80**: 4–18.
- Hazel, W.N., Smock R, and Johnson, D.M. 1990. A polygenic model for the evolution and maintenance of conditional strategies. *Proc. R. Soc. Lond. B. Biol. Sci.* **242**: 181–187.
- Heath, D.D., Devlin, R.H., Heath, J.W. and Iwama, G.K. 1994. Genetic, environmental and interaction effects on the incidence of jacking in *Oncorhynchus tshawytscha* (chinook salmon). *Heredity* **72**: 146–154.
- Henderson, M.A., and Cass, A.J. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* **48**: 988–994.

- Hooton, R.S., Ward, B.R., Lewynski, V.A., Lirette, M.G. and Facchin, A.R. 1987. Age and growth of steelhead in Vancouver Island populations. Province of British Columbia, Ministry of Environment and Parks Technical Circular No. 77.
- Hopelain, J.S. 1998. Age, growth, and life history of Klamath River Basin steelhead *Oncorhynchus mykiss irideus* as determined from scale analysis. Inland Fisheries Division, California Fish and Game, Sacramento, Calif. Admin. Rep. No. 98-3.
- Hosmer Jr, D.W., Lemeshow, S., and Sturdivant, R.X. 2013. Applied logistic regression. John Wiley and Sons, Hoboken, N.J.
- Hutchings, J.A. 2004. Norms of reaction and phenotypic plasticity in salmonid life histories. *In Evolution Illuminated: Salmon and Their Relatives. Edited by A.P. Hendry and S.C. Stearns.* Oxford University Press, Oxford pp. 154–174.
- Jepson, M.A., Keefer, M.L., Caudill, C.C., Clabough, T.S., Erdman, C.S., Blubaugh, T., and Sharpe, C.S. 2015. Migratory behavior, run timing, and distribution of radio-tagged adult winter steelhead, summer steelhead, spring Chinook salmon, and coho salmon in the Willamette River: 2011-2014. UI FERL for U.S. Army Corp of Engineers Portland District, Technical Report 2015-1, Portland, Oreg.

- Jonsson, N. and Jonsson, B. 2003. Energy allocation among developmental stages, age groups, and types of Atlantic salmon (*Salmo salar*) spawners. *Can. J. Fish. Aquat. Sci.* **60**: 506–516.
- Jonsson, N., Jonsson, B., and Hansen, L.P. 1991. Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). *J. Fish Biol.* **9**: 739–744.
- Kaeriyama, M., Nakamura, M., Edpalina, R., Bower, J.R., Yamaguchi, H., Walker, R.V. and Myers, K.W. 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fish. Oceanogr.* **13**: 197–207.
- Kendall, N.W., Hard, J.J. and Quinn, T.P. 2009. Quantifying six decades of fishery selection for size and age at maturity in sockeye salmon. *Evol. Appl.* **2**: 523–536.
- Kendall, N.W., McMillan, J.R., Sloat, M.R., Buehrens, T.W., Quinn, T.P., Pess, G.R., Kuzishchin, K.V., McClure, M.M., and Zabel, R.W. 2015. Anadromy and residency in steelhead and rainbow trout *Oncorhynchus mykiss*: a review of the processes and patterns. *Can. J. Fish. Aquat. Sci.* **72**: 319–342.
- Kesner, W.D., and Barnhart, R.A. 1972. Characteristics of the fallrun steelhead trout *Salmo gairdneri gairdneri* of the Klamath River system with emphasis on the half-pounder. *Calif. Fish Game.* **58**: 204–220.

- Koo, T.S.Y. 1962. Age and growth studies of red salmon scales by graphical means. *In* Studies of Alaska red salmon. *Edited by* T.S. Koo. University of Washington Press, Seattle, Wash. pp. 53–121.
- Kuparinen, A., Kuikka, S. and Merilä, J. 2009. Estimating fisheries-induced selection: traditional gear selectivity research meets fisheries-induced evolution. *Evol. Appl.* **2**: 234–243.
- Lee, R.M. 1920. A review of the methods of age and growth determination in fishes by means of scales. Fishery Investigations, Series II, Marine Fisheries, Great Britain Ministry of Agriculture, Fisheries and Food, 4.
- Light, J.T. 1985. Food and feeding of steelhead trout in the epipelagic waters of the North Pacific Ocean. (Document submitted to International North Pacific Fisheries Commission.) 25 p. FRI-UW-8507. Fish. Res. Inst., Univ. Washington, Seattle.
- Mangel, M. Climate change and salmonid life history variation. 1994. *Deep Sea Research, II (Topical Studies in Oceanography)* **41**: 75–106
- Martinson, E.C., Masuda, M.M., and Helle, J.H. 2000. Back-calculated fish lengths, percentages of scale growth, and scale measurements for two scale measurement methods used in studies of salmon growth. *N. Pac. Anadr. Fish Comm. Bull. No. 2* pp. 331–336.

- Martyniuk, C.J., Perry, G.M.L., Mogahadam, H.K., Ferguson, M.M. and Danzmann, R.G. 2003. The genetic architecture of correlations among growth-related traits and male age at maturation in rainbow trout. *J. Fish Biol.* **63**: 746–764.
- McMillan, J.R., Dunham, J.B., Reeves, G.H., Mills, J.S., and Jordan, C.E. 2012. Individual condition and stream temperature influence early maturation of rainbow and steelhead trout, *Oncorhynchus mykiss*. *Environ. Biol. Fish.* **93**: 343–355.
- Metcalf, N.B. and Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends Ecol. Evol.* **16**: 254–260.
- Moore, J. W., Yeakel, J.D., Peard, D., Lough, J., and Beere, M. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. *J. Anim. Ecol.* **83**:1035–1046.
- Morita, K., and Fukuwaka, M. 2006. Does size matter most? The effect of growth history on the probabilistic reaction norm for salmon maturation. *Evolution* **60**: 1516–1521.
- Morita, K., Morita, S.H., Fukuwaka, M., and Matsuda, H. 2005. Rule of age and size at maturity of chum salmon (*Oncorhynchus keta*): implications of recent trends among *Oncorhynchus* spp.. *Can. J. Fish. Aquat. Sci.* **62**: 2752–2759.

- Myers, K.W., Walker, R.V., Burgner, R.L. and Anma, G. 2001. Distribution, origins, biology, and ecology of juvenile steelhead (*Oncorhynchus mykiss*) in the Gulf of Alaska in summer 1993–2000. Nor. Pac. Anadr. Fish Comm. Technical Report, 2: 30–31. Available: www.npafc.org/new/pub_technical.html. (March 2016)
- Nagasawa, K. 2000. Winter zooplankton biomass in the subarctic North Pacific, with a discussion on the overwintering survival strategy of Pacific salmon (*Oncorhynchus* spp.). NPAFC Bull. 2: 21–32. (Available at www.npafc.org).
- Naydenko, S.V., and N.A. Kuznetsova. 2013. Food supply of juvenile pink salmon in the subarctic frontal zone of the western North Pacific Ocean in the winter and spring. NPAFC Tech. Rep. 9: 253–254. (Available at www.npafc.org).
- Nesbitt, H.K. and Moore, J.W. 2016. Species and population diversity in Pacific salmon fisheries underpin indigenous food security. *J. of Appl. Ecol.* doi: 10.1111/1365-2664.12717
- Nicieza, A.G. and Brana, F., 1993. Relationships among smolt size, marine growth, and sea age at maturity of Atlantic salmon (*Salmo salar*) in northern Spain. *Can. J. Fish. Aquat. Sci.* **50**:1632–1640.
- Nimon, K., Oswald, F., and Kyle Roberts, J. 2013. yhat: Interpreting Regression Effects. R package version 2.0-0.

- NMFS (National Marine Fisheries Service). 1999. Endangered and threatened species: threatened status for two ESUs of steelhead in Washington and Oregon. Federal Register 64:57 (25 March 1999):14517–14528.
- O'Connor, C.M., Norris, D.R., Crossin, G.T. and Cooke, S.J. 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere* 5: 1–11.
- ODFW (Oregon Department of Fish and Wildlife). 2004. Upper Willamette Steelhead HGMP 2004. Upper Willamette Summer Steelhead (Stock 24). ODFW, Salem.
- ODFW (Oregon Department of Fish and Wildlife) and NMFS (National Marine Fisheries Service). 2011. Upper Willamette River conservation and recovery plan for Chinook Salmon and steelhead. Report prepared for the ODFW, Salem and NMFS, Northwest Region, Portland, Oreg.
- Pearse, D.E., Miller, M.R., Abadía-Cardoso, A. and Garza, J.C. 2014. Rapid parallel evolution of standing variation in a single, complex, genomic region is associated with life history in steelhead/rainbow trout. *Proc. Biol. Sci.* **281**: 20140012.
- Peyronnet, A., Friedland, K.D., Ó Maoileidigh, N., Manning, M., and Poole, W.R. 2007. Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar*, L. *J. of Fish Biol.* **71**: 684–700.

- Phillis, C.C., Moore, J.W., Buoro, M., Hayes, S.A., Garza, J.C. and Pearse, D.E. 2016. Shifting thresholds: rapid evolution of migratory life histories in steelhead/rainbow trout, *Oncorhynchus mykiss*. *J. Hered.* **107**: 51–60.
- Piché, J., Hutchings, J.A. and Blanchard, W. 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. *Proc. Biol. Sci.* **275**: 1571–1575.
- Pevan, C.M., Whitney, R.R., and Williams, K.R. 1994. Age and length of steelhead smolts from the Mid-Columbia River Basin, Washington. *N. Am. J. Manage.* **14**: 77–86.
- Quinn, T.P. 2005. *The Behavior and Ecology of Pacific Salmon and Trout*. American Fisheries Society, Bethesda, Maryland.
- Quinn, T.P., Chamberlin, J., and Brannon, E.L. 2011a. Experimental evidence of population-specific marine spatial distributions of Chinook salmon, *Oncorhynchus tshawytscha*. *Environ. Biol. Fish.* **92**: 313–322.
- Quinn, T.P., Seamons, T.R., VØllestad, L.A., and Duffy, E. 2011b. Effects of growth and reproductive history on the egg-size fecundity trade-off in steelhead. *T. Am. Fish. Soc.* **140**: 45–51.

- Quinn, T.P., Seamons, T.R., and Johnson, S.P. 2012. Stable isotopes of carbon and nitrogen indicate differences in marine ecology between wild and hatchery-produced steelhead. *T. Am. Fish. Soc.* **141**: 526–532.
- Quist, M.C., Pegg, M.A., and DeVries, D.R. 2012. Age and Growth. *In Fisheries techniques*, 3rd edition. *Edited by* A.V. Zale, D.L. Parrish, and T.M. Sutton. American Fisheries Society, Bethesda, Maryland pp. 677-731.
- Randall, C.F., Bromage, N.R., Duston, J. and Symes, J. 1998. Photoperiod-induced phase-shifts of the endogenous clock controlling reproduction in the rainbow trout: a circannual phase–response curve. *J. Reprod. and Fertil.* **112**: 399–405.
- Rasband, W.S., 2014. ImageJ. US National Institutes of Health; Bethesda, Maryland, USA: 1997–2012.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. of Fish. Research Board Can.* **191**: 1–382.
- Roff, D.A. 1992. *The Evolution of Life Histories: Theory and Analysis*. Chapman and Hall, New York.
- Roff, D.A., 1996. The evolution of threshold traits in animals. *Q. Rev. Biol.* **71**: 3–35.

Ruzycki, J.R., Clarke, L.M., Flesher, M.W., Carmichael, R.W., and Eddy, D.L. 2009.

Performance of progeny from steelhead and rainbow trout crosses. Oregon Department of Fish and Wildlife, Fish Research and Development, NE Region.

Satterthwaite, W.H., Beakes, M.P., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G.,

Sogard, S.M. and Mangel, M. 2009. Steelhead life history on California's central coast: insights from a state-dependent model. *T. Am. Fish. Soc.* **138**: 532–548.

Schaffer, W.M. 2004. Life histories, evolution, and salmonids. *In* *Evolution illuminated:*

salmon and their relatives. *Edited by* A.P. Hendry and S.C. Stearns. Oxford University Press, USA, pp. 20–51.

Scheuerell, M.D. and Williams, J.G. 2005. Forecasting climate-induced changes in the

survival of Snake River spring/summer Chinook salmon (*Oncorhynchus tshawytscha*). *Fish. Oceanogr.* **14**: 448–457.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A. and

Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* **465**: 609–612.

Schwarz, G. 1978. Estimating the dimension of a model. *Ann. Stat.* **6**: 461–464.

The Science Sub-Committee (SSC) and Review Panels, Committee on Scientific Research and Statistics (CSRS). 2016. Review of 2011-2015 NPAFC Science Plan: forecast of

Pacific salmon production in the ocean ecosystems under changing climate. NPAFC Doc. 1661. 43 pp. The Science Sub-Committee (SSC) and Review Panels, Committee on Scientific Research and Statistics (CSRS) (Available at www.npafc.org).

Sloat, M.R., Fraser, D.J., Dunham, J.B., Falke, J.A., Jordan, C.E., McMillan, J.R., and Ohms, H.A. 2014. Ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines. *Rev. Fish Biol. Fisher.* **24**: 689–707.

Snyder, C.O. 1938. A study of the trout *Salmo irideus* Gibbons from Waddell Creek, California. *Calif. Fish Game.* **24**: 354–375.

Stearns, S.C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.

Stearns, S.C. and Koella, J.C. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* **40**: 893–913.

Sumpter, J.P., Scott, A.P., Baynes, S.M. and Witthames, P.R. 1984. Early stages of the reproductive cycle in virgin female rainbow trout (*Salmo gairdneri* Richardson). *Aquaculture* **43**: 235–242.

Taranger, G.L., Carrillo, M., Schulz, R.W., Fontaine, P., Zanuy, S., Felip, A., Weltzien, F.A., Dufour, S., Karlsen, Ø., Norberg, B. and Andersson, E. 2010. Control of puberty in farmed fish. *Gen. Comp. Endocr.* **165**: 483–515.

- Tattam, I.A., Ruzycki, J.R., McCormick, J.L. and Carmichael, R.W. 2015. Length and Condition of Wild Chinook Salmon Smolts Influence Age at Maturity. *T. Am. Fish. Soc.* **144**: 1237–1248.
- Thorpe, J.E., Mangel, M., Metcalfe, N.B. and Huntingford, F.A, 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar L.* *Evol. Ecol.* **12**: 581–599.
- Tomkins, J.L. and Hazel, W. 2007. The status of the conditional evolutionarily stable strategy. *Trends Ecol. Evol.* **22**: 522–528.
- Ueno, Y., Y. Ishida, K. Nagasawa, and T. Watanabe. 1997. Winter distribution and migration of Pacific salmon. NPAFC Doc. 271. 22 pp. (Available at www.npafc.org).
- Vischer, N. and Nastase, S . 2014. ObjectJ: non-destructive marking and linked results [Software]. Available from <https://sils.fnwi.uva.nl/bcb/objectj/>.
- Vøllestad, L.A., Peterson, J. and Quinn, T.P. 2004. Effects of freshwater and marine growth rates on early maturity in male coho and Chinook salmon. *T. Am. Fish. Soc.* **133**: 495–503.
- Ward, B.R. 2000. Declivity in steelhead (*Oncorhynchus mykiss*) recruitment at the Keogh River over the past decade. *Can. J. Fish. Aquat. Sci.* **57**: 298–306.

- Ward, B.R. and Slaney, P.A. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. *Can. J. Fish. Aquat. Sci.* **45**: 1110-1122.
- Welch, D.W., Ishida, Y., Nagasawa, K. and Eveson, J.P., 1998. Thermal limits on the ocean distribution of steelhead trout (*Oncorhynchus mykiss*). *Nor. Pac. Anadr. Fish Comm.* **1**: 396–404.
- Wells, B.K., Grimes, C.B., Sneva, J.G., McPherson, S. and Waldvogel, J.B., 2008. Relationships between oceanic conditions and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from California, Washington, and Alaska, USA. *Fish. Oceanogr.* **17**: 101–125.
- Wells, B.K., Grimes, C.B. and Waldvogel, J.B. 2007. Quantifying the effects of wind, upwelling, curl, sea surface temperature and sea level height on growth and maturation of a California Chinook salmon (*Oncorhynchus tshawytscha*) population. *Fish. Oceanogr.* **16**: 363–382.
- Winemiller, K.O. and Rose, K.A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Can. J. Fish. Aquat. Sci.* **49**: 2196–2218.

Table 3.1. Number of summer and winter steelhead from the Skeena, Nass, and Willamette River used to analyze the influence of ocean growth on age at maturity. Life history type refers to the number of years spent in freshwater (left of period) and the ocean (right on period) before returning to freshwater to spawn.

Life History Type	Brood Year	Capture Year	N
Skeena River Summer Steelhead			
4.2	2004	2010	46
4.3	2004	2011	22
4.2	2005	2011	49
4.3	2005	2012	30
4.2	2006	2012	43
4.3	2006	2013	24
4.2	2007	2013	39
4.3	2007	2014	15
Nass River Summer Steelhead			
3.2	2004	2009	39
3.3	2004	2010	10
3.2	2005	2010	40
3.3	2005	2011	19
3.2	2006	2011	48
3.3	2006	2012	14
3.2	2007	2012	50
3.3	2007	2013	15
3.2	2008	2013	44
3.3	2008	2014	22
Willamette River Winter Steelhead			
2.2	2008	2012	52
2.3	2008	2013	20
2.2	2009	2013	62
2.3	2009	2014	19
Willamette River Summer Steelhead			
1.2	2009	2012	49
1.3	2009	2013	15
1.2	2010	2013	49
1.3	2010	2014	6

Table 3.2. Candidate logistic regression models fit to age at maturity for Skeena, Nass, and Willamette River summer and winter steelhead. Loe = length at ocean entry. Gs1 = first ocean summer growth. Gw1 = first ocean winter growth. Gs2 = second ocean summer growth. L2 = length at the end of the second ocean summer. POP = population. Rel = relative growth increment. BIC = Bayesian information criterion.

Variables in model	Parameters	Δ BIC
Absolute growth models		
Loe + Gw1 + POP	6	0.00
Loe * Gw1 + POP	7	2.52
Loe + Gw1 + Gs2 + POP	7	5.07
Loe + Gs1 + Gw1 + POP	7	6.33
Gw1 + POP	5	6.74
Loe + Gs1 + Gw1 + Gs2 + POP	8	9.57
Gw1 + Gs2 + POP	6	11.64
Gs1 + Gw1 + POP	6	13.47
Gw1 * Gs2 + POP	7	17.23
Gs1 + Gw1 + Gs2 + POP	7	17.80
Gs1 * Gw1 + POP	7	20.09
Loe * Gw1 * Gs2 + POP	11	20.18
Loe * Gs1 * Gw1 + POP	11	27.86
Gs1 * Gw1 * Gs2 + POP	11	36.77
Loe + Gs2 + POP	6	47.64
Loe + Gs1 + POP	6	47.83
Loe * Gs2 + POP	7	53.17
Loe + Gs1 + Gs2 + POP	7	53.83
Loe * Gs1 + POP	7	54.37
Gs1 + POP	5	56.73
Gs2 + POP	5	57.55
Loe * Gs1 * Gw1 * Gs2 + POP	19	60.24
Gs1 + Gs2 + POP	6	61.96
Gs1 * Gs2 + POP	7	67.39
Loe * Gs1 * Gs2 + POP	11	72.53
Relative growth models		
Loe + relGs1 + relGw1 + POP	7	6.01
Loe + relGw1 + POP	6	7.01
Loe + relGs1 + relGw1 + relGs2 + POP	8	9.52
Loe * relGw1 + POP	7	11.21
Loe + relGw1 + relGs2 + POP	7	13.22
relGw1 + POP	5	20.57
relGw1 + relGs2 + POP	6	25.88
Loe * relGs1 * relGw1 + POP	11	26.44

relGs1 + relGw1 + POP	6	26.84
Loe * relGw1 * relGs2 + POP	11	27.30
relGs1 + relGw1 + relGs2 + POP	7	30.55
relGs1 * relGw1 + POP	7	30.76
relGw1 * relGs2 + POP	7	31.30
relGs1 * relGw1 * relGs2 + POP	11	39.27
Loe + relGs2 + POP	6	45.53
relGs1 + relGs2 + POP	6	46.87
Loe + relGs1 + POP	6	47.91
Loe + relGs1 + relGs2 + POP	7	50.13
Loe * relGs2 + POP	7	51.03
relGs1 + POP	5	51.23
relGs1 * relGs2 + POP	7	51.83
relGs2 + POP	5	53.97
Loe * relGs1 + POP	7	54.25
Loe * relGs1 * relGw1 * relGs2 + POP	19	55.63
Loe * relGs1 * relGs2 + POP	11	67.70
Length model		
L2 + POP	5	35.61

Table 3.3. Summary of results from a logistic regression model predicting the age at maturity of summer and winter steelhead from the Skeena, Nass, and Willamette rivers. The explanatory variables included in the model were length at ocean entry (Loe), first ocean winter growth (Gw1), and population (POP). Coefficients expressed as odds of maturing after two ocean years versus three ocean years. Parameter estimates shown in bold have 95% confidence intervals that do not include 1.

Parameter	Coefficient	95% confidence interval	
		Lower	Upper
Intercept	0.05	0.014	0.191
Loe	1.01	1.007	1.020
Gw1	1.02	1.015	1.028
POP (Skeena summer steelhead)	0.54	0.370	0.797
POP (Willamette summer steelhead)	1.19	0.661	2.189
POP (Willamette winter steelhead)	0.47	0.283	0.791

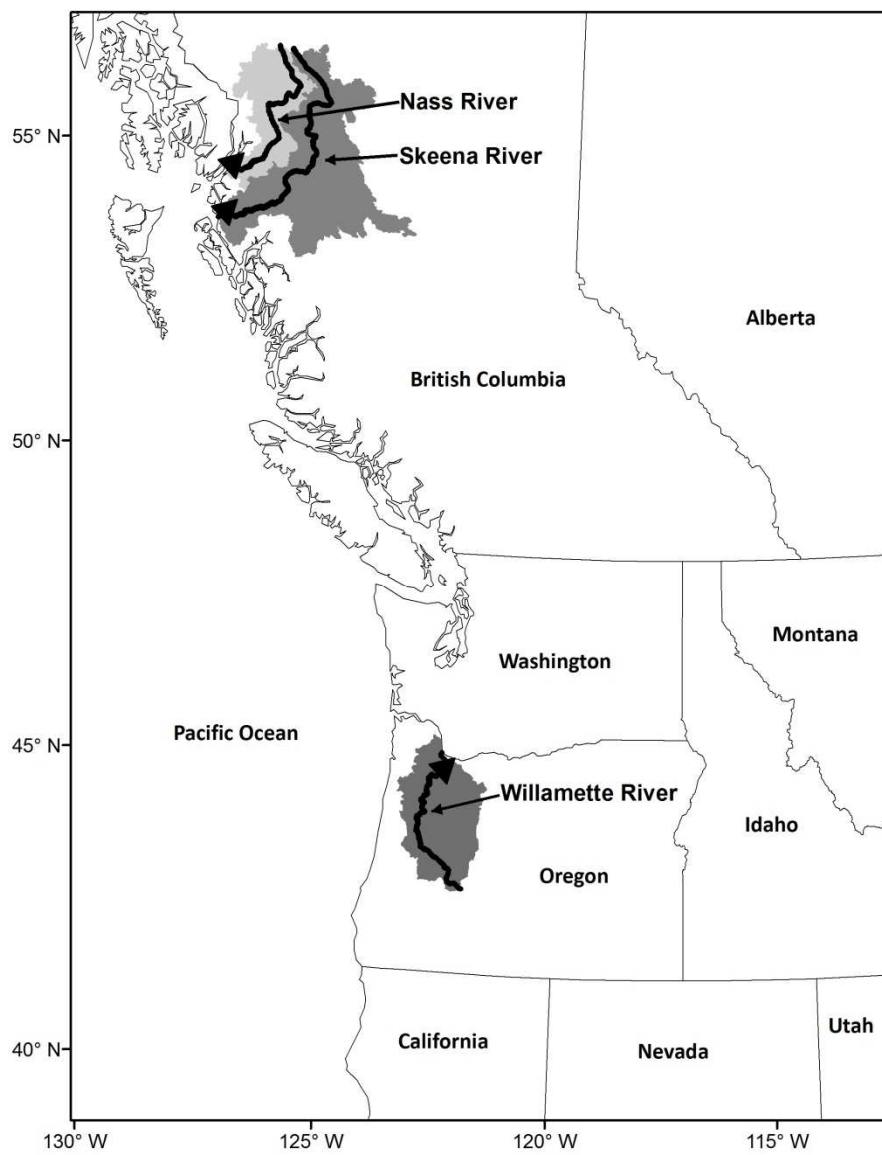


Figure 3.1. Map of Skeena, Nass, and Willamette River basins. Black triangles indicate capture locations of summer and winter steelhead used in the study.

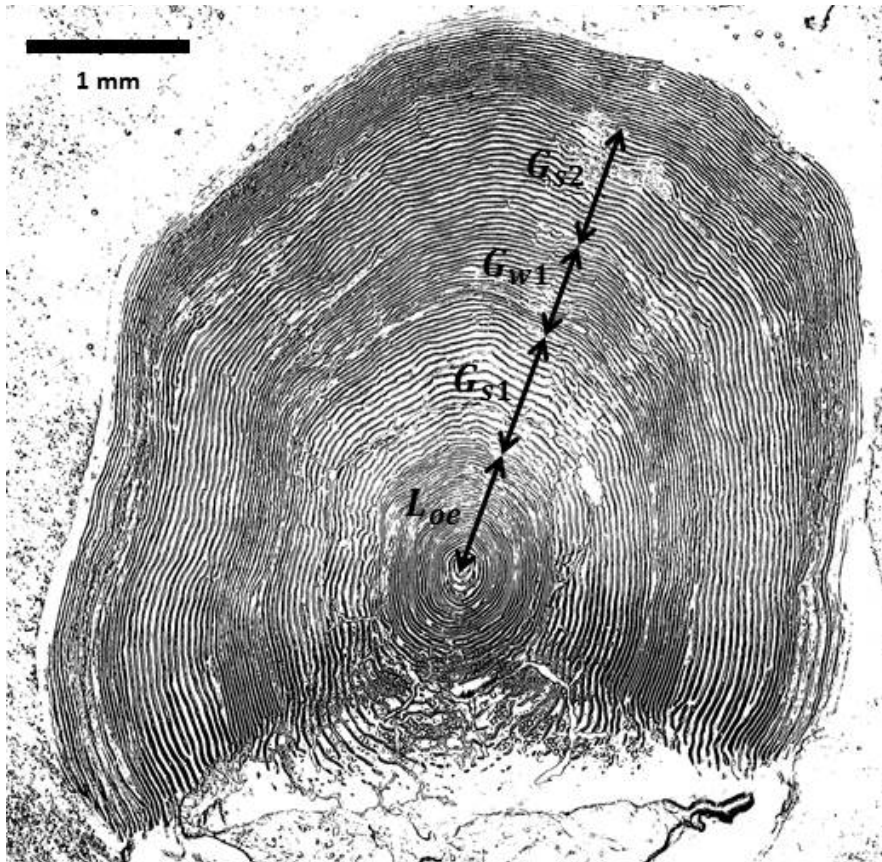


Figure 3.2. Scale of a mature 4.2 summer steelhead from the Skeena River, British Columbia. L_{oe} = length at ocean entry. G_{s1} = first ocean summer growth. G_{w1} = first ocean winter growth. G_{s2} = second ocean summer growth. L_2 = length at the end of the second ocean summer.

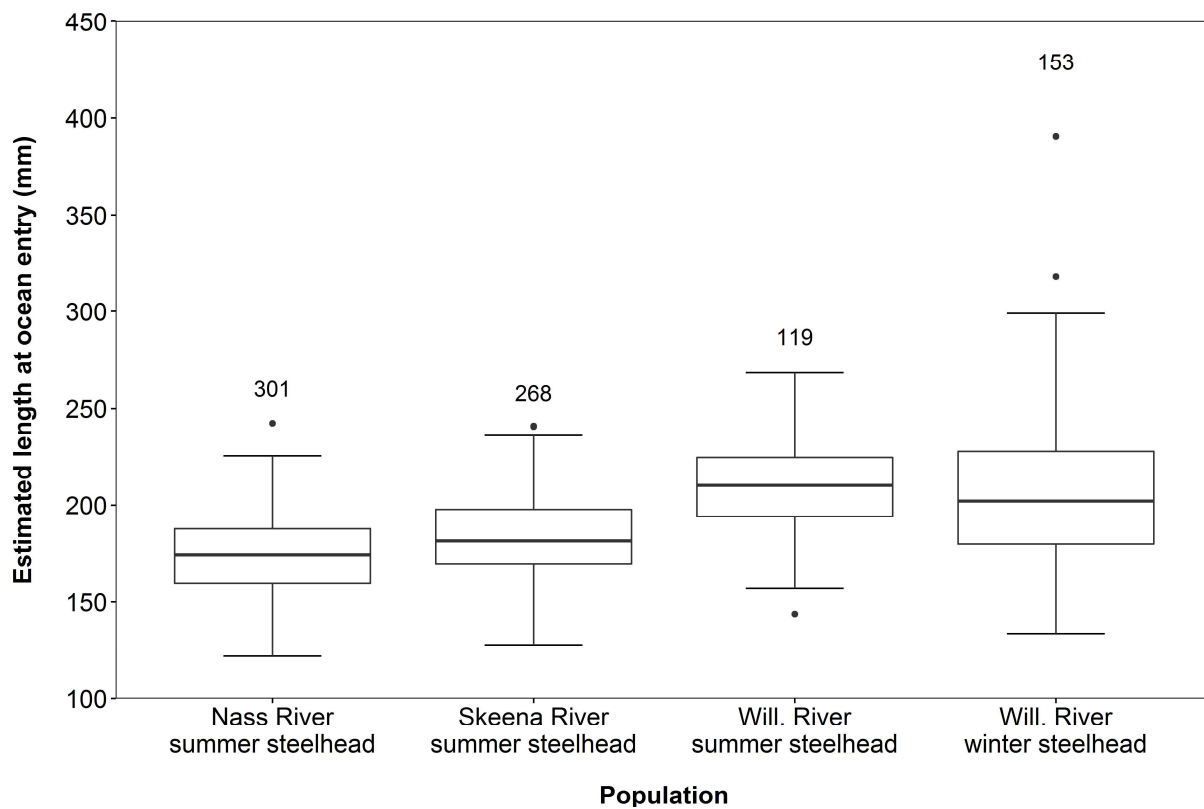


Figure 3.3. Estimated length at ocean entry for steelhead from four populations. Sample size is located above each box.

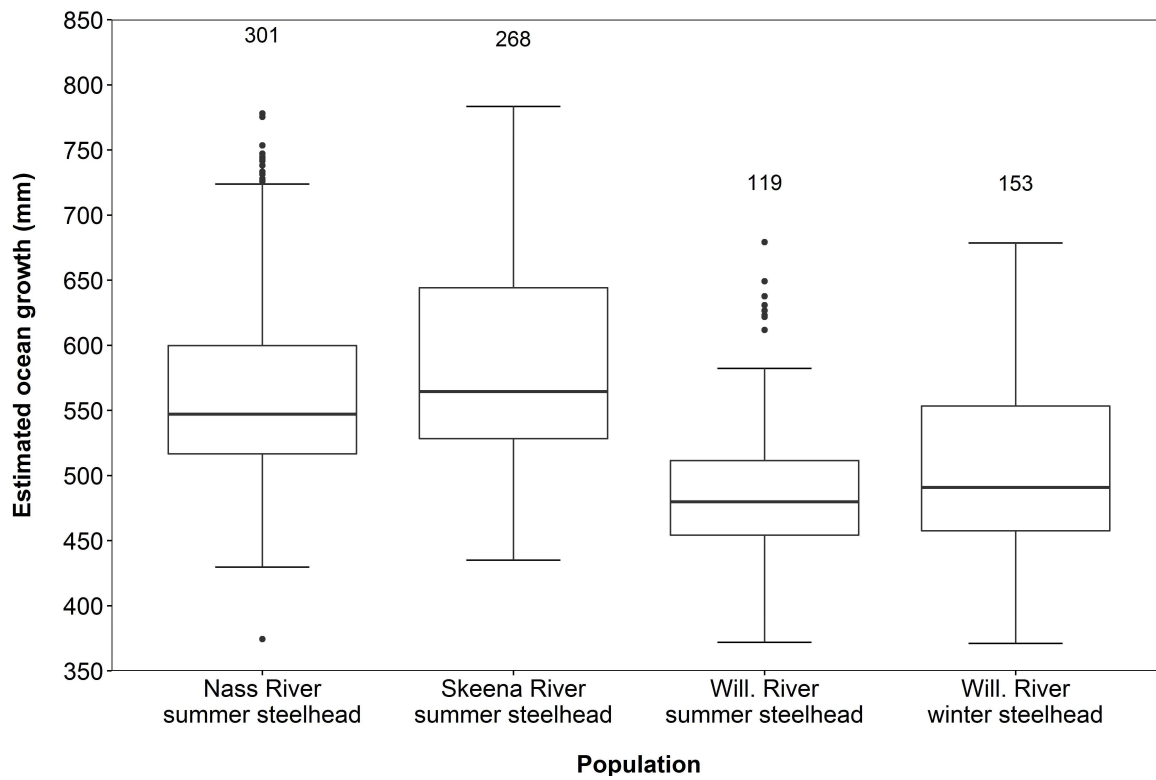


Figure 3.4. Estimated ocean growth for steelhead from four populations. Sample size is located above each box.

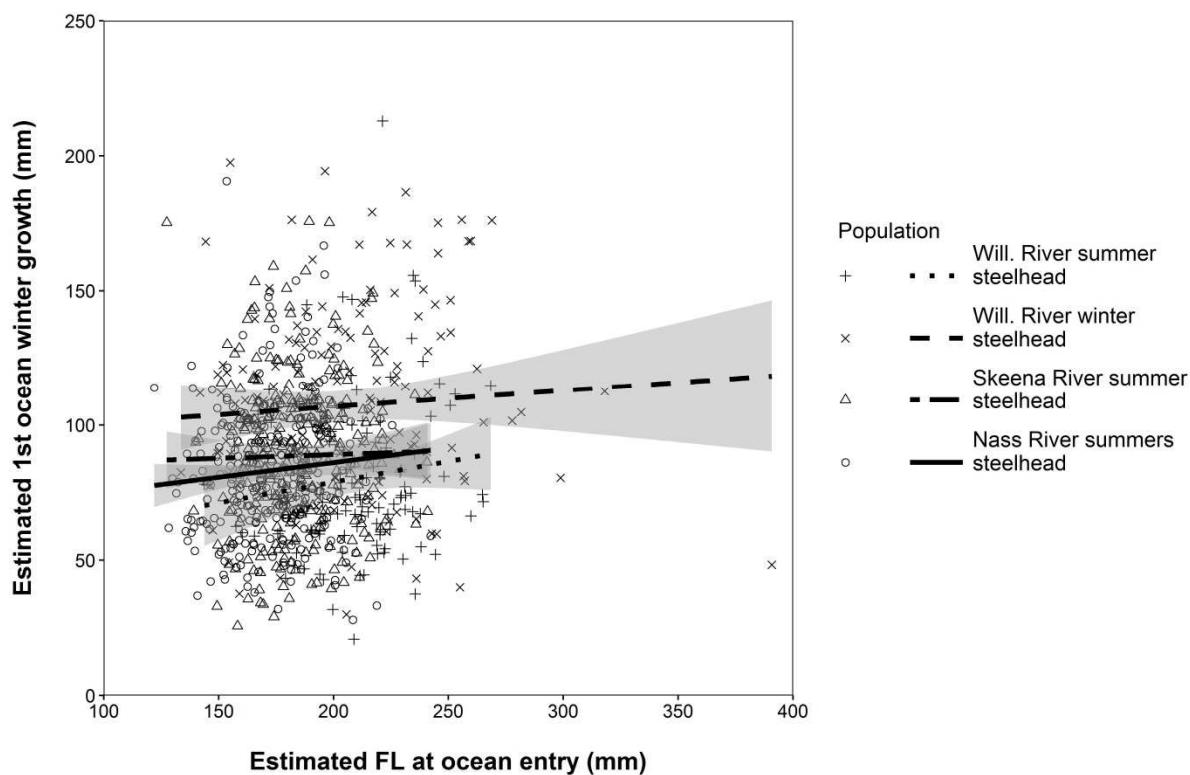


Figure 3.5. Relationship between estimated length at ocean entry (mm) and estimated first ocean winter growth (mm) for four populations of steelhead. Points = observed data. Lines = fitted linear regression for each population. Shaded areas represent 95% confidence intervals.

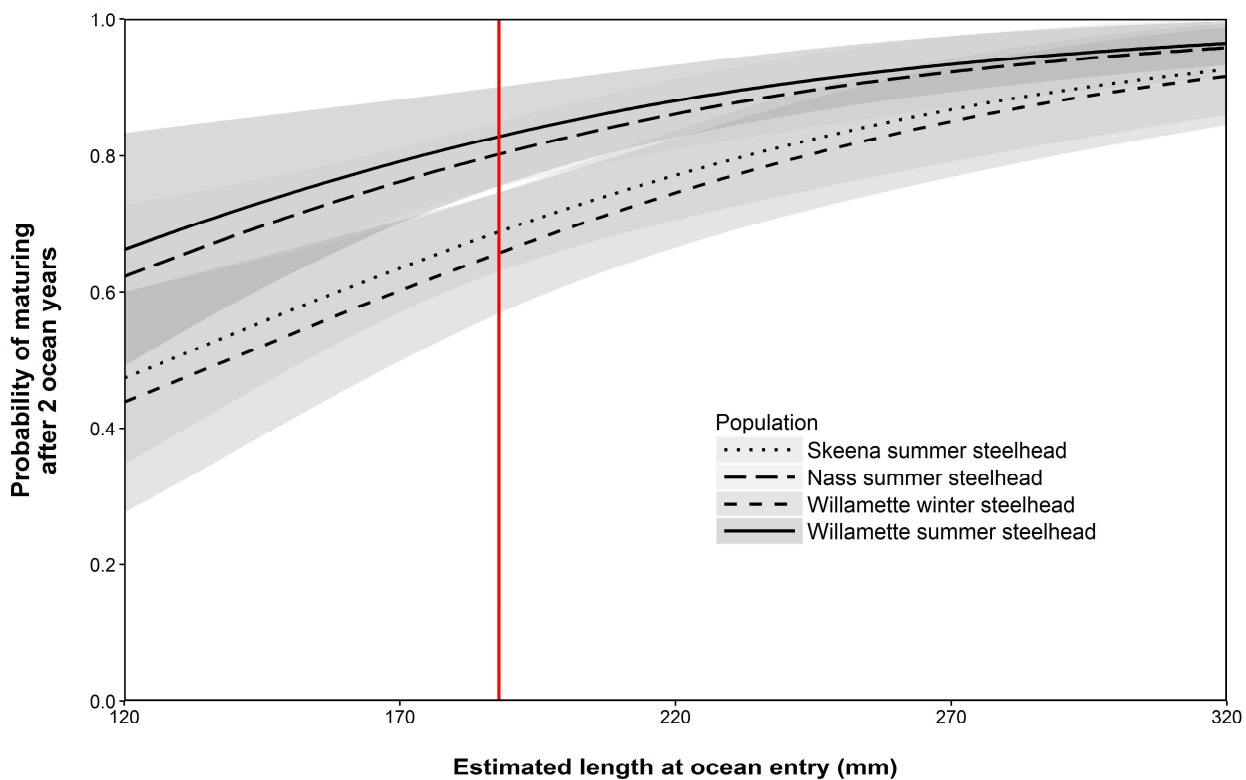


Figure 3.6. The probabilities of maturing after two ocean years for Skeena River summer steelhead, Nass River summer steelhead, Willamette River winter steelhead, and Willamette River summer steelhead across the observed range of estimated length at ocean entry. Estimated growth during the first ocean winter is held at the mean observed value (88.89 mm) while estimated length at ocean entry varies. Shaded areas represent 95% confidence intervals. Vertical line represents mean observed length at ocean entry (188.00 mm).

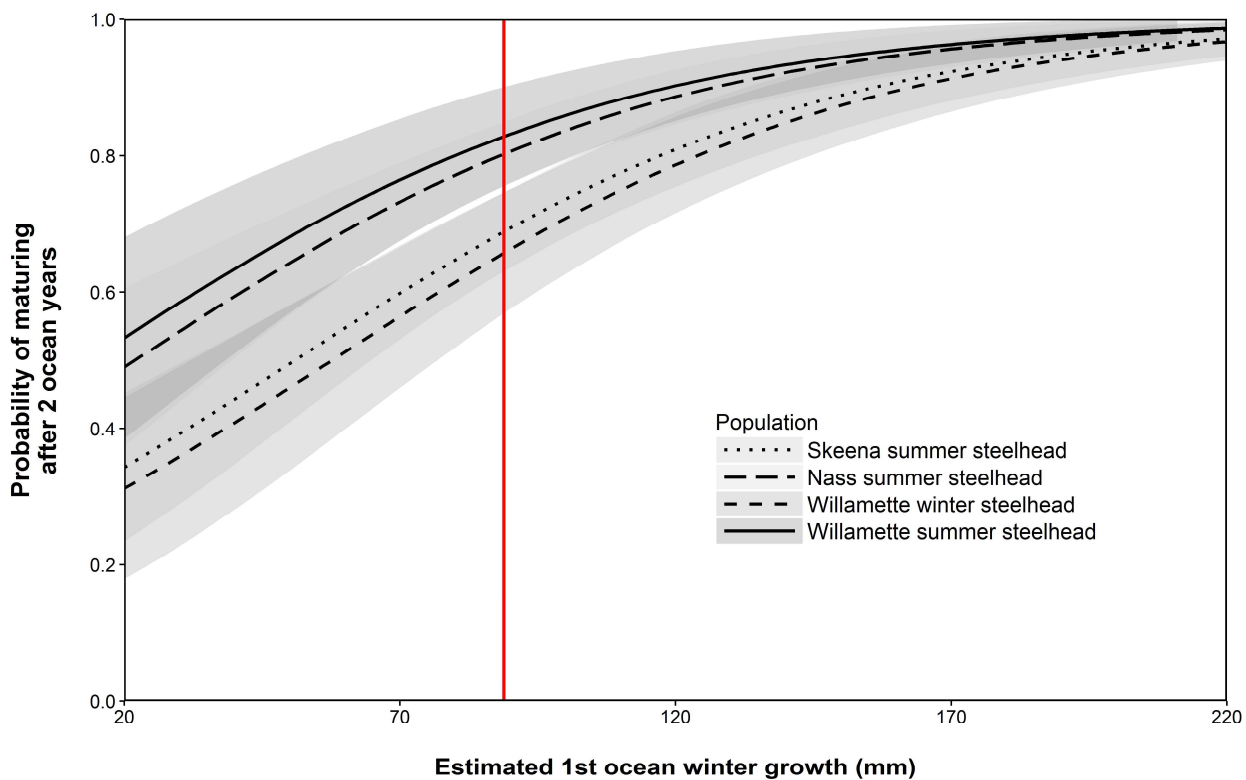


Figure 3.7. The probabilities of maturing after two ocean years for Skeena River summer steelhead, Nass River summer steelhead, Willamette River winter steelhead, and Willamette River summer steelhead across the observed range of estimated first ocean winter growth. Estimated length at ocean entry is held at the mean observed value (188.00 mm) while estimated first ocean winter growth varies. Shaded areas represent 95% confidence intervals. Vertical line represents mean observed length at ocean entry (88.89 mm).

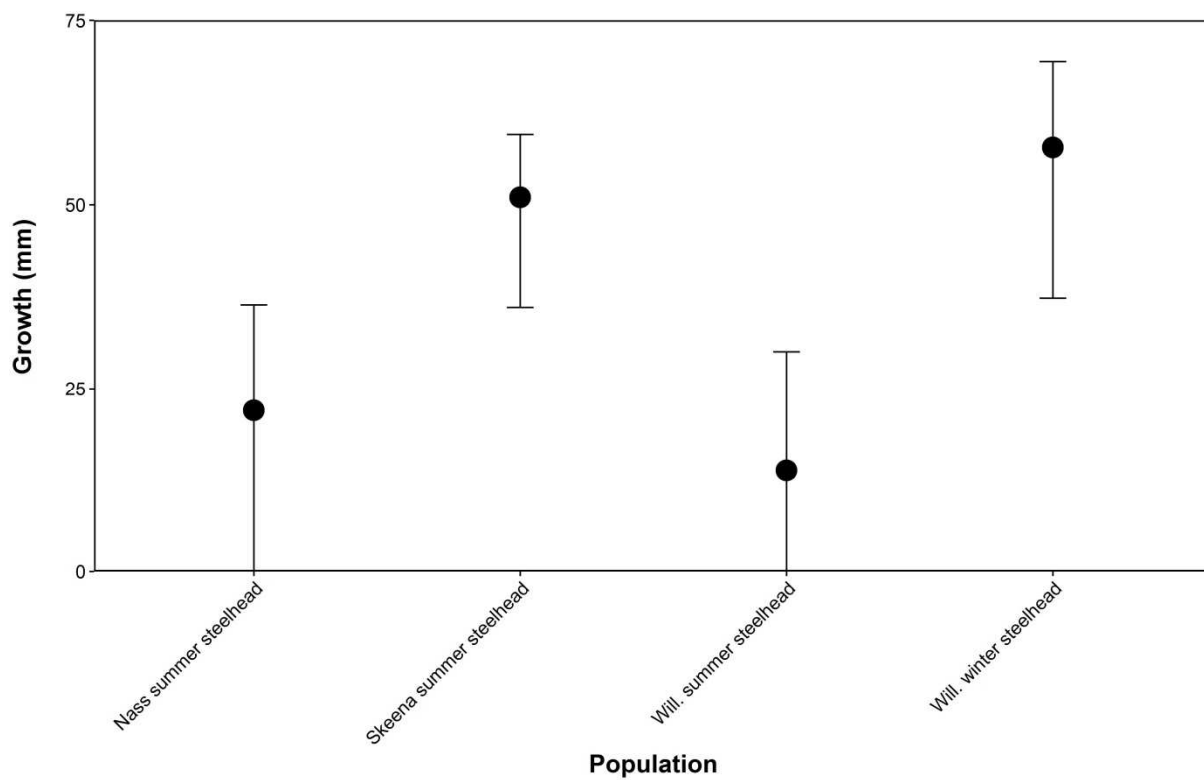


Figure 3.8. First ocean winter growth when the probability of maturing equals 50% for four winter and summer steelhead populations. 95% confidence intervals calculated using a nonparametric bootstrap percentile method, with 1,000 replications.

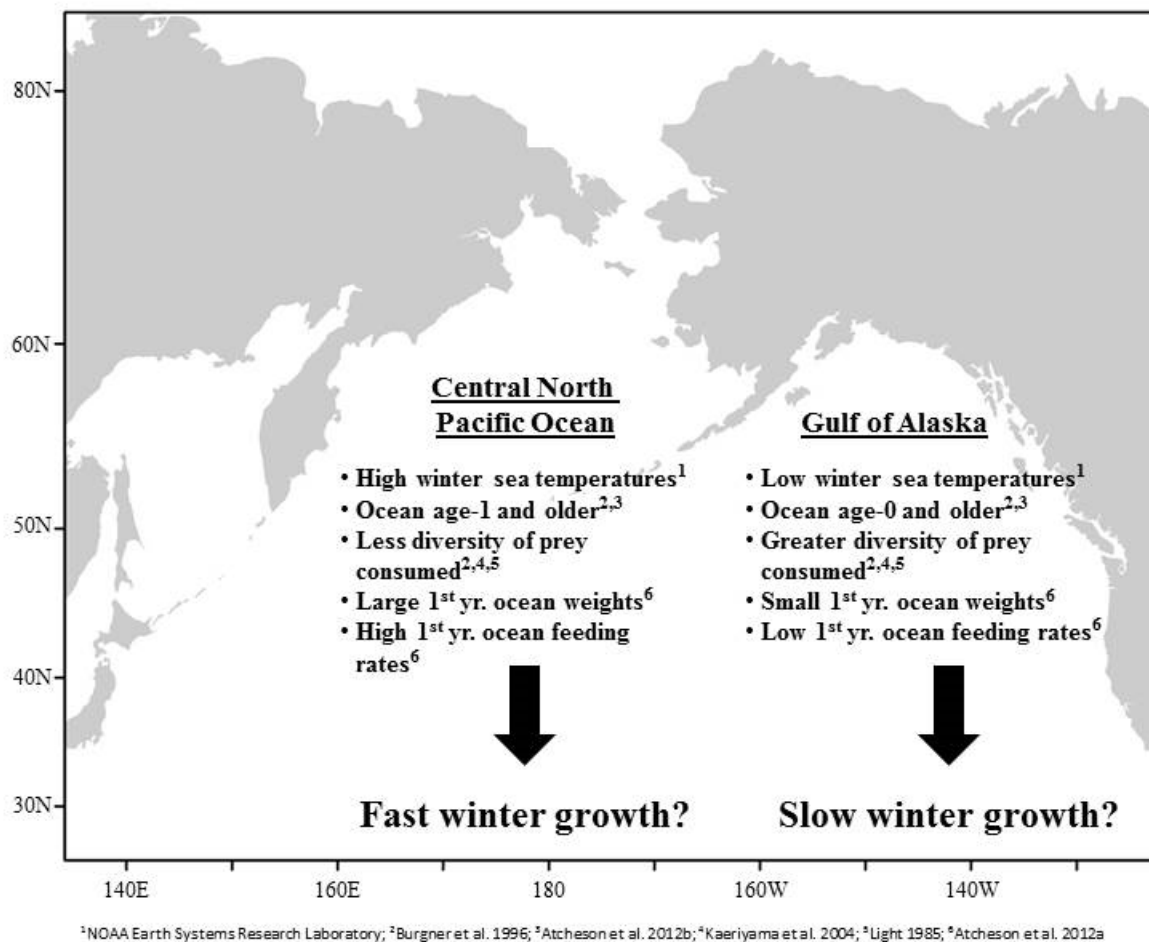


Figure 3.9. Summary of habitat characteristics and steelhead age, weight, and feeding rate differences in the Gulf of Alaska and the central North Pacific Ocean. We hypothesize that differences could lead to faster winter growth for steelhead in the central North Pacific Ocean, which, given the observed results, could lead to younger age at maturity.

Chapter 4: General Conclusions

Steelhead *Oncorhynchus mykiss* serve important ecological, economic, and social roles throughout their range. From a management perspective, steelhead pose a challenge due to their anadromous life history, wide-scale translocation to both native and nonnative watersheds, and importance in recreational fisheries. Ecologically, steelhead serve as an ideal species to study mechanisms driving life history diversity given their temporal variability in both freshwater and ocean residence. This thesis contributes to a broader understanding of both steelhead management and ecology. The first chapter addressed questions related to the management of a summer-run hatchery program in the Willamette River, Oregon, where a movement study was used to test assumptions associated with a recycling program. The second chapter focused on decoupling the relative importance of freshwater and ocean growth in determining steelhead age at maturity.

Recreational fishing opportunities are important from both a conservation and management perspective. Anglers can become engaged in both the protection and management of fish populations, and these opportunities should be provided. Recycling of anadromous salmonids is one option for allocating a surplus of fish that return to a hatchery or acclimation site and increasing angler opportunity. However, in basins where separation between recycled and endemic populations is warranted, the assumptions associated with such releases must be tested. The movement study in chapter two indicated that although a portion of recycled summer-run steelhead in the Willamette River are indeed harvested by anglers, a large portion remain in rivers to potentially interact with endemic winter-run steelhead. Expanded estimates of recycled steelhead that remain in rivers were larger than escapement estimates of Endangered Species Act-listed winter-run steelhead. Furthermore,

recycled steelhead were observed straying out of their respective release tributaries. Given the concern that hatchery-produced fish can pose a risk to naturally-produced fish, the recycling program in the Willamette River basin should be reviewed by managers to determine if the potential risks outweigh the benefit of a small increase in harvest.

Investigating the relationship between growth history and steelhead maturation showed that freshwater and first ocean winter growth both influenced age at maturity. Faster growth during both periods resulted in earlier maturation. The importance of growth during a resource-limited period (i.e., winter) illustrates the importance of understanding the ocean ecology of steelhead and possibly identifies the timing of the maturation “decision window”. Population-specific differences in the amount of freshwater and first ocean winter growth necessary to trigger maturation indicate selective forces act differently across the four populations to maximize fitness. These studies offer important insight into the management and ecology of steelhead and provide a foundation for future research.