

EFFECTS OF LARGE WOOD RESTORATION ON COHO SALMON IN A
NORTHERN CALIFORNIA WATERSHED: A BEFORE-AFTER-CONTROL-
IMPACT EXPERIMENT

By

Natalie B. Okun

A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Fisheries

Committee Membership

Dr. Mark J. Henderson, Committee Chair

Dr. Darren M. Ward, Committee Member

Dr. Nicholas A. Som, Committee Member

Seth J. Ricker, Committee Member

Dr. Erin C. Kelly, Graduate Coordinator

December 2021

ABSTRACT

EFFECTS OF LARGE WOOD RESTORATION ON COHO SALMON IN A NORTHERN CALIFORNIA WATERSHED: A BEFORE-AFTER-CONTROL- IMPACT EXPERIMENT

Natalie B. Okun

Substantial time, money, and effort are invested in river and stream restoration projects to aid in the recovery of imperiled salmonid populations, but there is little evidence that these efforts have had lasting positive impacts on juvenile fish growth and survival. To assess the effectiveness of large woody debris (LWD) restoration, which is one of the most common restoration practices, I evaluated the growth and survival response of endangered Central California Coast coho salmon (*Oncorhynchus kisutch*) in a paired watershed before-after impact-control (BACI) study. To determine if LWD supplementation influenced coho salmon growth and survival, two neighboring, similar watersheds in Northern California were selected to conduct long-term monitoring of both fish and habitat metrics. Fish and habitat monitoring consisted of summer and fall electrofishing surveys, juvenile outmigrant trapping, passive integrated transponder (PIT) array detections, and summer and winter habitat surveys. After three years of pre-treatment monitoring in both watersheds, Pudding Creek (the ‘experimental’ watershed) was supplemented with 1,365 cubic meters of LWD throughout 80% of the mainstem anadromous spawning habitat in 2015. Post-treatment monitoring then continued in both watersheds until 2020. Though wood density increased more in the experimental

watershed (31%) compared to the control watershed (13%) following wood treatment, there was no winter slow water habitat response, meaning the limiting factor to coho populations in these watersheds was not addressed. I used generalized linear mixed effects models with year as a random effect to predict summer and winter growth response to wood supplementation. I found that summer growth was positively associated with wood densities and winter growth was also associated with increased wood densities, but the experimental watershed had consistency higher winter growth compared to the control. Both summer and winter growth was associated with wood densities, but the wood treatment response did not align with the biological response (i.e., wood density increased more in the experimental watershed, but growth did not increase more in the experimental compared to the control watershed). To estimate winter survival rates, I used a Cormack-Jolly-Seber (CJS) model. I found that winter survival increased through time in the control while it stayed level in the experimental watershed. This thesis illuminates the utility of having a paired watershed study design with habitat and biological response analysis in tandem. The results from this experiment lead to a variety of questions and concerns relating to the treatment design and how treatment is paired with the study design. This thesis provides a foundation for a long-term monitoring to understand the effects of restoration efforts for a species at the southern extent of its range. This is particularly important given the at-risk status of these salmonid populations and the additional threats these fish face from a changing climate.

ACKNOWLEDGEMENTS

My advisor at Humboldt State University, Dr. Mark Henderson, has been a critical source of support and guidance and has committed an incredible amount of his energy and time into my development as a scientist. I am grateful to have a mentor that is committed to my personal and professional growth. I am fortunate to have been introduced to Mark by my former supervisor, California Department of Fish and Wildlife senior environmental scientist, Sean Gallagher. Sean Gallagher and Dave Wright came up with the premise of the BACI Experiment and carried the project for a large portion of its duration. Being able to analyze this dataset under Mark's guidance at the California Cooperative Fish and Wildlife Research Unit at Humboldt State aligns with the collaborative style held in all aspects of the study.

The BACI Experiment was made possible through funding from California Department of Fish and Wildlife's Fisheries Restoration Grant Program (P1610537), Trout Unlimited's North Coast Coho Project, The Nature Conservancy, NOAA Restoration Center and its Community-Based Restoration Program, Pacific States Marine Fisheries Commission, Columbia Habitat Monitoring Program (CHaMP), Lyme Redwood Forest Company, and Campbell Global. I am grateful for student funding from the California State University Council on Ocean Affairs, Science, and Technology (COAST), Richmond Rod and Gun Club, The Humboldt Area Foundation's Joseph Sidney Woolford Fund, and the California Cooperative Fish and Wildlife Research Unit.

My thesis is the culmination of nine years of intensive data collection by Pacific States Marine Fisheries Commission, California Department of Fish and Wildlife, Campbell Global, and Lyme Redwood Forest Company biologists and technicians. This represents a massive collaborative effort. Thanks to Stan Allan and Wendy Holloway with Pacific States Marine Fisheries Commission for administrative support. Thanks to Emily Lang with Lyme Redwood Forest Company for her diligence and commitment to the Pudding Creek watershed data collection and analysis. Thank you so much to all BACI Project technicians, particularly those who endured long habitat survey days with me. Thanks to Chris Blencowe and his team at Blencowe Watershed Management for their work performing the wood treatment implementation component of the project. Thanks to landowners Lyme Redwood Forest Company, and Jackson Demonstration State Forest for access to their properties and technical assistance with stream flow data. Thanks for Shaun Thompson for sharing vast knowledge about Caspar Creek and other Life Cycle Monitoring Stations along the Mendocino coast. Thanks to Anna Halligan at Trout Unlimited and her North Coast Coho Project team for the support in grant management. Thanks to Elizabeth Mackey for passing the BACI Project onto me and providing continuous collaboration and coordination throughout this process. Special thanks to Sarah Gallagher with the California Department of Fish and Wildlife and Jamie McGuire with Pacific States Marine Fisheries Commission for their collaboration and commitment to BACI Project. From ensuring that data collection could be completed in the midst of a pandemic to writing the technical report with me, I am forever grateful to your hard work that kept the BACI Project afloat.

Thank you to my graduate committee: Dr. Darren Ward, Dr. Nicholas Som, and Seth Ricker for your valuable statistical guidance and feedback. Thank you to Leslie Farrar and JoAnna Pifferini for your work in organizing and maintaining the California Cooperative Fish and Wildlife Research Unit. I am grateful to my fellow Natural Resources graduate students for their company, advice, and support during my time at Humboldt State. I am especially grateful to Emily Chen for her willingness to talk about fish and statistics at any time and her guidance through some of the more technical hurdles I needed to overcome. Thank you to Maddie Halloran, Samantha Kannry, Sam Rizza, Nick Van Vleet, John Deibner-Hanson, Emerson Kanawi, Nissa Kreidler, Chris Loomis, Max Ramos, Chris O'Keefe, Roxanne Roberston, Cori Flannery and Doyle Coyne for commiserating with me and, without fail, encouraging me to move towards my goals. Thank you so much to Jackie Bridegum for not only your superb habitat typing skills and field assistance, but more importantly, your constant willingness to listen and provide support. My time at Humboldt State would not have been the same without my dear friends Jasmine and Brian Williamshen. I am grateful to have such intelligent and compassionate friends and I feel lucky to have entwined our graduate school paths.

I want to thank my family for their never-ending love and faith in my abilities. You've supported my every move without waver, and I am so grateful for that. Lastly, thank you to Jeff Abrams, my best friend and partner in all things. Your encouragement has meant the world to me.

TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iv
TABLE OF CONTENTS.....	vii
LIST OF TABLES.....	ix
LIST OF FIGURES.....	xi
INTRODUCTION.....	1
METHODS.....	8
Study Area.....	8
Study Design.....	11
Large Wood Treatment.....	12
Habitat Response to Treatment.....	13
Life-cycle Monitoring.....	16
Summer and Fall Electrofishing.....	16
Summer Growth Estimates.....	17
Juvenile Outmigrant Trapping.....	18
Winter Growth Estimates.....	19
PIT Tag Arrays.....	20
Winter Survival Estimates.....	21
RESULTS.....	24
Habitat Response to Treatment.....	24
Summer Growth Results.....	31
Winter Growth Results.....	32

Winter Survival Results	37
DISCUSSION	43
Summer Growth.....	43
Winter Growth	45
Winter Survival.....	46
Restoration Effectiveness	48
Study Design.....	50
CONCLUSION.....	52
REFERENCES	54
APPENDIX.....	63

LIST OF TABLES

Table 1. Comparison of Caspar Creek (control) and Pudding Creek (experimental) as paired watersheds for the BACI experiment. (Cafferata and Reid 2013, Mackey et al. 2016, Okun et al. 2021).....	10
Table 2. The two-way Analysis of Variance (ANOVA) results stream temperature predicted by treatment time period (pre = 2011 to summer 2015, post = summer 2015 to 2020), watershed (control = Caspar Creek, experimental = Pudding Creek), and the interaction between treatment period and watershed.....	27
Table 3. The two-way Analysis of Variance (ANOVA) results using log(stream flow) as the dependent variable. Gauge refers to the flow gauge in each watershed (control gauge = North Fork Caspar Creek, experimental gauge = Pudding Creek). Treatment refers to before and after wood supplementation in the experimental watershed in summer 2015.	29
Table 4. The two-way Analysis of Variance (ANOVA) results using log(drainage area normalized stream flow) as the dependent variable. Gauge refers to the flow gauge in each watershed (control gauge = North Fork Caspar Creek, experimental gauge = Pudding Creek). Treatment refers to before and after wood supplementation in the experimental watershed in summer 2015.	30
Table 5. Summary results from top mixed effects model (selected through AIC) for coho salmon summer growth per day (log-transformed). Wood density refers to the annual summer wood volume per stream kilometer scaled with combined watersheds.....	31
Table 6. Summary results from top mixed effects model (selected through AIC) for coho salmon log-transformed winter growth per day (Wood Density Winter Growth Model). Wood density refers to the annual summer wood volume per stream kilometer scaled with combined watersheds. This data omits juvenile 2014-2015 due to 2014 run failure. Watershed compares Pudding Creek (experimental) against Caspar Creek (control). AICc score for this model is -2123.....	34
Table 7. Summary results from smolt density mixed effects model (selected through AIC) for coho salmon log-transformed winter growth per day (Smolt Density Winter Growth Model). Smolt density refers to the annual smolt estimates per watershed per stream kilometer scaled with combined watersheds. This data omits juvenile 2014-2015 due to 2014 run failure. Watershed compares Pudding Creek (experimental) against Caspar Creek (control). AICc score for this model is -2122.	36
Table 8. Juvenile coho survival (Φ) models ranked by Δ QAICc from RMark. The bold model was chosen as the top model based on the principle of parsimony (see text). In these models, watershed compares the experimental (Pudding) with the control (Caspar)	

and year is each year of the study from 2011 to 2020. Time refers to the occasion within the model. Capture probability for each of these models included watershed, year, and time. 39

Table 9. Coefficient estimates, standard errors, and lower and upper 95% confidence levels (Lower CL, Upper CL) for apparent survival (Φ) and capture probability (p) from the top CJS model in RMark predicting survival for juvenile coho in the BACI study. Pudding, the experimental watershed, is in comparison with Caspar, the control. The experimental watershed received wood supplementation in 2015. The four occasions of the study were: 1) summer electrofishing, 2) fall electrofishing, 3) downstream outmigrant trap, and 4) PIT tag array detection. 41

LIST OF FIGURES

- Figure 1. Study area for the Pudding Creek BACI Study, 2011-2020. Pudding Creek (experimental) and Caspar Creek (control) each have streamflow gauges, PIT tag arrays, temperature loggers, and outmigrant traps. Wood treatment only occurred in Pudding Creek. (Map by Sarah Gallagher, Okun et al. 2021) 8
- Figure 2. The four occasions of data collection used in the Cormack-Jolly-Seber model to estimate apparent survival and capture probability. Winter survival (Φ_2) is the interval between fall electrofishing and each creek’s outmigrant trap. 21
- Figure 3. Comparison of marginal means from the most parsimonious generalized linear mixed effects models for wood density (cubic meters per stream kilometer) and summer slow water volume (cubic meters). The points with the same letter indicate that there was no evidence of a difference in estimated habitat metric based on a Tukey Honestly Significant Difference post-hoc test..... 25
- Figure 4. Scaled annual wood density (cubic meters per stream kilometer) for the duration of the BACI study. Pudding Creek was the experimental watershed which received wood supplementation and Caspar Creek was the control watershed and did not receive active wood treatment. The gray vertical line denotes Pudding Creek wood treatment in summer 2015. 26
- Figure 5. Mean daily water temperatures on Pudding Creek (experimental) and Caspar Creek (control) through the BACI study period. Wood supplementation in Pudding Creek (experimental) took place in summer 2015. (Okun et al. 2021) 27
- Figure 6. Hydrograph of Pudding Creek (the experimental watershed) and North Fork Caspar Creek (representative of the control watershed) mean daily flow (cubic feet per second, cfs) during the BACI study period (2011 through 2020). Wood supplementation in Pudding Creek (the experimental watershed) took place in summer 2015. (Okun et al. 2021) 29
- Figure 7. Hydrograph of Pudding Creek (the experimental watershed) and North Fork Caspar Creek (representative of the control watershed) mean daily flow (cubic feet per second, cfs) normalized by the drainage area above each creek’s stream gauge during the BACI study period (2011 through 2020). Wood supplementation in Pudding (the experimental watershed) took place in summer 2015. (Okun et al. 2021) 30
- Figure 8. Predicted log-transformed coho salmon summer growth per day by wood density (volume of wood per stream kilometer) given the model that includes a random effect for year. The shaded gray region represents the 95% confidence interval. 32

Figure 9. Top model estimated marginal means and their 95% confidence intervals for log-transformed coho salmon winter growth per day for each watershed in the BACI study (Pudding is the experimental, Caspar is the control). 34

Figure 10. Predicted log-transformed coho salmon winter growth per day by wood density (volume of wood per stream kilometer) scaled by combined watersheds where the shaded gray region represents the 95% confidence interval. 35

Figure 11. The correlation between scaled annual wood density (volume of wood per km) and scaled annual smolt density (smolts per km) in the BACI study, $R = -0.73$, $p < 0.0001$ 35

Figure 12. Scaled wood density (volume per km) and scaled smolt density (smolts per km) through time for each watershed in the BACI experiment. The light blue vertical line denotes wood supplementation in the experimental watershed. The trend lines are the loess smoothed lines for the data. Circle data points and solid lines represent scaled wood density. Triangles and dashed lines represent smolt densities. The control watershed is in black while the experimental watershed is in yellow. Cohort year refers to the year at the start of winter (i.e., winter 2019-2020 is in cohort year 2019). 36

Figure 13. Predicted values from a model for log-transformed coho salmon winter growth per day predicted by scaled smolt density. Smolt density refers to the estimate of out migrating smolts at each watershed’s downstream trap in spring divided by the number of stream kilometers. Smolt density in the BACI study was collinear with wood density ($cor = -0.73$, $p < 0.001$). 37

Figure 14. The annual survival (ϕ) estimates from the RMark model for the control (Caspar) and experimental (Pudding) watersheds for the duration of the BACI study. Error bars show the estimated standard error around each survival estimate. The gray vertical line denotes wood treatment in the experimental watershed. Cohort year refers to the year at the start of winter (i.e., winter 2019-2020 is in cohort year 2019). 40

Figure 15. Tukey's Honestly Significant Difference multiple comparisons of means at the 95% family-wise level plot with every unique combination of watershed (Caspar = control, Pudding = experimental) with treatment (pre = 2011-2014, post= 2015-2020).. 42

INTRODUCTION

Using large woody debris to restore the habitats of imperiled salmonids is a pillar of recovery strategies, but studies rarely provide evidence that these restoration actions create lasting positive effects on population demographics such as abundance, growth, and survival (Roni et al. 2008, 2015, Whiteway et al. 2010). Despite this lack of evidence, huge amounts of energy and money are invested in restoration of freshwater habitats to aid in the recovery of threatened and endangered salmonid populations throughout the Pacific Northwest (Spence and Hughes 1996, Ricciardi and Rasmussen 1999, Naiman and Latterell 2005, Moyle et al. 2011). In California alone, the California Department of Fish and Wildlife awarded over \$15 million to restoration projects in the 2017-2018 season (CDFW 2018). Unfortunately, project effectiveness is most often gauged on physical habitat changes and lack conclusive long-term assessments of fish response to the projects (Beschta 1992, Roni et al. 2002). Evaluating the effectiveness of habitat restoration is critical as we continue to make difficult decisions about how to allocate funding for managing salmonid populations, especially for those populations facing the threat of extinction.

Many Pacific salmon populations are declining, particularly at the Southern extent of their range (Nehlsen et al. 1991, Spence et al. 1996, Ogston et al. 2014, NMFS 2016). For example, coho salmon (*Oncorhynchus kisutch*) populations in California have declined in excess of 95% over the past 50 years and coho salmon only exist in about half of their historic streams within California (Cal Trout 2018). The Central California Coast

(CCC) coho salmon evolutionarily significant unit (ESU) is at the southernmost part of the coho salmon range and was listed as threatened in 1996 and reclassified as endangered in 2005 (NMFS 2016). Endangered CCC coho salmon are expected to experience very high exposure and sensitivity to projected climate change effects including increases in stream and sea surface temperature as well as ocean acidification (Crozier et al. 2019). If these populations are to recover to sustainable abundances, it is critical that we understand how different habitat enhancement techniques influence critical population metrics (e.g., growth, survival, and abundance) and that we implement the most effective restoration measures possible. One of the primary threats to this ESU is degradation of freshwater habitats (NMFS 2016), which has resulted in increasing efforts to restore these habitats to make them more suitable for spawning and rearing.

There are numerous types of habitat restoration efforts intended to improve stream habitats and in turn, increase salmonid populations. Instream habitat improvement directly affects salmonids by increasing the capacity or productivity of stream habitat (Katz et al. 2007). Specific actions within this category include implementation of artificial log structures or natural LWD, weirs and deflectors and placement of boulders and rock-filled wire gabions (Roni et al. 2008). The implementation of LWD has become arguably the most widespread approach taken for Pacific Northwest stream restoration (Roni et al. 2014). These methods of instream habitat improvement can increase pool depth and frequency and lead to accumulation of woody debris and retention of sediment (Cederholm et al. 1997, Reeves et al. 1997). Each of these physical outcomes is expected to have some effect on salmonids utilizing the modified habitat. Specifically, the purpose

of these actions in the context of salmonid restoration is to: 1) recruit and store gravel to improve spawning habitat, 2) to create scour pools (i.e., pools made from the scouring action of current flowing against an obstruction) to improve slow-water over-winter refugia for juvenile fish and thermal refugia for over-summer survival of fish, and 3) to improve cover from predators, enhancing survival (Armantrout 1991, Nickelson 1992, National Research Council 1996). These restoration efforts are successful if they can create measurable habitat change leading to improved salmonid populations and if they continue to maintain their ecosystem functions over time without human intervention (Gregory and Bisson 1997).

LWD supplementation has become the most widespread approach for stream restoration because of the important role LWD plays in watershed processes and habitat formation and because of the history of intensive wood removal. Wood has been removed from watersheds directly to control the effects of floods, facilitate navigation, and allow for fish passage (Sedell and Froggat 1984, Wohl et al. 2016, Dominguez and Cederholm 2020). Wood has been removed indirectly from watersheds through reduction of wood input sources from timber harvest and reduction of riparian zones, channelization through bank stabilization, dredging, and log floating for the purpose of transportation of timber, and flow regulation which has changed wood transport and recruitment processes (Boulton 2007, Wohl 2014, Wohl et al. 2016).

Restoration treatment via LWD supplementation is expected to positively impact watershed processes and lead to self-sustaining dynamics if there are sufficient existing riparian wood sources for interaction. Collins et al. (2012) describe the ‘floodplain large-

wood cycle' hypothesis as an interaction between wood, water, and sediment that creates a positive feedback loop. Large, stable riparian trees that fall into the channel can initiate wood jams, altering the floodplain and causing deposition that forms stable alluvial patches that allows for colonization of more trees, which continues the cycle. Some of the processes affected by these wood jams include: habitat and pool formation, island formation by inducing sediment deposition and vegetation colonization, creation of anastomosing channel patterns, and augmentation of the floodplain area by water, sediment, and wood routing (Collins et al. 2012). If restoration practitioners can strategically place woody debris into rivers that have existing stable riparian trees, they could promote the floodplain large-wood cycle which would allow the system to restore many other ecological processes and have lasting effects. The floodplain large-wood cycle breaks down if there are not existing wood sources in and outside of the channel. If there are wood sources to recruit into the system and treatment designed to move dynamically and collect wood, LWD supplementation can be a cost-effective approach with positive, watershed-wide long-term effects.

Effectiveness monitoring of biological response to restoration is often limited. Restoration projects often fail to achieve their objectives for rehabilitating river functions (Katz et al. 2007, Palmer et al. 2014, Wohl et al. 2015). For many instream restoration projects, their effectiveness is assessed solely by whether or not the planned manipulations were implemented, and whether or not the targeted physical habitat was realized; however, physical changes from restoration actions may not be meaningful if they do not produce the desired biological outcome (Bernhardt et al. 2005, Roni et al.

2002, Roni et al. 2008). In particular, if the goals of the restoration efforts are to help salmonid populations recover, then the restoration effectiveness should be measured by a long-term quantitative measurement of the life stage-specific rate being addressed.

Although large woody debris restoration can provide valuable rearing habitat for all salmonid species, it is often targeted toward the recovery of coho salmon populations due to their habitat preferences (Solazzi et al. 2000). Juvenile coho salmon use woody debris as important cover and protection from high flow events in winter (McMahon and Hartman 1989). Rearing coho have a preference for complex (spatially and structurally diverse) cover and seek shelter from high current velocities, preferring pools with average velocities less than 20 cm/s (Bisson et al. 1988, McMahon and Hartman 1989, Tullos and Walter 2015, Bair et al. 2019). Kaufmann (1987) found positive relationships between the structural complexity of woody debris, the size of pools, and volume of low velocity zones suggesting that woody debris placed in streams should be useful in creating habitat for overwintering juvenile coho salmon. This is particularly important because winter rearing habitat for coho salmon has been identified as a limiting factor in many populations (Nickelson et al. 1992, Solazzi et al. 2000, Romer et al. 2008, Gallagher et al. 2012). During spring and summer months, juvenile coho favor pools over riffles or glides (Nickelson et al. 1992). Adult coho salmon stream occupancy can be predicted by complex pools (pools with varied depth and structural diversity including cover elements like wood), percent bedrock, site distance to the ocean, and capacity of the habitat to support parr during winter (Anlauf-Dunn et al. 2014). Thus, the physical

effects of large wood restoration align well with the habitat requirements for coho salmon.

Despite this evidence to suggest that LWD supplementation should be beneficial for coho salmon populations, very few studies have shown a long-term, watershed-scale positive response to large wood restoration (Roni et al. 2008, Foote et al. 2020). Whiteway et al. (2010) synthesizes results from 211 LWD restoration projects and describes short term effects of increased pool area, average pool depth, and percent cover. In this meta-analysis, 73% of the LWD projects resulted in increased local salmonid densities; however, most do not distinguish between increased population abundance and increased concentrations of fish. Of the projects in review, 41% were only monitored for one year and, on average, monitoring lasted only 3 years (Whiteway et al. 2010). It can be necessary to monitor the effects of LWD additions for longer durations since salmonids have a 2-7 year lifespan. Furthermore, effects on geomorphological processes may require a longer transition period to become measurable (Whiteway et al. 2010, Collins et al. 2012). This emphasizes a major concern regarding the long-term effectiveness of LWD restoration projects. Additionally, it is important to look at actual demographic rates, not just abundance estimates, if we want to specifically understand how wood implementation is affecting fish populations (Roni et al. 2015), yet survival is not mentioned in the most recent major meta-analysis of the impact of instream restoration on salmonids (Foote et al. 2020). Most of the investigations of biological response to restoration focus on changes in fish abundance, yet changes in fish abundance can be the result of changes in fish distribution, recruitment, survival, or some

combination of these factors (Whiteway et al. 2010). Reviewing these projects, it is apparent that most are not watershed scale, long-term experiments and that their focus is not on vital rates, so it is difficult to make claims on changes to salmonid populations, river processes and their lasting effects on the watershed (Johnson et al. 2005, Palmer et al. 2014, Roni et al. 2015).

Given the substantial resources invested in LWD restoration projects, and the at-risk status of the target salmonid populations, it is prudent to quantitatively assess the population response of salmonids to those LWD restoration projects. Those responses are necessary to inform best management and restoration practices aimed at recovering coho salmon populations. Therefore, my thesis focuses on the biological response of endangered Central California Coast coho salmon (*Oncorhynchus kisutch*) to large wood treatments throughout a northern California coastal watershed using a Before-After-Control-Impact (BACI) experiment. My study objectives were to:

- 1) Determine whether wood implementation in the experimental watershed resulted in increased summer and winter growth rates.
- 2) Determine whether wood treatment resulted in improved winter survival in the experimental watershed.

METHODS

Study Area

This thesis is part of a BACI study that was conducted on Pudding Creek (the experimental watershed) and Caspar Creek (the control watershed) in Fort Bragg, California (Figure 1). These are unregulated, rainfall-driven watersheds that flow directly into the Pacific Ocean. High stream flows occur with winter storms and each watershed's bar-built estuary closes to the ocean during low flow periods.

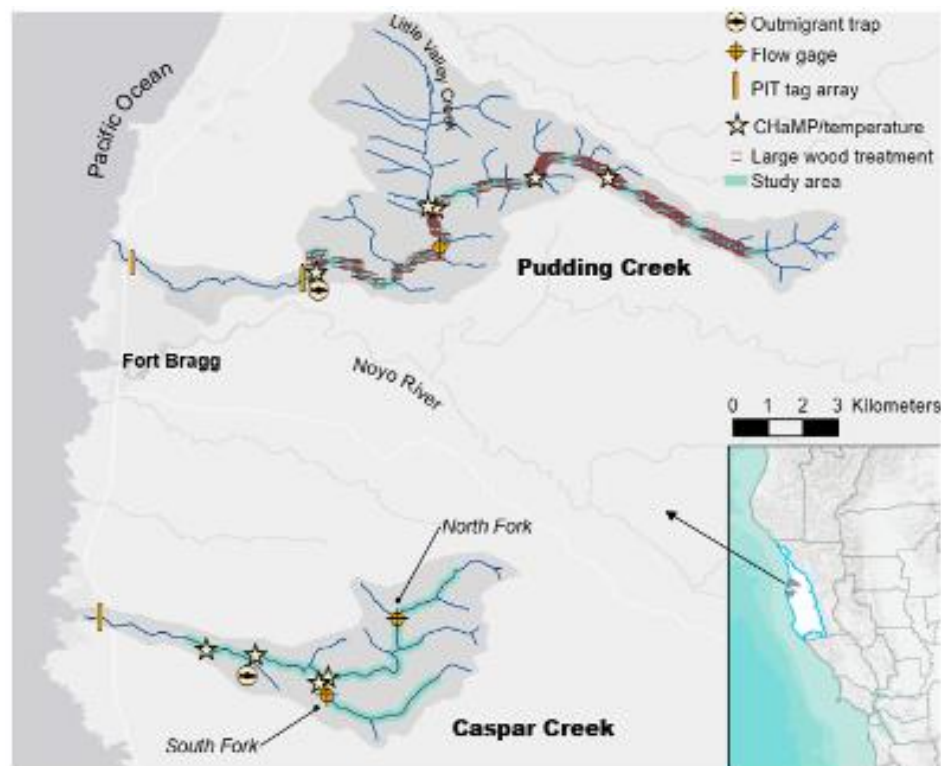


Figure 1. Study area for the Pudding Creek BACI Study, 2011-2020. Pudding Creek (experimental) and Caspar Creek (control) each have streamflow gauges, PIT tag arrays, temperature loggers, and outmigrant traps. Wood treatment only occurred in Pudding Creek. (Map by Sarah Gallagher, Okun et al. 2021)

Pudding Creek acts as the experimental site in the BACI study. It drains a watershed that is 45 km², has an average gradient of 1.8%, and an average bankfull width of 6.09 m (Mackey et al. 2016). Mixed coast redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*) dominate the watershed with a nearly continuous riparian canopy of primarily red alder (*Alnus rubra*), willow (*Salix* spp.), and big-leaf maple (*Acer macrophyllum*) (Mackey et al. 2016). The Pudding watershed is privately owned by Lyme Redwood Forest Company and is managed for residential use, timber production, and recreation. The average low temperature is 7.1 °C and the average high temperature is 15.8 °C with an average of 102.2 cm of annual precipitation by rainfall and no annual snowfall (WRCC 2018).

Pudding Creek has a lowhead dam less than 2 m above the water surface elevation at high tide located just under 0.25 km upstream of the creek's confluence with the ocean. This impoundment, built in 1953, is earthen and concrete and previously served as an adult trapping site and a passive integrated transponder (PIT) tag array site. A high flow event in December 2016 severely damaged much of the structure (Campbell Global Fisheries 2014). To continue to trap returning adults, a resistance board weir was installed in November 2017 6.6 km upstream from the mouth.

Caspar Creek is the control site in this BACI study and has many similarities to Pudding Creek (Table 5). Caspar Creek is a coastal watershed that drains an area that is 22 km², has an average gradient of 1.5%, and an average bankfull width of 5.36 m (Mackey et al. 2016). Caspar Creek watershed is dominated by coast redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*) with some grand fir (*Abies*

grandis) and western hemlock (*Tsuga heterophylla*) (Cafferata and Reid 2013). The riparian stand is dominated by red alder (*Alnus rubra*) (Cafferata and Reid 2013). Caspar Creek watershed is within Jackson Demonstration State Forest and includes the Caspar Creek Experimental Watersheds in the North and South Forks of Caspar Creek. Caspar Creek is managed for timber harvest, recreation, and research. The watershed has experienced historic heavy clear-cutting and floodplain modification (Cafferata and Reid 2013). At each fork on Caspar Creek, there is a v-notch weir and fish ladder leading to a sediment pond used in bedload transport studies.

Table 1. Comparison of Caspar Creek (control) and Pudding Creek (experimental) as paired watersheds for the BACI experiment. (Cafferata and Reid 2013, Mackey et al. 2016, Okun et al. 2021)

	<i>Caspar Creek</i>	<i>Pudding Creek</i>
watershed drainage area	22 km ²	45 km ²
average gradient	1.80%	1.50%
average bankfull width	5.36 m	6.09 m
ownership	Jackson Demonstration State Forest	Lyme Redwood Forest Company
dominant plant species	coast redwood, Douglas-fir, grand fir, western hemlock, red alder	coast redwood, Douglas-fir, red alder, willow, big-leaf maple
Life Cycle Monitoring Station	Yes, est. 2000	Yes, est. 2006
impoundments	Yes, v-notch weirs with fish ladders	Yes, flashboard dam with fish ladder
road access	>60%	>60%
salmonids species supported	Central California Coast coho salmon and Northern California steelhead	Central California Coast coho salmon and Northern California steelhead

Both watersheds currently experience timber harvest and experienced significant instream large wood removal during the 1970's (Mackey et al. 2016). Pudding and Caspar creeks both support independent populations of the endangered Central California Coast coho salmon evolutionarily significant unit (ESU) and the threatened Northern California steelhead distinct population segment (DPS). Both creeks have been operated as Life Cycle Monitoring (LCM) stations within California's Coastal Salmonid Monitoring Plan (CMP). The CMP was initiated in the control watershed in 2000 and in the experimental watershed in 2006. The goals within the CMP for these creeks are to estimate adult escapement, summer juvenile abundance, out-migrant production, and to characterize salmonids life history patterns within the creek (Wright et al. 2012).

Study Design

This thesis examines the biological responses (growth and survival) from a paired watershed BACI study that included annual habitat surveys and fish abundance, survival, and morphological data from 2011 through 2020. A paired watershed BACI design allows for the changes from an experimental treatment to be distinguished from background effects (i.e., large-scale, time effects) shared by both sites in addition to any background site differences that exist between the pair (Stewart-Oaten et al. 1986, Conner et al. 2016). Paired watersheds do not have to be identical because the analysis involves comparing each watershed's changes with itself through time to identify treatment impacts in the experimental watershed. The key to identifying a treatment effect in the paired watershed BACI design is to look at the interaction between

watershed and treatment or the habitat change resulting from treatment (i.e., a change in wood density following wood supplementation). In both study watersheds, baseline data were collected starting 2011, large wood was placed into Pudding Creek in 2015, and post-treatment monitoring concluded in 2020. During the pre-and post-treatment phase of the BACI study, we monitored salmonid populations on both the control and the experimental creeks to observe population trends in these two watersheds. Monitoring data that was used in this thesis included: tag releases and length measurements from summer and fall electrofishing surveys, downstream migrant trap recaptures and length measurements, passive integrated transponder (PIT) tag array detections, and winter and summer habitat surveys. Throughout this monitoring effort, the creek reaches that we surveyed on the control and experimental creeks were selected using the Generalized Random Tessellation Stratified (GRTS) method for spatially balanced sampling (Stevens and Olsen 2004, Holloway et al. 2015).

Large Wood Treatment

In summer 2015, LWD was strategically placed into 80% of the mainstem anadromous spawning habitat reaches in the experimental watershed (Fig 1). Wood was placed into the channel using rubber-tired grapple skidders and rubber-tired backhoes or by felling riparian trees directly into the channel at locations that were expected to collect and retain other woody debris as it moves downstream (Blencowe 2015). This approach is known as ‘Accelerated Recruitment’ and is meant to be a cost-effective approach to wood implementation that mimics the natural process of wood recruitment (Carah et al.

2014). Often, LWD was wedged amongst riparian trees, streambanks, stumps, or other ‘roughness elements’ to minimize wood treatment’s downstream mobility (Mackey et al. 2016). Treatment consisted of 236 unique instream wood structures using a total of 438 pieces (1,365 cubic meters) of LWD consisting of logs and rootwads. (Mackey et al. 2016). Wood treatment was designed to increase the creek’s connection to floodplains during winter flows, enhance pool habitat through scour, and sort and store bedload material (Carah et al. 2014). Each piece of treatment wood was tagged with unique identification markers and their locations were recorded. No LWD was actively placed in the control watershed.

Habitat Response to Treatment

The habitat changes in response to the LWD treatment were analyzed separately from this thesis to assess restoration effectiveness and satisfy grant deliverables (Okun et al. 2021), but I will briefly summarize the habitat survey and data analysis methods pertinent to my thesis. Onset HOB0 Pro V2 data loggers at multiple sites in each creek recorded stream temperature hourly for each year of the study. Stream flow data was recorded at gaging stations in each watershed (Figure 1). Flow data from the control watershed came from the stream gauge on the North Fork of the creek. The control watershed stream gauge data were provided by the Caspar Creek Experimental Watersheds project, which was funded by the USDA Forest Service Pacific Southwest Research Station and the California Department of Forestry and Fire Protection. The experimental watershed stream gauge data were provided by Lyme Redwood Forest

Company. The control stream gauge drains 4.79 km² while the experimental gauge drains 32.17 km² meaning the control gauge drains a smaller proportion of its entire watershed compared to experimental. I scaled flow by drainage area to compare the time series of flow in these watersheds throughout the study; however, in my statistical analyses, I used the absolute flow from the stream gauges to approximate the flows experienced by fish.

Each summer and winter, habitat data were collected using the Columbia Habitat Monitoring Program protocol (Bouwes et al. 2014), modified by Holloway et al. (2015), Holloway et al. (2016a), and Holloway et al. (2016b). The entire study extent was classified by unit type and measurements of fish cover, substrate composition, depth, wetted length and width, and large woody debris were collected. Large wood was assigned diameter-length size categories based on visual estimations and systematic calibration. Minimum size for LWD was 10 cm diameter and 1 m length. In spring 2020, crews recorded treatment wood tag numbers and locations which were used in ArcMap™ by ESRI to assess the movement of treatment wood in the experimental watershed from each piece's initial placement location (ESRI 2011). The goal of the winter habitat survey was to classify habitat units as either fast or slow water by observing gradient, relative stream velocity, and/or turbulence, then to further classify slow water units by pool type following methods at consistent winter flow levels each year. Once classified into unit type, each habitat unit's water surface area was visually estimated with a systematic sample measured for calibration.

Based on hypotheses about how fish grow and survive in response to their habitat, habitat metrics and candidate models were selected for analysis. All modeling in Okun et

al. (2021) and in this thesis was performed in RStudio versions 2021.09.1+372 (RStudio Team 2021). Model responses were residual pool depth, pool frequency, summer slow water volume, LWD density, LWD frequency, and winter slow water to fast water ratio. The two LWD metrics (density and frequency) both had a large number of survey units in which no LWD was observed which led to skewed distributions and poor model diagnostics (e.g., lack of homogeneity of variance, skewed QQ-plots). To compensate for this lack of model fit, we fit zero-inflated models to both the large wood metrics. Multiple habitat units (e.g., pools, riffles) were surveyed within each GRTS reach and, therefore, units from within the same GRTS reach lacked independence. To account for the variation related to GRTS reach, we included a random effect for GRTS in the models. Similarly, year was included as a random effect to account for the variation through time due to annual-scale differences in environmental conditions (e.g., precipitation).

Candidate models for each habitat response included fixed effects for watershed, treatment (pre vs post), and the interaction between watershed and treatment. We included an interaction between watershed and treatment based on the hypothesis that treatment would cause a habitat change evident in the experimental watershed that would not be evident in the control watershed.

We used an information theoretic approach (i.e. Akaike's Information Criterion, AIC) to compare models with different sets of covariates. AIC is a metric used for model selection where the best model is selected based on a score calculated as a trade-off between fit and number of parameters in the model (Burnham and Anderson 2001). AICc

is corrected for small sample sizes (Hurvich and Tsai 1989). AICc was used to determine the most parsimonious model for each habitat response metric. Models with ΔAICc less than 2 were assumed to fit the data equally well, in which case I selected the model with the fewest parameters based on the principle of parsimony. The Final Technical Report provides more details regarding the habitat data collection and statistical analysis (Okun et al. 2021).

Life-cycle Monitoring

Summer and Fall Electrofishing

Summer and fall electrofishing surveys were used to tag and recapture salmonids to evaluate seasonal growth and survival rates. After performing summer habitat surveys, in which the entire anadromous length of both creeks were delineated by habitat unit type (i.e. scour pool, riffle, non-turbulent fast water), electrofishing surveys were conducted in a systematic sample of 50 habitat units in the control watershed, and 50 habitat units in the experimental watershed (Gallagher et al. 2014). All selected habitat units were electrofished twice yearly during summer (July to mid-August) and fall (October). Three-pass depletion electrofishing methods described in Reynolds (1996) were used where block nets were set up at the upstream and downstream end of units being sampled.

All captured salmonids larger than 60mm were anesthetized, measured, weighed, examined for tags, and any untagged salmon were surgically implanted with a PIT tag. Fish were anesthetized using buffered, diluted tricaine mesylate (MS 222) and were

released back to the unit they were captured from after all necessary data had been collected and the depletion survey was complete. Prior to release, we ensured that all fish had fully recovered from the anesthetic in aerated buckets. Tagging of fish, as well as all handling of fish, was performed under the auspices of Humboldt State University IACUC #2020C76.

Summer Growth Estimates

I used generalized linear mixed effects models (GLMMs), and model selection with AICc to evaluate evidence for which covariates influenced the growth rate between summer and fall captures. GLMMs for summer growth were built with the R package ‘lme4’ version 1.1-27.1 in RStudio (Bates et al. 2015). Growth per day (gpd) was the difference in fork length for recaptured salmonids within one electrofishing season divided by the days between initial summer capture and fall recapture. For each species, I tested summer growth predicted by watershed (control vs experimental), and wood density (annual m³ summer wood per km stream length in each watershed) with a random effect for year (2011-2020). I also included an interaction between watershed and LWD density based on the *a priori* hypothesis that growth rates would stay constant in the control watershed throughout the study but change in the experimental watershed following the supplementation of wood. I hypothesized that wood treatments would create refugia from high winter flows, and slower velocity habitat can allow fish to conserve energy for foraging and growth, even in winter (Giannico and Hinch 2003, Ebersole et al. 2006). LWD density, hereafter referred to as wood density or LWD density, is the volume of wood per kilometer in each watershed measured annually in the summer habitat census.

This allows wood volume on each creek to be compared relatively despite the difference in watershed size between the two creeks. I scaled wood density by subtracting the mean and dividing by the standard deviation. A scaled wood density value of zero represents the mean for both watersheds observations combined. To determine which terms were the most important in this juvenile salmonid growth model, I ranked models based on AICc and determined the most parsimonious model. I used the R statistical package Diagnostics for Hierarchical Regression Models ('DHARMA') to check for violations of model assumptions (Hartig 2017) and the package Multi-model Inference ('MuMin') to check for goodness of fit (Bartón 2020).

Juvenile Outmigrant Trapping

The estimates of annual smolt abundances, and PIT tag recaptures necessary to estimate overwinter survival, were based on data collected at the juvenile outmigrant traps operated as an essential component of the life-cycle monitoring stations in each watershed. In the experimental watershed, we installed a rotary screw trap at a site 6.6 km upstream from the Pacific Ocean. Due to limited depths in the control watershed, we used a fyke net to capture downstream migrants, which was installed 2.5 km upstream of the Pacific Ocean. Traps were installed in late-February in each stream and sampled daily through early June every year of the study.

At these traps, out-migrating coho salmon had morphometric data collected and PIT tags surgically implanted. Salmonids larger than 60 mm in the experimental watershed and larger than 70 mm in the control watershed were implanted with PIT tags due to differences in antenna tag-reading types in each watershed. No tagging occurred in

the control watershed during spring 2015 due to low adult escapement and low number of juveniles that were encountered. We examined all trap-captured salmonids for marks each day.

Annual smolt abundance was estimated in the 2021 Final Technical Report for this study using Darroch Analysis with Rank Reduction and a one-trap design (Bjorkstedt 2003, Okun et al. 2021). These annual estimates were used to calculate smolt density which I had hypothesized would be a predictor of winter growth rate in this project.

Winter Growth Estimates

I used a generalized linear mixed effects model and AICc model selection to identify which covariates were correlated with coho salmon winter growth. Generalized linear mixed effects models for summer growth were built with the R package 'lme4' version 1.1-27.1 in RStudio (Bates et al. 2015). Winter growth-per-day is the over winter growth difference between fall electrofishing capture and recapture at the downstream outmigrant trap divided by the days between capture. I tested winter growth rate predicted by watershed (control vs experimental), scaled wood density, and a random effect for year. I hypothesized that winter growth would remain constant throughout the study in the control watershed, but increase in the experimental watershed post-treatment because placed wood was intended to increase slow water rearing habitat in winter. I expected wood treatments to slow winter flows and to create pools, improving the quality and quantity of habitat and allowing fish to allocate energy towards growth that may otherwise be allocated to holding in high velocity flow. I included all possible combinations of my predictors in model selection. I included the interaction between

watershed and wood density to see if adding wood to the experimental creek allowed for greater winter growth than in control. Watershed is categorical independent variable while wood density is a continuous independent variable. I used the AICc score to select the most parsimonious generalized linear model to see which predictors are significantly informative to the top model. Once I selected the best model predicting winter growth, I used the R package 'DHARMA' (Hartig 2017) to check model assumptions and 'MuMin' to check for goodness of fit (Bartón 2020).

PIT Tag Arrays

PIT tag antenna arrays were placed on the control and experimental watersheds to detect movement of tagged salmonids and used for survival analysis (Figure 1).

Locations of the arrays used in this study were chosen based on proximity to the ocean and land access. Arrays were maintained from fall through early summer. Previous analysis has shown very limited movement of salmonids over summer in both watersheds when flows are low, therefore we did not operate arrays during this period.

This study used data collected at the downstream-most PIT tag arrays in each watershed. The control watershed's downstream-most array was located 450 m from the creek's mouth and the experimental watershed's two downstream-most arrays used in the study were located at 800 m and 4 km from the mouth (Figure 1). The control watershed's array consisted of HDX pass-through antennas that run on deep-cycle lead batteries with an Oregon RFID multi-plex reader and tuners. The experimental watershed's arrays are FDX pass-over arrays that run on a combination of solar panels and deep-cycle lead batteries with Biomark Qube controller/readers.

Winter Survival Estimates

To estimate over-winter survival, I used a Cormack-Jolly-Seber (CJS) model with the detection data from electrofishing, downstream out-migrant traps, and downstream PIT arrays. I used the R package ‘RMark’ (Laake 2013) which calls Program MARK (White and Burnham 1999). I created capture histories with four occasions: 1) summer electrofishing, 2) fall electrofishing, 3) capture at downstream migrant traps, and 4) detection at the downstream-most arrays (Figure 2). The CJS model estimates both apparent survival (Φ) and capture probability (p). Apparent survival (Φ) is the product of fish surviving through an occasion and not emigrating from the area so that they can be detected. The capture probability (p) is the probability of marked individuals being re-captured at a given time.



Figure 2. The four occasions of data collection used in the Cormack-Jolly-Seber model to estimate apparent survival and capture probability. Winter survival (Φ_2) is the interval between fall electrofishing and each creek’s outmigrant trap.

The CJS model assumes the following (Lebreton 1992, Pledger 2003):

1. Every individual in the population during sampling has the same probability of being captured or recaptured.

2. Every individual in the population during sampling has the same probability of surviving from time i to time $i+1$.
3. Marks are not lost, missed, or recorded incorrectly during the sampling period.
4. Samples are instantaneous relative to the interval between detection occasions (i and $i+1$) and animals are released immediately after being sampled.
5. Emigration from the sampled study area is permanent.
6. Each individual's capture and survival is independent of one another.

Covariates used to predict apparent survival were watershed, year, time (the occasion within the model), and the interaction between watershed and year. I expected differences in survival response between watersheds because wood treatment only occurred in the experimental watershed and I expected fish survival would change through time due to natural variation in a wide variety of biological (e.g., density of fish) and physical (e.g., stream flow and temperature) factors expected to occur over the nine-year study period. The interaction between watershed and year was included to see if there was a positive treatment effect, where winter survival would increase more in the experimental watershed following treatment than in the control. I used watershed, year, and time as covariates for capture probability because I expected capture probability to vary by capture technique at each occasion in each watershed, and through time.

After adjusting for an estimate of overdispersion (median c -hat) derived in Program MARK for each species, I ranked models based on ΔQAICc . ΔQAICc is the difference in overdispersion-adjusted AICc for each model with that of the best model.

Parameter estimates for apparent survival and capture probability and model coefficients were outputs from the RMark function for the CJS model.

Using RMark's watershed and year-specific parameter estimates from the most parsimonious model predicting winter survival, I bootstrapped data to estimate the average changes in survival in each watershed from the pre- to post-treatment time periods. I used the watershed-year specific survival estimates and their standard errors to simulate distributions of survival estimates for each unique watershed-year combination. I then calculated the means for each watershed-year grouped by treatment time period where pre-treatment was 2011 through 2014 and post-treatment was 2015 through 2020. I performed a two-way ANOVA on a linear model where watershed-treatment period mean survival from the simulated data was predicted by watershed, treatment (pre vs post), and the interaction between watershed and treatment. I used Tukey's Honestly Significant Difference (Tukey HSD) test to look at each contrast of watershed and treatment in the model.

RESULTS

Habitat Response to Treatment

Habitat surveys conducted as part of the larger BACI study found that the only habitat metrics with a treatment effect from pre- to post- treatment were wood density and summer slow water volume (Figure 3). There was a greater increase in wood density in the experimental watershed (pre-treatment = 189.9 cubic meters per kilometer, post-treatment = 248.9 cubic meters per kilometer, 31% increase) than in the control watershed (pre-treatment = 282.4 cubic meters per kilometer, post-treatment = 318.7 cubic meters per kilometer, 13% increase) (Figure 4). Wood density was lower in the experimental than in the control watershed during the pre-treatment period and increased to reach similar wood densities as the control watershed in the post-treatment period. The binomial portion of the zero-inflated models for LWD density included an interaction between treatment and watershed, indicating that more summer habitat units had large wood present post-treatment and that the increase was greater in the experimental than the control watershed. Summer slow water increased more in the experimental than the control watershed and there was a wide range of summer slow water volumes throughout the study (Figure 3). The top models for winter slow water to fast water ratio and for pool frequency were models that did not include any covariates, indicating there were no differences between watershed or treatment period. Wood movement analysis showed 80% of the wood treatment pieces were resighted, 10% of which moved downstream. For

those pieces that were resighted downstream, movement was an average of 200m downstream from initial placement locations.

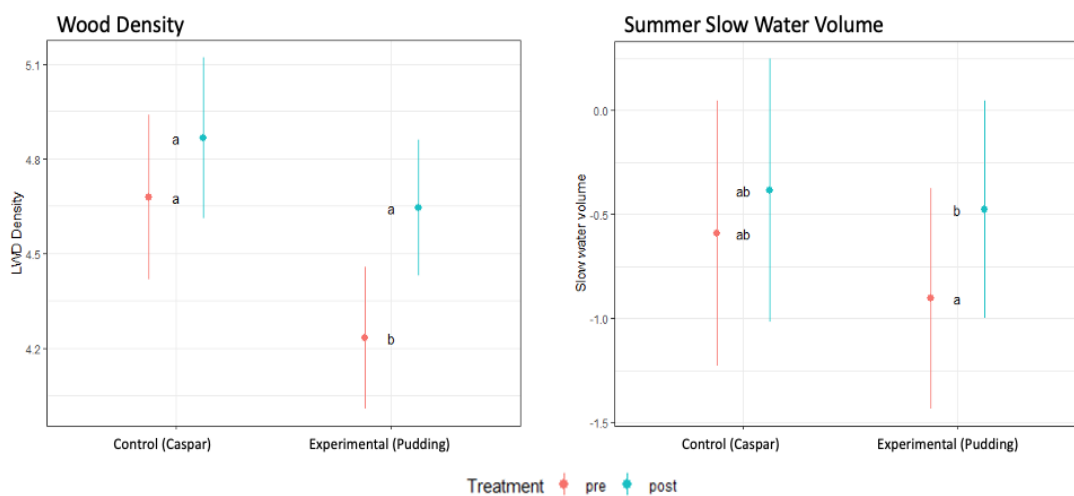


Figure 3. Comparison of marginal means from the most parsimonious generalized linear mixed effects models for wood density (cubic meters per stream kilometer) and summer slow water volume (cubic meters). The points with the same letter indicate that there was no evidence of a difference in estimated habitat metric based on a Tukey Honestly Significant Difference post-hoc test.

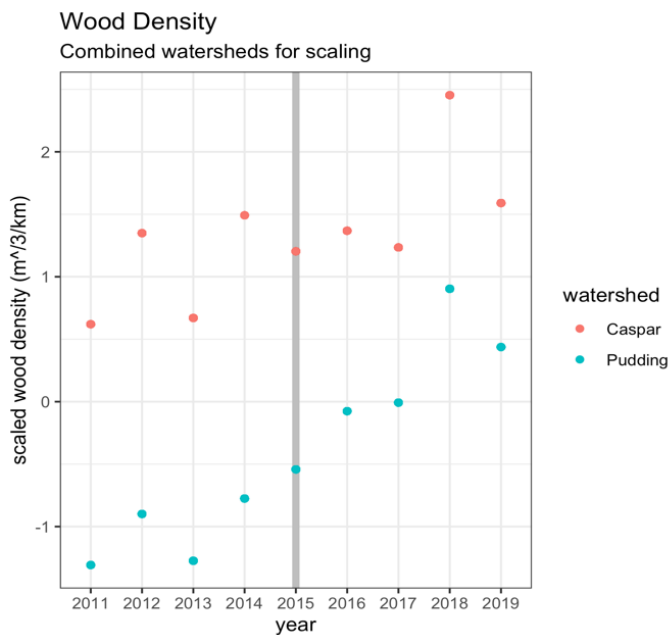


Figure 4. Scaled annual wood density (cubic meters per stream kilometer) for the duration of the BACI study. Pudding Creek was the experimental watershed which received wood supplementation and Caspar Creek was the control watershed and did not receive active wood treatment. The gray vertical line denotes Pudding Creek wood treatment in summer 2015.

A two-way ANOVA with watershed, treatment (pre vs post), and their interaction revealed that there was strong evidence ($p < 0.001$) that the control watershed was slightly warmer than the experimental watershed and that the pre-treatment period of the study was colder than the post-treatment period (Figure 5, Table 2). The treatment-related difference in water temperature was most substantial when comparing winter temperatures. There was no evidence ($p=0.72$) of an interaction between watershed and treatment period indicating that the temperatures changed similarly in both watershed through time.

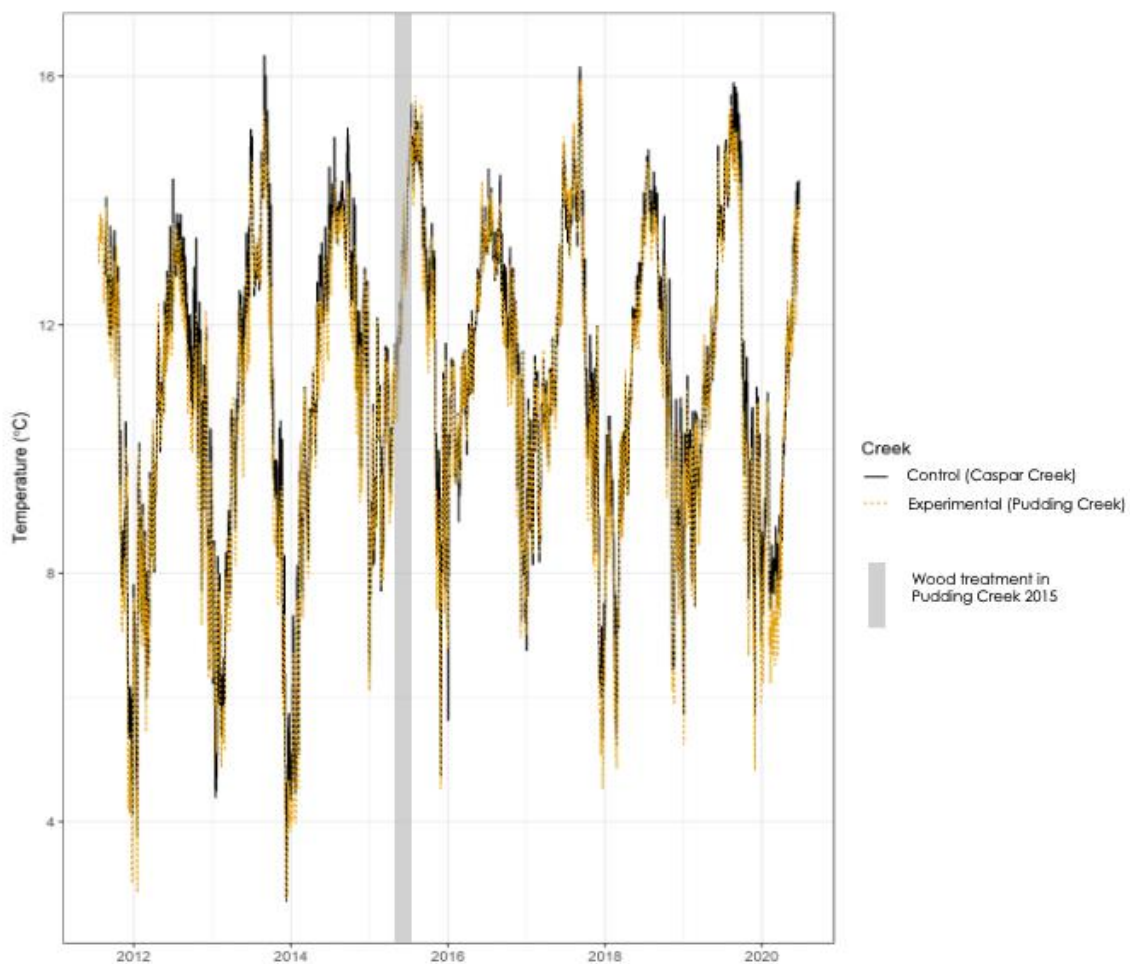


Figure 5. Mean daily water temperatures on Pudding Creek (experimental) and Caspar Creek (control) through the BACI study period. Wood supplementation in Pudding Creek (experimental) took place in summer 2015. (Okun et al. 2021)

Table 2. The two-way Analysis of Variance (ANOVA) results stream temperature predicted by treatment time period (pre = 2011 to summer 2015, post = summer 2015 to 2020), watershed (control = Caspar Creek, experimental = Pudding Creek), and the interaction between treatment period and watershed.

Predictor	Sum of Sq.	df	Mean Sq.	F	p
(Intercept)	746697.59	1	746697.59	117654.00	<0.001
treatment	813	1	813.26	128.14	<0.001
watershed	147	1	146.68	23.11	<0.001
treatment x watershed	1	1	0.81	0.13	0.721
Error	41138.02	6482	6.35		

We used a two-way ANOVA to test the effects of watershed, treatment, and the interaction between watershed and treatment on logged mean daily flow (cubic feet per second, cfs) and logged mean daily flow normalized by drainage area (square kilometers, sq km) upstream of the stream gages (Table 3, Table 4). Log-transforming the response variables, flow and normalized flow, for each linear model allowed model assumptions to be met. For the logged mean daily flow, there was strong evidence ($p < 0.001$) for differences between watershed and treatment period as well as strong evidence ($p < 0.001$) for an interaction effect between watershed and treatment (Figure 6, Table 3). For the drainage area normalized flow, there was also strong evidence ($p < 0.001$) of a difference in flow between watersheds and treatments (pre- vs post) and strong evidence ($p < 0.001$) of an interaction between watershed and treatment (Figure 7, Table 4). There was more flow in the post-treatment period and the stream flow change from pre- to post-treatment was more dramatic in the experimental watershed.

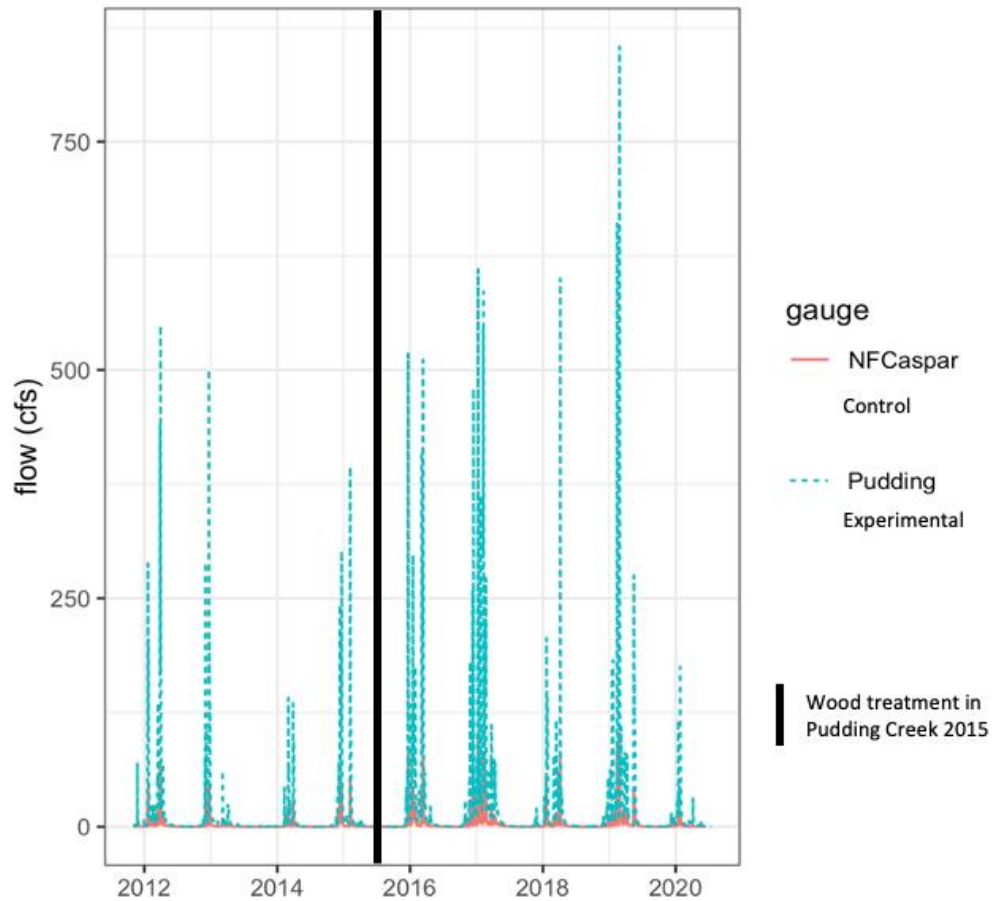


Figure 6. Hydrograph of Pudding Creek (the experimental watershed) and North Fork Caspar Creek (representative of the control watershed) mean daily flow (cubic feet per second, cfs) during the BACI study period (2011 through 2020). Wood supplementation in Pudding Creek (the experimental watershed) took place in summer 2015. (Okun et al. 2021)

Table 3. The two-way Analysis of Variance (ANOVA) results using log(stream flow) as the dependent variable. Gauge refers to the flow gauge in each watershed (control gauge = North Fork Caspar Creek, experimental gauge = Pudding Creek). Treatment refers to before and after wood supplementation in the experimental watershed in summer 2015.

Predictor	Sum of Sq.	df	Mean Sq.	F	p
gauge	2695.5	1	2695.5	695.86	<0.001
treatment	1468.2	1	1468.2	379.02	<0.001
gauge x treatment	51.7	1	51.75	13.36	<0.001
Residuals	24500.8	6325	3.87		

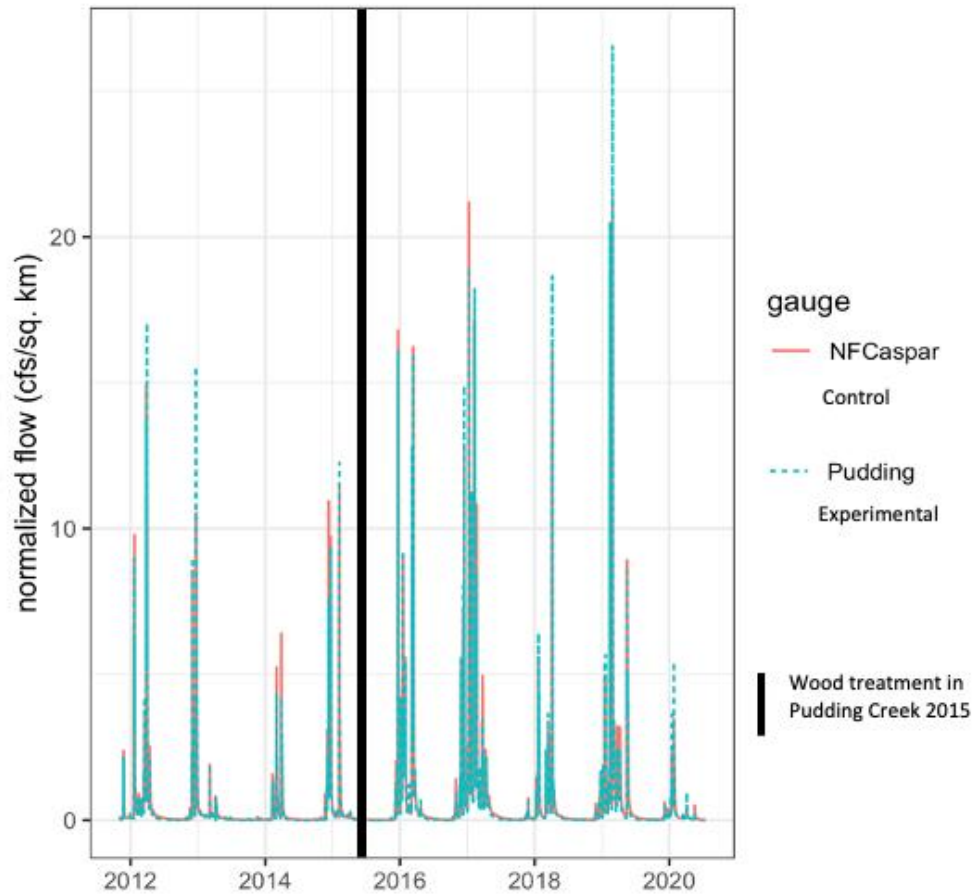


Figure 7. Hydrograph of Pudding Creek (the experimental watershed) and North Fork Caspar Creek (representative of the control watershed) mean daily flow (cubic feet per second, cfs) normalized by the drainage area above each creek's stream gauge during the BACI study period (2011 through 2020). Wood supplementation in Pudding (the experimental watershed) took place in summer 2015. (Okun et al. 2021)

Table 4. The two-way Analysis of Variance (ANOVA) results using $\log(\text{drainage area normalized stream flow})$ as the dependent variable. Gauge refers to the flow gauge in each watershed (control gauge = North Fork Caspar Creek, experimental gauge = Pudding Creek). Treatment refers to before and after wood supplementation in the experimental watershed in summer 2015.

Predictor	Sum of Sq.	df	Mean Sq.	F	p
gauge	2696	1	2695.5	695.7	<0.001
treatment	1468	1	1468.2	379.0	<0.001
gauge x treatment	52	1	51.7	13.4	<0.001
Residuals	24501	6325	3.9		

Summer Growth Results

The most parsimonious model for summer growth rate included wood density as a fixed effect and year as a random effect (Table 5). The top model had the response, summer growth rate, log-transformed. There was strong evidence ($p < 0.001$) that with increasing wood densities, summer growth rates increased (Figure 8). The top model's variance associated with the random effect for year was $4.948e-05$, which is virtually zero. The pseudo- R^2 for GLMM from the R package 'MuMin' for generalized mixed effects models indicated that variation in summer growth is not well explained by the model. The marginal R^2 for GLMM, representing the variance explained by the fixed effects, was 0.089, while the conditional R^2 for GLMM, representing the variance explained by the entire model, including both fixed and random effects, was slightly higher at 0.116. DHARMA model diagnostics indicated that model assumptions had been met for the summer growth model.

Table 5. Summary results from top mixed effects model (selected through AIC) for coho salmon summer growth per day (log-transformed). Wood density refers to the annual summer wood volume per stream kilometer scaled with combined watersheds.

Effect	Covariate	Estimate	St. Error	Variance	St. Deviation
fixed	intercept	0.0581	0.0036	-	-
	wood density	0.0134	0.0023	-	-
random	year	-	-	0.0005	0.007

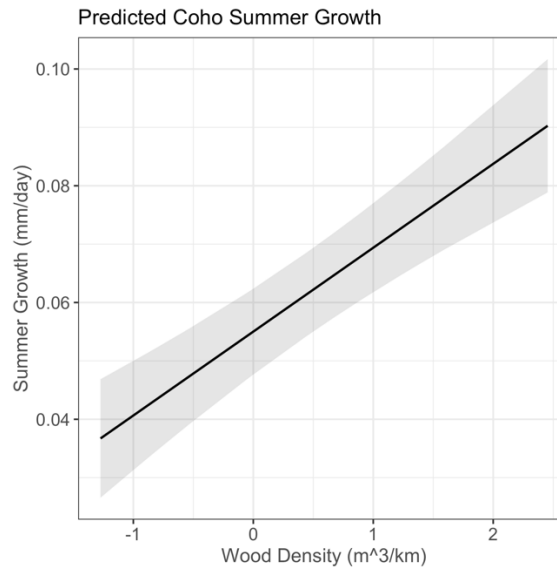


Figure 8. Predicted log-transformed coho salmon summer growth per day by wood density (volume of wood per stream kilometer) given the model that includes a random effect for year. The shaded gray region represents the 95% confidence interval.

Winter Growth Results

The top model predicting winter growth for coho included watershed, wood density, and a random effect for year (Table 6). There was strong evidence ($p < 0.001$) that the experimental watershed had higher winter growth than the control watershed (Figure 9). There was moderate evidence ($p = 0.01$) that with increasing wood density, winter growth increased (Figure 10). The random effect for year had a variance of 0.002 and the conditional R^2 for GLMM was 0.34 which was greater than the marginal R^2 for GLMM at 0.16. This indicates that variance explained by the entire model, including both fixed and random effects, is better than the model without the random effect for year.

Unfortunately, smolt density was collinear with wood density ($\text{cor} = -0.73$, $p < 0.001$), so I could not use both covariates in the same model (Figure 11,). Due to the study design and purpose, I decided to keep wood density in the model to understand the treatment effect. This meant that ultimately, I used the winter growth model with wood density instead of smolt density. The AIC score for the growth model predicted by the random effect for year with watershed and wood density (Wood Density Winter Growth Model) was -2123 and the AIC score for the growth model predicted by the random effect for year with watershed and smolt density (Smolt Density Winter Growth Model) was -2122. A difference between two AICc scores that is less than 2 indicates no difference between the models' ranks and that these models explain the data equally well. DHARMA model diagnostics indicated that model assumptions had been met for the both the Smolt Density and Wood Density Winter Growth Models.

Despite not using smolt density as the predictive model to address my study question, there are some interesting trends to note. With higher smolt densities, this model predicts that coho winter growth rate declines (Table 7, Figure 13). In years with higher smolt densities, there was lower wood densities and smolt densities varied greatly between watersheds (Figure 11, Figure 12). Based on population estimates from spring trapping, the mean smolt density in the pre-treatment period was 969 smolts per kilometer in the experimental watershed and 267 smolts per kilometer in the control watershed, while in the post-treatment period, it was 818 smolts per kilometer in the experimental watershed and 287 smolts per kilometer in the control watershed. This

additional information is important to note for interpretation of the winter growth model that does not include smolt density as a predictor.

Table 6. Summary results from top mixed effects model (selected through AIC) for coho salmon log-transformed winter growth per day (Wood Density Winter Growth Model). Wood density refers to the annual summer wood volume per stream kilometer scaled with combined watersheds. This data omits juvenile 2014-2015 due to 2014 run failure. Watershed compares Pudding Creek (experimental) against Caspar Creek (control). AICc score for this model is -2123.

Effect	Covariate	Estimate	St. Error	Variance	St. Deviation
fixed	intercept	0.031	0.024	-	-
	wood density	0.045	0.017	-	-
	watershed(Pudding)	0.157	0.025		
random	year	-	-	0.002	0.04

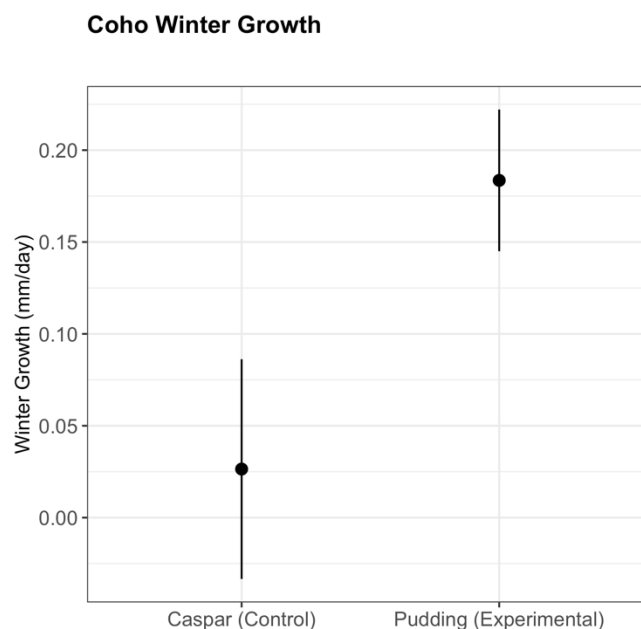


Figure 9. Top model estimated marginal means and their 95% confidence intervals for log-transformed coho salmon winter growth per day for each watershed in the BACI study (Pudding is the experimental, Caspar is the control).

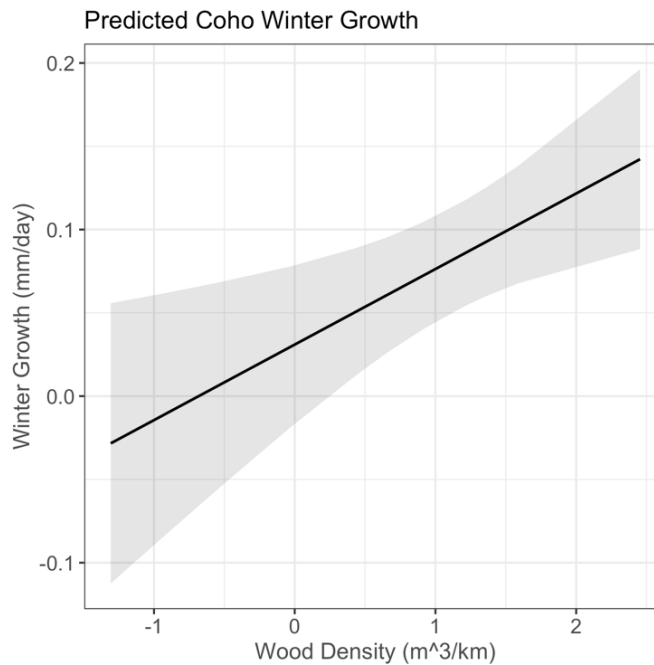


Figure 10. Predicted log-transformed coho salmon winter growth per day by wood density (volume of wood per stream kilometer) scaled by combined watersheds where the shaded gray region represents the 95% confidence interval.

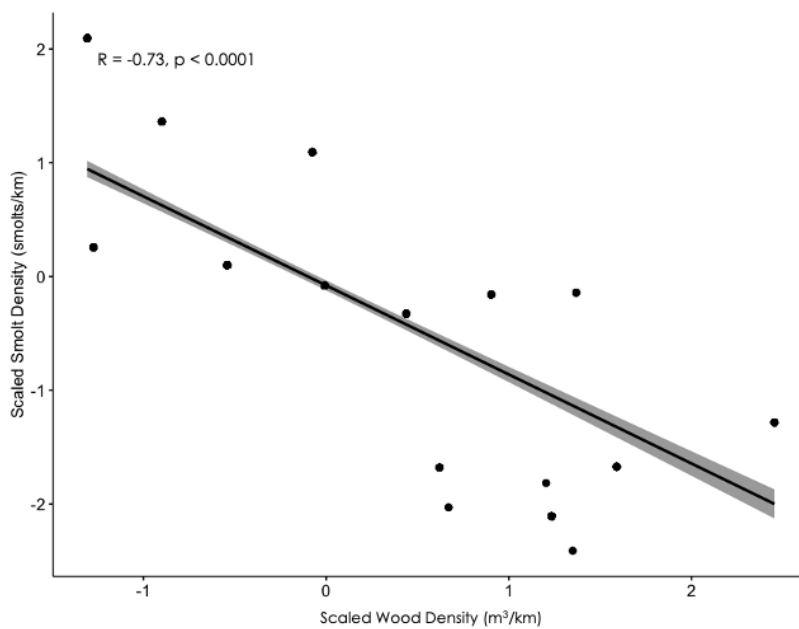


Figure 11. The correlation between scaled annual wood density (volume of wood per km) and scaled annual smolt density (smolts per km) in the BACI study, $R = -0.73, p < 0.0001$.

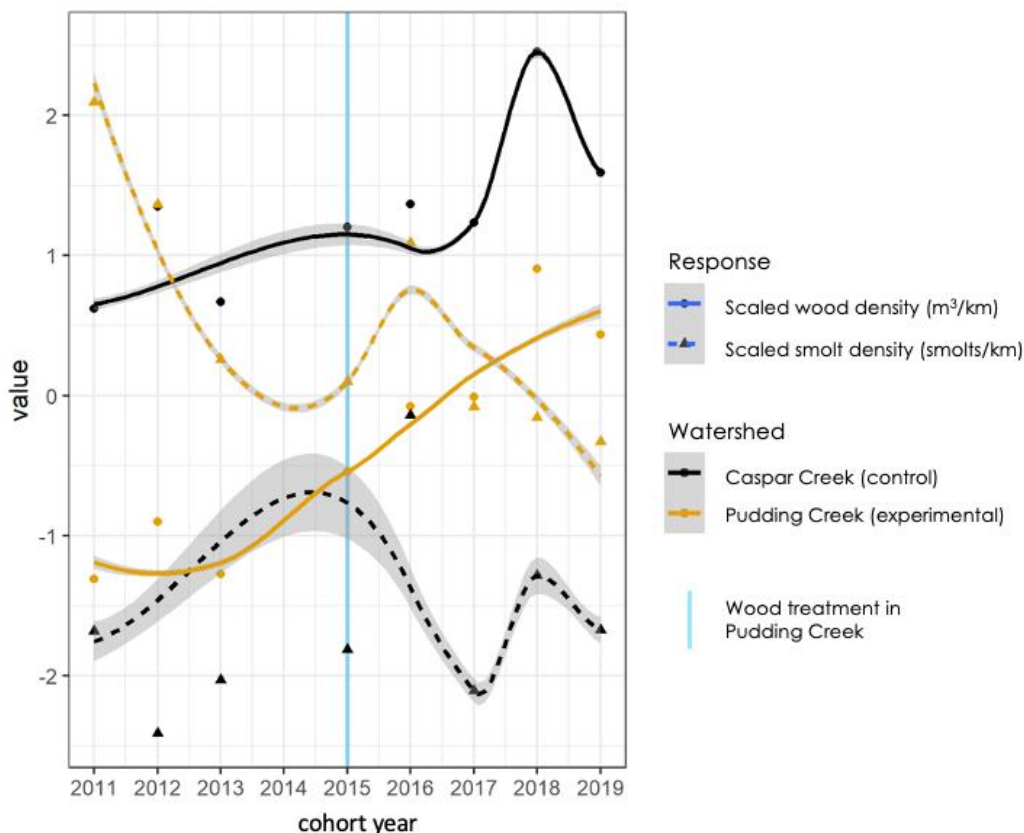


Figure 12. Scaled wood density (volume per km) and scaled smolt density (smolts per km) through time for each watershed in the BACI experiment. The light blue vertical line denotes wood supplementation in the experimental watershed. The trend lines are the loess smoothed lines for the data. Circle data points and solid lines represent scaled wood density. Triangles and dashed lines represent smolt densities. The control watershed is in black while the experimental watershed is in yellow. Cohort year refers to the year at the start of winter (i.e., winter 2019-2020 is in cohort year 2019).

Table 7. Summary results from smolt density mixed effects model (selected through AIC) for coho salmon log-transformed winter growth per day (Smolt Density Winter Growth Model). Smolt density refers to the annual smolt estimates per watershed per stream kilometer scaled with combined watersheds. This data omits juvenile 2014-2015 due to 2014 run failure. Watershed compares Pudding Creek (experimental) against Caspar Creek (control). AICc score for this model is -2122.

Effect	Covariate	Estimate	St. Error	Variance	St. Deviation
fixed	intercept	0.050	0.022	-	-
	smolt density	-0.021	0.009	-	-
	watershed(Pudding)	0.134	0.019		
random	year	-	-	0.002	0.05

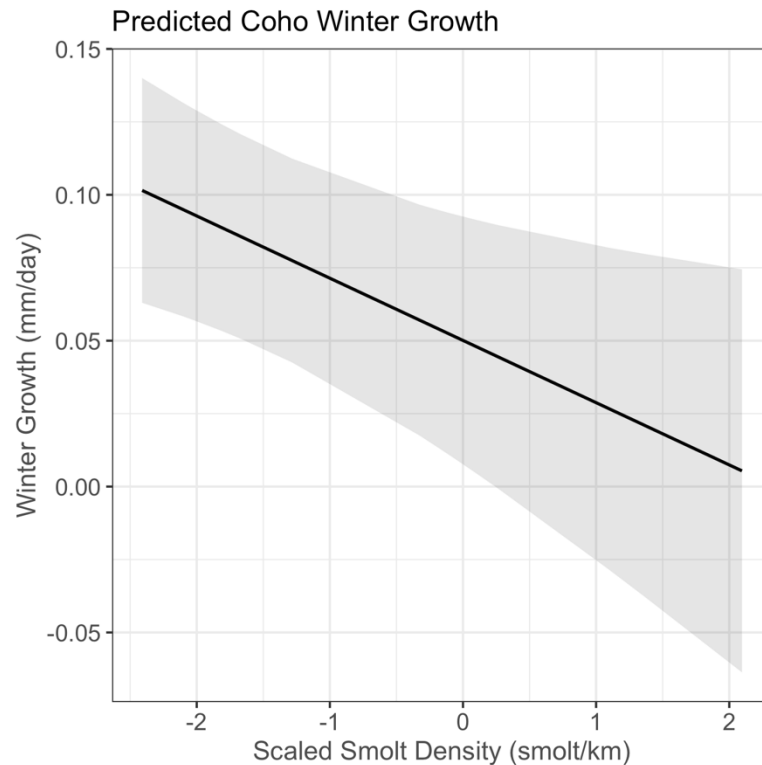


Figure 13. Predicted values from a model for log-transformed coho salmon winter growth per day predicted by scaled smolt density. Smolt density refers to the estimate of out migrating smolts at each watershed's downstream trap in spring divided by the number of stream kilometers. Smolt density in the BACI study was collinear with wood density ($cor = -0.73$, $p < 0.001$).

Winter Survival Results

The most parsimonious mark-recapture model estimating survival of coho salmon included watershed, year, time, and the interaction between watershed and year (Table 8). This model had the lowest QAICc, the AICc score adjusted for the quasi-likelihood parameter, estimated \hat{c} , based on the bootstrap goodness-of-fit approach in Program MARK (median $\hat{c} = 3.86$). The estimated \hat{c} for survival suggests that the data are

overdispersed, that is, there is greater variability in the observed data than what would be expected given the survival model. The effect of overdispersion is an underestimation of the variance and can be corrected for by using QAICc ranking for model selection. One explanation for overdispersion is omitted variables which is likely the case in this survival model. In order to include annual covariates that could be affecting winter survival (e.g., smolt density, stream flow), I would need to include a random effect accounting for the variation related to year.

The top survival model showed that from the start of the experiment to the end, winter survival in the control watershed increased, while the survival in the experimental watershed stayed the same (Figure 14, Table 9). A two-way ANOVA on the simulated watershed-year survival estimates grouped into pre- and post-treatment time periods predicted by watershed, treatment, and the interaction between watershed and treatment indicated that there is evidence ($p = 0.002$) for the interaction. Post-hoc analysis with Tukey's Honestly Significant Difference contrasts of means of simulated data, based on the RMark parameter estimates, showed that there was strong evidence ($p = 0.001$) of an increase in survival from pre- to post-treatment in the control watershed, but there was no evidence ($p = 0.85$) of a difference in survival in the experimental watershed (Figure 15).

Table 8. Juvenile coho survival (Φ) models ranked by $\Delta QAICc$ from RMark. The bold model was chosen as the top model based on the principle of parsimony (see text). In these models, watershed compares the experimental (Pudding) with the control (Caspar) and year is each year of the study from 2011 to 2020. Time refers to the occasion within the model. Capture probability for each of these models included watershed, year, and time.

<i>Model</i>	<i>nPar</i>	<i>deltaQAICc</i>
Phi~ watershed + year + time + watershed: year	32	0
Phi~ watershed + year + time	24	70
Phi~ watershed + time	23	111
Phi~ year + time	16	137
Phi~ time	15	172

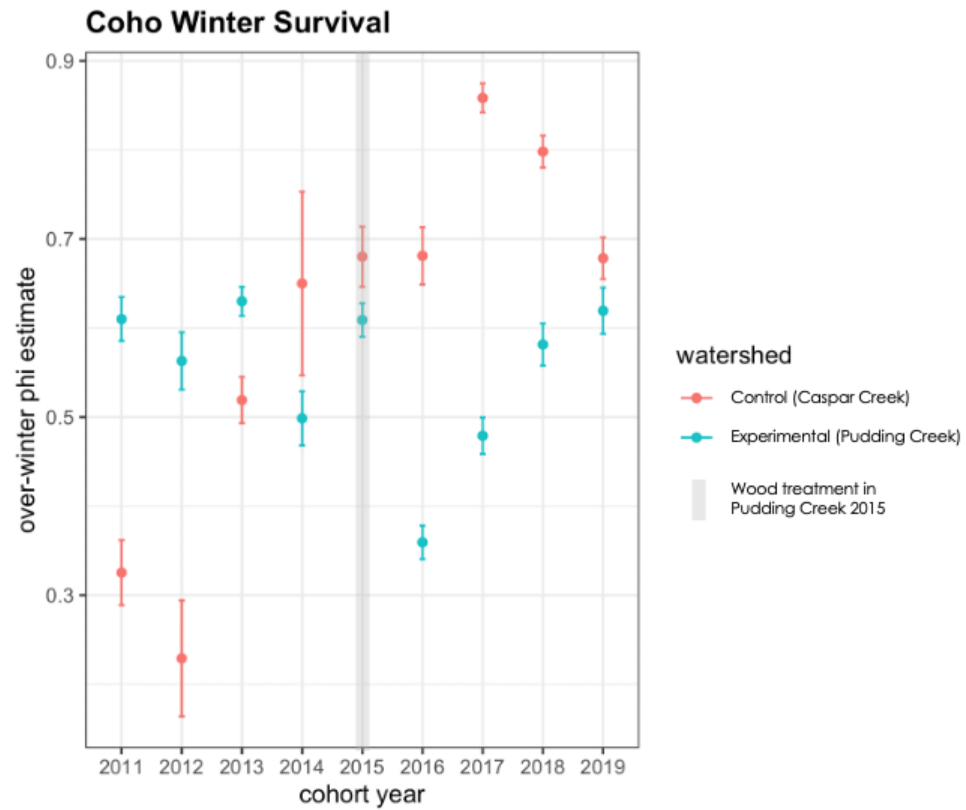


Figure 14. The annual survival (ϕ) estimates from the RMark model for the control (Caspar) and experimental (Pudding) watersheds for the duration of the BACI study. Error bars show the estimated standard error around each survival estimate. The gray vertical line denotes wood treatment in the experimental watershed. Cohort year refers to the year at the start of winter (i.e., winter 2019-2020 is in cohort year 2019).

Table 9. Coefficient estimates, standard errors, and lower and upper 95% confidence levels (Lower CL, Upper CL) for apparent survival (Φ) and capture probability (p) from the top CJS model in RMark predicting survival for juvenile coho in the BACI study. Pudding, the experimental watershed, is in comparison with Caspar, the control. The experimental watershed received wood supplementation in 2015. The four occasions of the study were: 1) summer electrofishing, 2) fall electrofishing, 3) downstream outmigrant trap, and 4) PIT tag array detection.

Parameter	Covariate	Estimate	St. Error	Lower CL	Upper CL
Survival	Intercept	1.153	0.285	0.594	1.711
	Pudding	1.178	0.180	0.825	1.530
	2012	-0.484	0.398	-1.264	0.295
	2013	0.806	0.180	0.454	1.159
	2014	1.349	0.477	0.415	2.284
	2015	1.484	0.214	1.065	1.904
	2016	1.489	0.209	1.079	1.898
	2017	2.533	0.199	2.142	2.923
	2018	2.105	0.184	1.744	2.466
	2019	1.476	0.182	1.120	1.833
	fall to trap	-1.883	0.249	-2.371	-1.395
	trap to array	-1.932	0.239	-2.401	-1.463
	Pudding:2012	0.290	0.422	-0.537	1.118
	Pudding:2013	-0.722	0.204	-1.122	-0.322
	Pudding:2014	-1.803	0.496	-2.775	-0.831
	Pudding:2015	-1.489	0.238	-1.956	-1.022
	Pudding:2016	-2.515	0.235	-2.975	-2.055
	Pudding:2017	-3.064	0.226	-3.507	-2.621
	Pudding:2018	-2.224	0.218	-2.651	-1.797
Pudding:2019	-1.437	0.221	-1.871	-1.003	
Capture Probability	Intercept	-0.895	0.143	-1.175	-0.615
	Pudding	0.560	0.069	0.424	0.697
	2012	0.752	0.208	0.345	1.159
	2013	-0.484	0.136	-0.749	-0.218
	2014	0.718	0.180	0.365	1.070
	2015	0.696	0.147	0.409	0.983
	2016	0.442	0.155	0.139	0.746
	2017	0.826	0.145	0.543	1.110
	2018	-0.432	0.150	-0.726	-0.138
	2019	0.586	0.148	0.297	0.876
	trap capture	-0.725	0.078	-0.878	-0.573
	array detection	17.609	636.596	-1230.120	1265.337

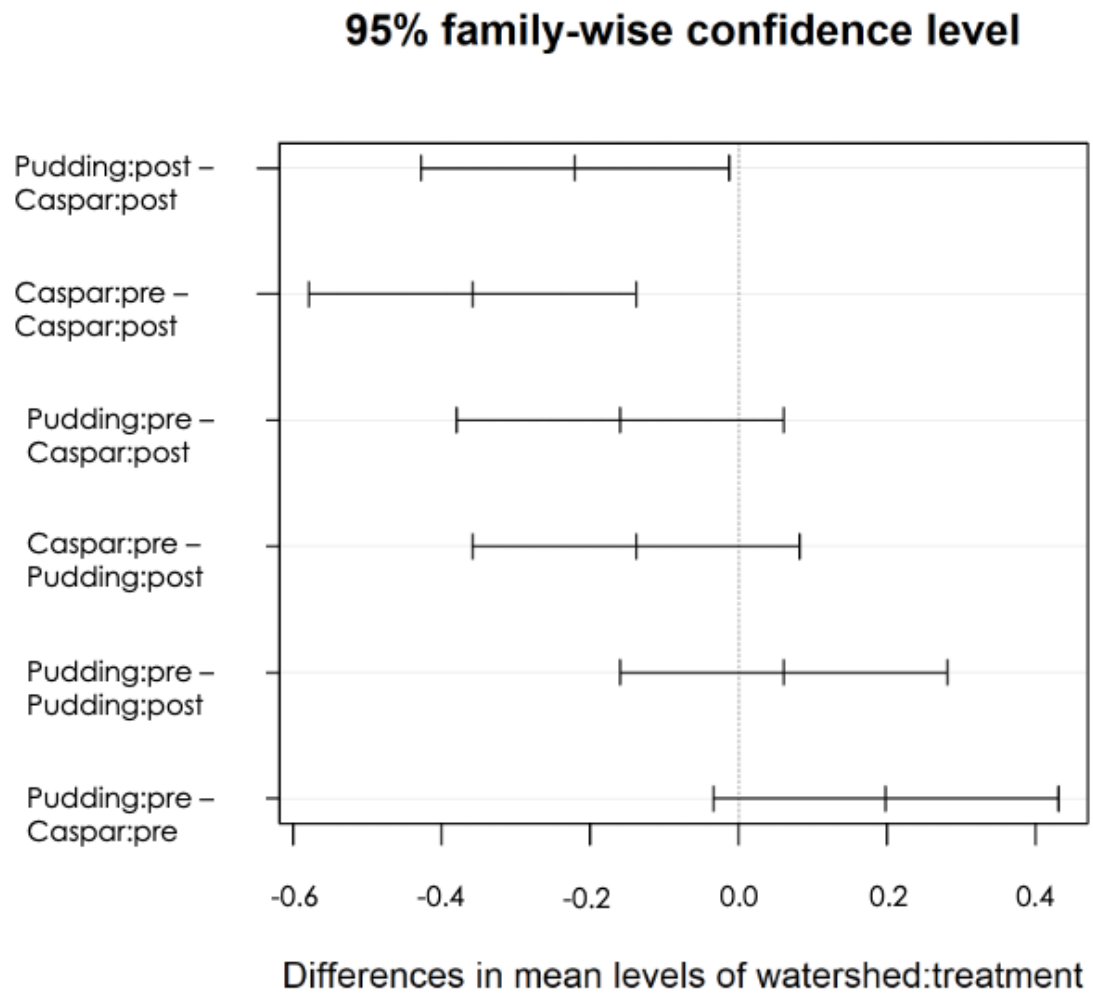


Figure 15. Tukey's Honestly Significant Difference multiple comparisons of means at the 95% family-wise level plot with every unique combination of watershed (Caspar = control, Pudding = experimental) with treatment (pre = 2011-2014, post= 2015-2020).

DISCUSSION

The goal of this thesis was to evaluate fish response to large wood restoration treatment. To assess the effectiveness of this restoration, I analyzed data from 9 years of survey data collected as part of a BACI experiment, looking at each watershed's change in juvenile coho growth and survival response. The addition of large wood to the experimental watershed was expected to increase channel complexity and restore processes that lead to future wood recruitment and floodplain connectivity, improving habitat thought to limit salmon production; however, in this experiment, only wood density and summer slow water volume increased following treatment. There was no evidence of an increase in winter slow water habitat. I hypothesized that adding large wood would improve growth and survival of juvenile coho salmon, but that hypothesis relied on the idea that wood supplementation would lead to more winter slow water habitat for juvenile salmon.

Summer Growth

Coho summer growth increased with increasing wood density in both watersheds, but there was no evidence that the treatment had an impact on summer growth in the experimental watershed. Increased summer growth with increased wood densities could be due to improved flow velocity diversification and food availability associated with instream wood. By diversifying flow, wood can create more habitat along velocity gradients where fish can rest and still take advantage of drifting invertebrate food (Fausch 1984, Hafs et al. 2014, Tullos and Walter 2015). This creates an ideal situation for

growth. Additionally, instream wood can support food resources for fish. Wood can increase particulate organic matter retention, allowing for greater access by macroinvertebrate and microbial communities, affect hyporheic zones, providing habitat to some aquatic macroinvertebrates at various life stages, and can serve as a substrate for aquatic macroinvertebrate biomass (Hernandez et al. 2005, Boulton 2007, Battin et al. 2008, Wohl et al. 2016). I did not collect information on the foodscape of the watersheds in this experiment and it may have provided important context to the growth trends that I observed.

There may have been other, more informative covariates to test in the model selection for summer growth that may have improved the model fit (e.g., summer fish density, summer stream flows, summer water temperatures, food availability). The GLMM conditional R^2 of the summer growth model was rather low ($R^2_{\text{conditional}} = 0.116$), indicating it was not a very informative model. It is likely that there are density dependent effects that are related to the differences in growth rates between watersheds, which could help to explain some of this unexplained variance. Unfortunately, I could not use summer density as an additional covariate in the summer growth models because there were multiple sources of sampling error during our summer electrofishing surveys that led to large margins of error in our summer abundance estimates. If these abundance estimation methods could be improved, it would be valuable to look at the relationship between summer parr abundance and summer growth rates through time for these watersheds as there have been studies demonstrating this connection (Gee et al. 1978, Eglishaw and Shackley 1985, Crisp 1993). However, summer is also a period of low

growth for coho in the experimental and control watersheds (Gallagher et al. 2012), so model development will be challenging due to the large amount of variability compared to the relatively small response.

Winter Growth

I found that winter growth was higher with increasing wood densities in both watersheds and that winter growth was always higher in the experimental compared to the control. Similar to summer growth, I did not find evidence that winter growth in the experimental watershed improved following the large wood supplementation. This is likely because we also did not see a winter slow water habitat effect from the large wood treatment. As a result, the hypothesized benefits of LWD supplementation (i.e., velocity refugia, increased foraging habitat) were not realized.

It is possible that differences in winter growth related to watersheds and wood densities are related to landscape-scale dissimilarities between creeks and climatic shifts through time. Though there are many similarities between the two watersheds, the experimental watershed has a wider floodplain through portions of the system and experiences higher winter flows compared to the control watershed (Figure 6Figure 1). These higher flows in the experimental watershed may have supported higher growth rates by improving access to food and alleviating pressure from crowding (Sommer et al. 2001, Rosenfeld et al. 2005, Ward et al. 2006, Bellmore et al. 2013). During the post-treatment period, both creeks experienced more frequent and higher intensity winter high flow events compared to the pre-treatment period (Figure 6Figure 6). Increased wood

densities did not result in deeper pools, but they may have provided improved connection to floodplain habitat in winter flows (Okun et al. 2021). The degree of floodplain connectivity was not a habitat metric we investigated. Increased winter flows in both watersheds may have led to more invertebrate food available for fish and/or alleviation of habitat issues associated with lower water levels (Bêche et al. 2009, Timusk et al. 2016).

Smolt density had a negative effect on winter growth rates, but unfortunately, smolt density was collinear with wood density (Figure 11). Therefore, I could not include both wood and smolt densities and I removed smolt density from the winter growth model to maintain my focus on wood treatment. The smolt density winter growth model indicated higher winter growth rates in the experimental watershed and a negative relationship between growth rate and smolt density. This model was just as informative in terms of AICc score as the wood density winter growth model (Table 6, Table 7). At lower smolt densities, winter growth rates increased (Figure 13). The experimental watershed smolt densities declined through time while the control watershed smolt densities stayed approximately the same. The combined decrease in pressure from crowding with the increase in available floodplain habitat from higher flows in the experimental watershed compared to the control watershed may have been important to the observed trends in winter growth rates.

Winter Survival

Winter survival in the experimental watershed stayed relatively constant through time, while survival in the control watershed increased from the pre- to post-treatment

period. Based on the preliminary data indicating that the lack slow water in winter was limiting juvenile coho survival in the experimental watershed, the lack of an increase in survival in the experimental watershed at higher stream flows in the post-treatment period is not surprising given that there is no evidence of increased winter slow water habitat following wood supplementation (Figure 6).

It is likely that improved coho winter survival in the control watershed compared to the experimental watershed from the pre- to post-treatment period was related to more favorable environmental conditions in the control watershed post-treatment. However, because the CJS model in RMark does not support mixed effects, I was unable to test the effects of annual environmental covariates (e.g., annual wood density, smolt density, or stream flow) in the presence of the random effect accounting for the variation related to year. From 2012 to 2015 (BACI study pre-treatment), California experienced its most extreme drought in over a 1,200-year period (Robeson 2015). Then, starting in 2016, precipitation increased, resulting in much higher stream flows (Figure 6). There is strong evidence that flows were higher in the experimental watershed throughout the study, the post-treatment period had higher flows compared to the pre-treatment period, and that fish in the experimental watershed have a known negative relationship with winter survival and winter flow (Gallagher et al. 2012, Okun et al. 2021). What is considered a ‘high’ winter flow is dramatically different between the study watersheds. High flows in the post-treatment period were possibly beneficial to coho in the control creek compared to high flows in the experimental creek. Juvenile coho have shown a decreased ability to maintain position in high flows, resulting in excessive energetic costs and preference for

low velocity habitats (Huusko et al. 2007, Bair et al. 2019). The high flows in the control watershed may have increased access to floodplain habitat and velocity gradients useful for cover from predators and positioning for foraging while high flows in the experimental watershed may have been relatively much more energetically costly. This could support an increase in survival within the control watershed compared to the experimental watershed in the post-treatment, high flow time period.

Restoration Effectiveness

Though wood density increased more in the experimental watershed compared to the control watershed following treatment, winter slow water habitat was not affected and there was no evidence of improved growth and survival in the experimental watershed resulting from treatment. From the pre- to post-treatment period, there was a 13% increase in wood density in the control watershed compared to a 31% increase in wood density in the experimental watershed; however, the control watershed started with 49% more wood than the experimental watershed (Figure 4). Wood densities at the start of the experiment were extremely low in the experimental watershed and, even following treatment, wood densities never became higher than the control watershed's initial wood densities. The increase in wood density in the control watershed is from natural wood loading processes.

The wood treatment in the experimental watershed may have been unsuccessful in creating the anticipated habitat response for a variety of reasons relating to treatment and study design. It is possible that the 'accelerated recruitment' approach to treatment was

inappropriate for the watershed's available wood sources and the duration of the study. The idea of 'accelerated recruitment' is that the treatment pieces are meant to collect naturally occurring instream wood and move dynamically as the watershed changes through time and space (Carah et al. 2014). Thus, the treatment in the experimental watershed is meant to support the existing relationship between the floodplain, wood, and water in the creek and assist in creating positive, watershed-wide long-term effects for habitat and fish. It is possible that the experimental watershed's available wood inputs in the form of riparian vegetation are not sufficient to create impactful, natural wood-related habitat changes. For example, if the riparian stand age is relatively young and homogenous as a relic of timber harvest practices, woody debris may not be ready to fall into the channel during the study period. To see the treatment effects from this method of wood supplementation, it is possible that the duration of the study was too short. It is also possible that the magnitude of wood treatment was not sufficient to create slow water habitat. Even with a 31% increase in wood density in the experimental watershed, wood levels only just reached the levels existing in the control watershed (Figure 3). It could be useful to add more wood into the creek to see at what magnitude of supplementation wood treatment-mediated winter slow water habitat forms. It is also possible that winter habitat survey methods failed to capture some change in habitat that did exist. Winter habitat census in this study was a snapshot of winter conditions compared to the fine-scaled approach to summer habitat census. The winter habitat census protocol is flow-dependent, making a relatively short window to complete data collection. Additionally, surveying at high winter flows is difficult and can be dangerous. If winter habitat data

collection had involved more surveys throughout winter with finer-scale measurements on metrics like water velocity, floodplain connection, and actual slow water volume, we may have detected some habitat change.

It would be useful to re-evaluate the experimental watershed in the future to see how the habitats have changed and how fish populations have responded. Based on the large investments made in restoration projects annually, it is critical to evaluate if the restoration tools we are using are having the desired effect (Bernhardt et al. 2005, Roni et al. 2010).

Study Design

By having a paired watershed- BACI design, I was able to gain perspective on the growth and survival rates that I observed that I would not have had context for if I had only looked at one watershed through time. In my thesis, I would have seen the winter growth increase in the experimental watershed with increasing wood density and I would have had reason to say that restoration improved growth. In reality, there was no treatment-specific winter growth response. Winter growth increased with increasing wood density in both watersheds, not more so in the experimental watershed. By pairing year-round habitat and biological data collection and analyses, there is a clearer route for quantifying restoration effectiveness. Wood treatment did not create winter slow water, so the limiting factor in the experimental was not addressed. If I had only looked at a biological response to treatment without knowing the habitat response, I would have interpreted growth and survival responses differently. Having climatic shifts coincide

perfectly with the pre- and post- treatment period of the study, altering the stream flows in each group of years, complicated interpretation of my results and make it clear that it will be important to include flow as a predictor of biological response in future work on restoration effectiveness.

CONCLUSION

This study was a massive undertaking with year-round fish and habitat data collection that produced an extensive and comprehensive dataset of fish and their habitat and provided important details of the population dynamics of listed salmonids at the southern extent of their range. I found that summer growth was positively associated with wood densities, both watersheds had increases in winter growth associated with increased wood densities, and the experimental watershed had consistency higher winter growth compared to the control. Both summer and winter growth was associated with wood densities, but the wood treatment response did not align with the biological response (i.e., wood increased more in the experimental watershed, but growth did not increase more in the experimental watershed). I found that winter survival increased through time in the control while it stayed level in the experimental watershed.

One way to improve our understanding of fish response to wood implementation would be to extend the duration of the post-treatment monitoring to capture more variability in climate and to allow for treatment structures to serve their purpose of acting as part of the wood recruitment process within the experimental watershed. Long-term monitoring is critical to understanding population structure and dynamics and to developing and implementing management strategies that can best recover imperiled salmonids. An important aspect of long-term monitoring is collecting data throughout the widest possible range of environmental and population conditions so that models can perform better. For example, if this study's post treatment period had extended longer, I

may have been able to collect data post treatment in flows similar to the pre-treatment conditions in addition to allowing for more process-based change to take place within the experimental watershed. I believe, as many other studies suggest (Whiteway et al. 2010, Collins et al. 2012, Roni et al. 2015), that the appropriate time scale to measure response to restoration is that of watershed and river-processes, and that a study that can encompass effects at a wide range of environmental conditions will be particularly useful with our rapidly changing climate. As we attempt to untangle the ways that environmental conditions, physical habitat and biological interactions intertwine, it becomes apparent that if we are interested in longer-term effects of restoration, we need to lengthen the study scale and allow for processes to be restored.

REFERENCES

- Anlauf-Dunn, K.J., Ward, E.J., Strickland, M., & Jones, K. (2014). Habitat connectivity, complexity, and quality: predicting adult coho salmon occupancy and abundance. *Canadian journal of fisheries and aquatic sciences*, 71(12), 1864-1876.
- Armantrout, N.B. (1991). Restructuring streams for anadromous salmonids. In *Fisheries Bioengineering Symposium: American Fisheries Society Symposium 10* (p. 136).
- Bair, R.T., Segura, C. & Lorion, C.M. (2019). Quantifying the restoration success of wood introductions to increase coho salmon winter habitat. *Earth Surface Dynamics*, 7(3), pp.841-857, doi:10.5194/esurf-7-841-2019.
- Bartón, K. (2020). MuMin: Multi-model Inferences. R Package version 1.43.17
- Bates, D., Mächler M, Bolker B, & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1-48.
- Battin, T.J., Kaplan, L.A., Findlay, S., Hopkinson, C.S., Marti, E., Packman, A. I., Newbold, J.D., & Sabater, F. (2008). Biophysical controls on organic carbon fluxes in fluvial networks. *Nature geoscience*, 1(2), 95-100.
- Bêche, L.A., Connors, P.G., Resh, V. H., & Merenlender, A.M. (2009). Resilience of fishes and invertebrates to prolonged drought in two California streams. *Ecography*, 32(5), 778-788.
- Bellmore, J.R., Baxter, C.V., Martens, K., & Connolly, P.J. (2013). The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. *Ecological Applications*, 23(1), 189-207.
- Bernhardt, E.S., Palmer, M.A., Allan, J.D., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C., Follstad-Shah, J. & Galat, D. (2005). Synthesizing US river restoration effort.
- Beschta, R.L., W.S. Platts, J.B. Kauffman, & M.T. Hill. (1994). Artificial stream restoration—money well spent or expensive failure? In *Proceedings of Environmental Restoration. UCOWR 1994 Annual Meeting, Big Sky, Montana*. pp. 76-104.
- Bisson, P.A., Sullivan, K., & Nielsen, J.L. (1988). Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. *Transactions of the American Fisheries Society*, 117(3), 262-273.

- Bjorkstedt, E.P. (2003). DARR (Darroch analysis with rank reduction) A method for analysis of stratified mark-recapture data for small populations, with application to estimating abundance of smolts from out-migrant trap data. National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz, CA. Administrative Report SC-00-02. 24 pp.
- Blencowe, C. (2015). Using large wood to increase salmon abundance in Pudding Creek: A BACI Experiment, 2015 Instream Habitat Implementation Final Report. Blencow Watershed Management. Fort Bragg, CA. 27 pp.
- Boulton, A.J. (2007). Hyporheic rehabilitation in rivers: restoring vertical connectivity. *Freshwater Biology*, 52(4), 632-650.
- Bouwes, N., Moberg, J., Weber, N., Bouwes, B., Beasley, C., Bennett, S., Hill, A., Jordan, C., Miller, R., Nelle, P., Polino, M., Rentmeester, S., Semmens, B., Volk, C., Ward, M.B., Wathen, G., & White, J. (2014). Scientific protocol for salmonid habitat surveys within the Columbia Habitat Monitoring Program. Prepared by the Integrated Status and Effectiveness Monitoring Program and published by Terraqua, Inc., Wauconda, WA.
- Burnham, K. P., & Anderson, D. R. (2001). Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife research*, 28(2), 111-119.
- Cafferata, P.H., & Reid, L. (2013). Applications of long-term watershed research to forest management in California: 50 years... Technical Report for State of California Department of Forestry and Fire Protection. Report No. 5. 111 pp.
- Cal Trout Inc. (2018). CENTRAL CALIFORNIA COAST COHO SALMON *Oncorhynchus kisutch* (Walbaum). Retrieved on 10 November 2018 from: <https://caltrout.org/central-california-coast-coho-salmon/>
- California Department of Fish and Wildlife Fisheries Restoration Grants Program. (2018). "2017- 2018 FRGP awards" [PDF]. Retrieved on 20 October 2018 from: <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=154248&inline>
- Carah, J.K., Blencowe, C. C., Wright, D. W., & Bolton, L. A. (2014). Low-cost restoration techniques for rapidly increasing wood cover in coastal coho salmon streams. *North American Journal of Fisheries Management*, 34(5), 1003-1013.
- Cederholm, C.J., Bilby, R.E., Bisson, P.A., Bumstead, T.W., Fransen, B.R., Scarlett,

- W.J., & Ward, J.W. (1997). Response of juvenile coho salmon and steelhead to placement of large woody debris in a coastal Washington stream. *North American Journal of Fisheries Management* 17(4):947-963.
- Collins, D.L., Langlois, T.J., Bond, T., Holmes, T.H., Harvey, E.S., Fisher, R., McLean, D.L. Crawford, B.A., & Rumsey, S.M. (2011). Guidance for monitoring recovery of pacific salmon and Steelhead listed under the Federal Endangered Species Act: Guidance to salmon recovery partners concerning prioritizing monitoring efforts to assess the viability of salmon and steelhead populations protected under the Federal Endangered Species Act. NOAA, National Marine Fisheries Service, Northwest Region. 160pp.
- Conner, M., Saunders, W., Bouwes, N., & Jordan, C. (2016). Evaluating impacts using a BACI design, ratios, and a Bayesian approach with a focus on restoration.
- Crisp, D.T. (1993). Population densities of juvenile trout (*Salmo trutta*) in five upland streams and their effects upon growth, survival and dispersal. *Journal of Applied Ecology*, 759-771.
- Crozier, L.G., McClure, M.M., Beechie, T., Bograd, S.J., Boughton, D.A., & Carr, M. (2019). Climate vulnerability assessment for Pacific salmon and steelhead in the California Current Large Marine Ecosystem. *PLoS ONE* 14(7): e0217711. <https://doi.org/10.1371/journal.pone.0217711>
- Dominguez, L.G., & Cederholm, C. J. (2020). Rehabilitating stream channels using large woody debris with considerations for salmonid life history and fluvial geomorphic processes. In *Sustainable Fisheries Management* (pp. 545-563). CRC Press.
- Ebersole, J.L., Wigington, P.J. Baker, J.P., Cairns, M.A., Robbins Church, M. Hansen, B.P., Miller, B.A., LaVigne, H.R., Compton, J.E., & Leibowitz, S.G. (2006). Juvenile Coho Salmon Growth and Survival across Stream Network Seasonal Habitats. *Transactions of the American Fisheries Society*. 135:1681-1697.
- Egglisshaw, H.J., & Shackley, P. E. (1985). Factors governing the production of juvenile Atlantic salmon in Scottish streams. *Journal of Fish Biology*, 27, 27-33.
- ESRI (2011). ArcGIS Deskto Release 10. Environmental Systems Research Institute, Inc. Redlands, California.
- Fausch, K.D. (1984). Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian journal of zoology*, 62(3), 441-451.
- Foote, K.J., Biron, P. M., & Grant, J. W. (2020). Impact of in-stream restoration

structures on salmonid abundance and biomass: an updated meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 77(9), 1574-1591.

- Gallagher, S.P., Thompson, S., & Wright, D.W. (2012). Identifying factors limiting coho salmon to inform stream restoration in coastal Northern California. *California Fish and Game*, 98(4), 185-201.
- Gallagher, S.P., Ferreira, J., Lang, E., Holloway, W.E., & Wright, D.W. (2014). Investigation of the relationship between physical habitat and salmonid abundance in two coastal northern California streams. *California Fish and Game*. 100(4):683-702.
- Gee, A.S., Milner, N. J., & Hemsworth, R. J. (1978). The production of juvenile Atlantic salmon, *Salmo salar* in the upper Wye, Wales. *Journal of Fish Biology*, 13(4), 439-451.
- Gerhard, M., & Reich, M. (2000). Restoration of streams with large wood: Effects of accumulated and built-in wood on channel morphology, habitat diversity and aquatic fauna. *International Review of Hydrobiology*, 85(1), 123-137.
- Giannico, G.R., & Hinch, S. G. (2003). The effect of wood and temperature on juvenile coho salmon winter movement, growth, density and survival in side-channels. *River Research and Applications*, 19(3), 219-231.
- Gregory, S. V., & Bisson, P. A. (1997). Degradation and loss of anadromous salmonid habitat in the Pacific Northwest. In *Pacific Salmon & Their Ecosystems* (pp. 277-314). Springer, Boston, MA.
- Hafs, A.W., Harrison, L. R., Utz, R. M., & Dunne, T. (2014). Quantifying the role of woody debris in providing bioenergetically favorable habitat for juvenile salmon. *Ecological Modelling*, 285, 30-38.
- Hartig, F. (2017). DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R Package version 0.1.5. URL <http://florianhartif.github.io/DHARMA>
- Hernandez, O., Merritt, R. W., & Wipfli, M. S. (2005). Benthic invertebrate community structure is influenced by forest succession after clearcut logging in southeastern Alaska. *Hydrobiologia*, 533(1), 45-59.
- Holloway, W., Gallagher, S. P., Thompson, S., Wright, D., & Lang, E. (2015). Coastal Mendocino County Salmonid Life Cycle and Regional Monitoring: Monitoring Status and Trends for 2015. 2014-15 Administrative Report. Pacific States Marine

Fisheries Commission and the California State Department of Fish and Wildlife, Coastal Watershed Planning and Assessment Program, 1487 Sandy Prairie Court, Suite A., Fortuna, CA 95540 54pp

- Holloway, W., Mackey, E., McClary, A., & Gallagher, S.P. (2016a). Summer habitat data collection protocol version 4.0. California Department of Fish and Wildlife 32330 North Harbor Drive. 11 pages.
- Holloway, W., Mackey, E., McClary, A., & Gallagher, S.P. (2016b). Winter Habitat Data Collection Protocol Version 4.0. California Department of Fish and Wildlife 32330 North Harbor Drive. 11 pages.
- Hurvich, C.M., & Tsai, C. L. (1989). Regression and time series model selection in small samples. *Biometrika*, 76(2), 297-307.
- Huusko, A.R.I., Greenberg, L., Stickler, M., Linnansaari, T., Nykänen, M., Vehanen, T., Kolionen, S., Louhi, P., & Alfredsen, K. (2007). Life in the ice lane: the winter ecology of stream salmonids. *River research and applications*, 23(5), 469-491.
- Johnson, S.L., Rodgers, J.D., Solazzi, M.F., & Nickelson, T.E. (2005), Effects of an increase in large wood on abundance and survival of juvenile salmonids (*Oncorhynchus* spp.) in an Oregon coastal stream, *Can. J. Fish. Aquat. Sci.*, 62(2), 412–424, doi:10.1139/f04-222.
- Kaufmann, P.R. (1987). Channel morphology and hydraulic characteristics of torrent-impacted forest streams in the Oregon Coast Range, USA.
- Katz, S.L., Barnas, K., Hicks, R., Cowen, J., & Jenkinson, R. (2007). Freshwater habitat restoration actions in the Pacific Northwest: a decade's investment in habitat improvement. *Restoration Ecology*, 15(3), 494-505.
- Laake, J.L. (2013). RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.
- Lebreton, J.D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological monographs*, 62(1), 67-118.
- Mackey, E., Gallagher, S.P., Holloway, W., McClary, G., Lang, E., & Blencowe, C. (2016). *Using Large Wood to Increase Salmon Abundance in Pudding Creek, CA: A BACI Experiment, Technical Report*. Trout Unlimited.

- McMahon, T.E., & Hartman, G.F. (1989). Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) Canadian Journal of Fisheries and Aquatic Sciences 46(9): 1551-1557.
- Moyle, P.B., Katz, J. V., & Quiñones, R. M. (2011). Rapid decline of California's native inland fishes: a status assessment. *Biological Conservation*, 144(10), 2414-2423.
- Naiman, R.J. & Latterell, J. J. (2005), Principles for linking fish habitat to fisheries management and conservation. *Journal of Fish Biology*, 67: 166-185.
- National Research Council. (1996). *Upstream: salmon and society in the Pacific Northwest*. National Academies Press.
- Nehlsen, W., Williams, J. E., & Lichatowich, J. A. (1991). Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries*, 16(2), 4-21.
- Nickelson, T.E., Rodgers, J. D., Johnson, S. L., & Solazzi, M. F. (1992). Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(4), 783-789.
- National Marine Fisheries Service (NMFS). (2016). Final Coastal Multispecies Recovery Plan for California Coastal Chinook Salmon, Northern California Steelhead and Central California Coast Steelhead. National Marine Fisheries Service, Southwest Region, Santa Rosa, California.
- Okun, N., McGuire, J., Henderson, M., Gallagher, S., Lang, E., & Mackey, E. (2021). Final Technical Report: Large Wood Restoration Effectiveness Monitoring in a Coastal Northern California Stream: A Paired Watershed Before-After-Control-Impact Study. Fisheries Restoration Grant Program Number P1610537. Pacific States Marine Fisheries Commission and the California State Department of Fish and Wildlife, Fort Bragg, California.
- Ogston, L., Gidora, S., Foy, M., & Rosenfeld, J. (2014). Watershed-scale effectiveness of floodplain habitat restoration for juvenile coho salmon in the Chilliwack River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(4), 479-490.
- Palmer, M.A., Hondula, K. L., & Koch, B. J. (2014). Ecological restoration of streams and rivers: shifting strategies and shifting goals. *Annual Review of Ecology, Evolution, and Systematics*, 45, 247-269.

- Pledger, S., Pollock, K. H., & Norris, J. L. (2003). Open capture-recapture models with heterogeneity: I. Cormack-Jolly-Seber model. *Biometrics*, 59(4), 786-794.
- RStudio Team. (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL <http://www.rstudio.com/>.
- Reeves, G. H., Hohler, D. B., Hansen, B. E., Everest, F. H., Sedell, J. R., Hickman, T. L., & Shively, D. (1997). Fish habitat restoration in the Pacific Northwest: fish creek of Oregon. *Watershed Restoration: Principles and Practices.*, 335-359.
- Reynolds, J.B. (1996). Electrofishing. Pages 221-253 in B.R. Murphy and D.W. Willis, editors. *Fisheries Techniques*, 2nd Edition. American Fisheries Society, Bethesda Maryland.
- Ricciardi, A., & Rasmussen, J. B. (1999). Extinction rates of North American freshwater fauna. *Conservation biology*, 13(5), 1220-1222
- Robeson, S.M. (2015). Revisiting the recent California drought as an extreme value. *Geophysical Research Letters*, 42(16), 6771-6779.
- Romer, J. D., Anlauf, K. J., & Jones, K. K. (2008). *Status of Winter Rearing Habitat in Four Coho Population Units, 2007* (p. 3). Monitoring Program Report Number OPSW-ODFW-2008-7, Oregon Department of Fish and Wildlife, Salem, OR.
- Roni, P., Liermann, M., & Steel, A. (2002). 12. Monitoring and Evaluating Fish Response to Instream Restoration. *RESTORATION PUGET SOUND RIVERS* (p), 318.
- Roni, P., Hanson, K., & Beechie, T. (2008). Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. *North American Journal of Fisheries Management*, 28(3), 856-890.
- Roni, P., Pess, G., Beechie, T., & Morley, S. (2010). Estimating changes in coho salmon and steelhead abundance from watershed restoration: how much restoration is needed to measurably increase smolt production?. *North American Journal of Fisheries Management*, 30(6), 1469-1484.
- Roni, P., Pess, G. R., Beechie, T. J., & Hanson, K. M. (2014). Fish-habitat relationships and the effectiveness of habitat restoration.
- Roni, P., Beechie, T., Pess, G., & Hanson, K. (2015). Wood placement in river restoration: fact, fiction, and future direction. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(3), 466-478.

- Rosenfeld, J.S., Leiter, T., Lindner, G., & Rothman, L. (2005). Food abundance and fish density alters habitat selection, growth, and habitat suitability curves for juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62(8), 1691-1701.
- Sedell, J. R., & Froggatt, J. L. (1984). Importance of streamside forests to large rivers: The isolation of the Willamette River, Oregon, USA, from its floodplain by snagging and streamside forest removal: With 2 figures and 1 table in the text. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, 22(3), 1828-1834.
- Spence, B. C., & Hughes, R. M. (1996). *An ecosystem approach to salmonid conservation* (p. 23). ManTech Environmental Research Services, Corporation.
- Solazzi, M.F., Nickelson, T. E., Johnson, S. L., & Rodgers, J. D. (2000). Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. *Can. J. Fish. Aquat. Sci*, 57, 906-914.
- Sommer, T.R., Nobriga, M. L., Harrell, W. C., Batham, W., & Kimmerer, W. J. (2001). Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(2), 325-333.
- Stevens, D.L., Olsen, A.R. (2004). Spatially Balanced Sampling of Natural Resources. *Journal of American Statistical Association*. 99(1):262-278.
- Stewart-Oaten, A., Murdoch, W.W., Parker, K.R. (1986). Environmental impact assessment: "pseudoreplication" in time? *Ecology* 67: 929-940
- Timusk, E.R., Smokorowski, K. E., & Jones, N. E. (2016). An experimental test of sub-hourly changes in macroinvertebrate drift density associated with hydropeaking in a regulated river. *Journal of Freshwater Ecology*, 31(4), 555-570.
- Tullos, D., & Walter, C. (2015). Fish use of turbulence around wood in winter: physical experiments on hydraulic variability and habitat selection by juvenile coho salmon, *Oncorhynchus kisutch*. *Environmental biology of fishes*, 98(5), 1339-1353.
- Ward, A.J., Webster, M. M., & Hart, P. J. (2006). Intraspecific food competition in fishes. *Fish and Fisheries*, 7(4), 231-261.
- Western Regional Climate Center (WRCC). (2018). FT BRAGG 5 N, CALIFORNIA

(043161) Period of Record Monthly Climate Summary. Retrieved on 12 December 2018 from: <https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca3161>

- White, G.C. & Burnham, K.P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 Supplement, 120-138.
- Whiteway, S.L., Biron, P.M., Zimmerman, A., Venter, O., & Grant, J.W. (2010). Do In-Stream Restoration Structures Enhance Salmonid Abundance? A Meta-Analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 67(5):831-841.
- Wohl, E. (2014). A legacy of absence: Wood removal in US rivers. *Progress in Physical Geography*, 38(5), 637-663.
- Wohl, E., Lane, S. N., & Wilcox, A. C. (2015). The science and practice of river restoration. *Water Resources Research*, 51(8), 5974-5997.
- Wohl, E., Bledsoe, B. P., Fausch, K. D., Kramer, N., Bestgen, K. R., & Gooseff, M. N. (2016). Management of large wood in streams: an overview and proposed framework for hazard evaluation. *JAWRA Journal of the American Water Resources Association*, 52(2), 315-335.
- Wright, D.W., Gallagher, S. P., & Hannon, C. J. (2012). Measurements of key life history metrics of Coho salmon in Pudding Creek, California. In: *Standiford, R.B., Weller, T.J., Piirto, D.D., Stuart, J.D., tech. coords. Proceedings of coast redwood forests in a changing California: A symposium for scientists and managers. Gen. Tech. Rep. PSW-GTR-238. Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture. pp. 459-470 (Vol. 238, pp. 459-470).*

APPENDIX

Appendix: From Okun et al. 2021, summary of generalized linear mixed model results fit to six key metrics measured during summer and winter habitat surveys. The different models for the LWD metrics (density and frequency) are the two components of the zero-inflated models. The random effects column summarizes the variance (standard deviation) of the model's random effects components.

Metric	n	Random Effects	Fixed Effect	Estimate	SE	p-value
Residual Pool Depth	8513	GRTS: 0.14 (0.38) Year: 0.004 (0.07) Residual: 0.26 (0.51)	Intercept	-0.9	0.1	<0.001
Slow Water Volume	9213	GRTS: 0.59 (0.77) Year: 0.02 (0.13) Residual: 0.60 (0.78)	Intercept Treatment (pre) Watershed (Pudding) Treatment:Watershed	-0.38 -0.21 -0.09 -0.22	0.32 0.1 0.41 0.04	0.23 0.05 0.82 <0.001
Pool frequency	105	GRTS: 0.12 (0.35) Year: 0.002 (0.04) Residual: 0.01 (0.12)	Intercept	1.58	0.09	<0.001
LWD Density (positive)	21931	GRTS: 0.09 (0.29) Year: 0.01 (0.09) Residual: 2.93 (1.71)	Intercept Treatment (pre) Watershed (Pudding) Treatment:Watershed	4.87 -0.19 -0.22 -0.22	0.12 0.08 0.16 0.06	<0.001 0.014 0.162 <0.001
LWD Density (binomial)	21931	GRTS: 0.06 (0.25) Year: 0.03 (0.18) Residual: 2.93 (1.71)	Intercept Treatment (pre) Watershed (Pudding) Treatment:Watershed	-1.45 0.33 0.06 0.15	0.14 0.14 0.14 0.07	<0.001 0.021 0.661 0.019
LWD Frequency (positive)	21931	GRTS: 0.09 (0.30) Year: 0.01 (0.09) Residual: 0.86 (0.93)	Intercept Treatment (pre)	3.68 -0.18	0.09 0.07	<0.001 0.01
LWD Frequency (binomial)	21931	GRTS: 0.06 (0.25) Year: 0.03 (0.17) Residual: 0.86 (0.93)	Intercept Treatment (pre) Watershed (Pudding) Treatment:Watershed	-1.43 0.33 0.07 0.16	0.14 0.14 0.14 0.06	<0.001 0.019 0.628 0.013
Winter Slow-Water: Fast-Water Ratio	105	GRTS: 0.60 (0.78) Year: 0.29 (0.54) Residual: 0.33 (0.58)	Intercept	-0.6	0.29	0.04

