GEOMORPHIC AND HYDRAULIC CONTROLS ON COHO SALMON OUTMIGRATION IN THE RUSSIAN RIVER WATERSHED, CALIFORNIA

Brian Kastl, Lukas Winklerprins, Kyle Leathers, Zack Dinh, and Shelby Witherby

Term paper for *Landscape Architecture 227 Restoration of Rivers and Streams*
December 2018

Abstract

Declining global salmon populations necessitate attention to the environmental conditions that support salmon life cycle bottlenecks. The migration from natal streams to the ocean by juveniles is a dynamic life stage event, but little is known about the hydraulic conditions required for downstream movement. This study focuses on California's Russian River tributaries to investigate: i) water depths that support coho (*Onchorynchus kisutch*) outmigration, ii) variability in flow-to-depth relationships between streams, and iii) geomorphic influences on these relationships. From 12 sites across five streams in the Russian River watershed, we collected flow and water depth measurements throughout the spring 2018 outmigration season. We relate water depth measurements to recorded coho smolt movement. Additionally, we took geomorphic measurements, including channel gradient, geometry, and particle size at 5-6 sites per stream. Findings indicate that outmigration is concentrated during high flow events. Outmigration occurs below the 12 cm riffle crest thalweg depth threshold set by the Department of Fish and Wildlife for coho outmigration. We find that flows required to reach 12 cm riffle crest thalweg depths vary by a factor of eight among streams. Researching the drivers of variation in flow-to-depth relationships is thus highly valuable. Our findings indicate that streams with low flow-to-depth ratios are associated with narrow active channels and large particle sizes. A geomorphic approach to understanding flow-to-depth relationships can inform hydrograph management to facilitate outmigration. In turn, this has the potential to improve coho salmon metapopulation resilience.

Introduction

Overharvesting, pollution, poor hatchery practices, climate change, and landscape degradation have reduced coho salmon (*Oncorhynchus kisutch*) populations to historic lows in California (Brown et al. 1994). Restoring coho abundance across California will require significant management interventions, focusing on vulnerable coho life stages. One such life stage is outmigration, the movement of juvenile coho salmon (smolts) from natal freshwater streams to the Pacific Ocean. Juvenile coho in California typically spend one year in their natal stream and outmigrate during the following spring, with an outmigration season of almost two months (Spence & Dick 2014). The chances of outmigrating smolts surviving and later returning to their natal streams to breed significantly increase if they arrive to the ocean during a strong ocean upwelling period, which typically supports high food availability (Braun et al. 2016, Lestelle 2007). However, seasonal upwelling varies significantly in timing (Ainley et al. 1995). Thus, a large window when smolts enter the ocean increases the likelihood that a subset of the population will arrive in environmentally favorable conditions (Satterthwaite et al. 2014). Consequently, large variation in outmigration timing between streams is expected to stabilize returns (Carlson et al. 2011). This phenomenon, in which asynchrony in subpopulation dynamics contributes to overall population stability has been coined the "portfolio effect" and has been documented in other salmon populations (Schindler et al. 2015; Carlson et al. 2011; Schindler et al. 2010). However, little is known about the underlying mechanisms that promote this stabilizing asynchrony and control outmigration timing.

Literature Review: Overview of Outmigration Timing Drivers

Previous studies examined various spatial scales of outmigration effects, from single reaches to full species geographic ranges, with the greatest number of studies conducted at the stream and watershed scales. We focused outmigration predictors at reach scales across a watershed, but our conclusions may stand for any watershed with similar seasonality in streamflow. Precedent research on outmigration timing shows that outmigration is driven by both biotic and abiotic factors, including those that are biologic, climatic, hydrologic, and geomorphic in nature. Our literature review (Appendix I and II) categorizes previous studies by driver, and through this we found that biologic drivers (including genetic differences and food availability), hydrologic drivers (including water temperature and flow), and geomorphic drivers (including stream gradient and interruptions like lakes along an outmigration path) have similar counts of acknowledgement in precedent work. Our research focuses on hydrologic and geomorphic drivers because of their immediate management implications—dams, diversions, and legislation around their management allow for some control of flow. Specifically, we focus on flow and water depth—a combined hydrologic and geomorphic effect—as a bottleneck that may interrupt otherwise typical coho life stage timing. We will first address a broader scope of outmigration drivers.

In-stream temperature is a widely discussed control on outmigration timing, but the relationship is location-dependent, correlated with other factors, and only applies up to a point. Spence and Dick (2014) demonstrate that the same system may see outmigration across significantly different stream temperatures, and consider that fish may migrate due to a "cumulative thermal experience" rather than a specific thermal threshold, which echoes earlier studies by Solomon (1978). Stream temperature positively affects growth rates (Beechie et al. 2006, Lestelle 2007) and earlier maturation is linked to earlier outmigration (Johnson 2016), but stream temperature and development are also both linked to photoperiod (McCormick et al. 2000). Lunar phase is also a driver, associated with outmigration timing across 27 groups of salmonids and trout (Grau et al. 1981). The association between lunar phase and outmigration is complicated, however, by potentially low survivorship: full-moon, well-illuminated nights make smolts more visible to predators (Moser et al. 1991, Moyle 2002).

The presence of lakes along the migration passage delays outmigration (Lisi et al. 2013, Barlaup et al. 2018) and estuaries at the river mouth are correlated with smolts entering the ocean later in the year (Carr-Harris et al. 2018, Moser et al. 1991). At reach scales, in-stream obstacles (generally large wood) contribute to scour, riffle formation, and general habitat complexity that may additionally affect movement by juveniles (Buffington et al. 2002). Grain size correlates with bed roughness, affecting water velocity, and is a major control on stream morphology, helping determine, for instance, riffle-pool or step-pool forms (Montgomery & Buffington 1997). Coho depend on certain channel morphologies for spawning and juvenile development (Montgomery et al. 1999), but it is unclear if juveniles stay in or prefer these bed types as they mature.

Streamflow is a crucial element in salmonid outmigration survival. High flows may mobilize sediment and are correlated with increased stream turbidity. Gregory & Levings (1998) suggest that low visibility, due to high turbidity after the spring freshet (first snowmelt flood), may reduce predation and correlate with high outmigration counts. However, high flows can also negatively impact juvenile survival, as the energy expenses to hold position during high flow events may lead to juvenile fish death (Riddell & Leggett 1981).

One of the most important flow-dependent outmigration controls is connectivity between natal streams and the ocean (i.e. a navigable path for coho to move downstream). Biologic effects from connectivity are difficult to assess because smolts' ability to navigate obstacles and the importance of individual barriers versus cumulative effects are poorly understood. Connectivity depends on a variety of interrelated physical factors as well, including channel geometry, obstacles, flow, water depth, bedform, and more. Despite this complexity, connectivity has often been assessed via a single metric: the riffle crest thalweg depth. The riffle crest is the shallowest cross section along a stream's longitudinal profile. The thalweg is the deepest point within a cross section, so the riffle crest thalweg is the deepest point within the crest of a riffle. The riffle crest

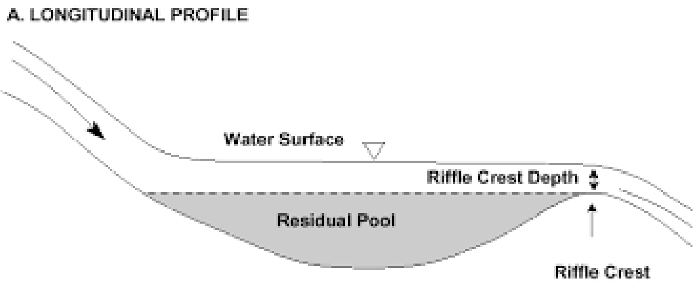

Figure 1a: Schematic diagram displaying the shallow riffle crest location at the inflection between a pool tail and riffle (UC Cooperative Extension).

Figure 1b: Riffle crest thalweg location marked by rebar in Willow Creek of the Russian River watershed. Arrow indicates flow direction.

thalweg depth (hereafter “RCT”) is the minimum water depth through which outmigrants must pass on their oceanward journey (Figure 1). Grantham (2013) supports the need for minimum RCT values throughout a stream to ensure connectivity, but rivers with strong seasonal variation, such as those in California’s Mediterranean climate, may render minimum-depth requirements less applicable, with percent-of-flow management more appropriate (Mierau et al. 2017). The Department of Fish and Wildlife sets a minimum riffle depth requirement of 0.4 feet (12 cm) for at least 25% of total riffle width and 10% contiguous width for 1- to 2-year-old steelhead passage, based on Thompson’s (1972) hydraulic criteria.

Flow-to-Depth Relationship

Relationships between flow through a given channel cross-section and the associated average water depth generally follow power-law relationships, as published by Leopold & Maddock (1953). Mierau et al. (2017) update this form to reflect directly-measured RCT values; we follow this form and thus anticipate the following relationship:

$$Q = a(RCT)^{d}$$

where Q is the volumetric flow rate, RCT is the riffle crest thalweg depth, and a and d are empirically-determined values that we refer to as the “coefficient” and “exponent” hereafter, respectively. This relationship is called an RCT-Q curve. While, intuitively, flow and RCT always positively correlate, exact relationships, set by coefficient and exponent values, can vary from stream to stream. We focus on building RCT-Q curves in and across spawning tributaries in our studied watershed as they are useful in evaluating the relationship between flow and morphology between streams.

Methods

During the coho salmon outmigration season, from February to June 2018, we measured 12 riffle crest thalweg depths (Figure 1b) in 0.5 – 2 km reaches of five Russian River Tributaries (Figure 2). These were measured immediately upstream of Passive Integrated Responder (PIT) tag antenna arrays, which record the outmigration timing and unique identification of PIT tagged juveniles and are operated by the *Russian River Coho Salmon Captive Broodstock Program*. We used in-situ pressure transducer gages at each tributary to measure stage water depth. We conducted a linear regression between stage and median RCT depth to interpolate discrete RCT measurements and generate continuous RCT values over time. Flows were measured with a FlowTracker, handheld acoustic doppler velocimeter. Using median RCT depths and associated flows and a power-law regression, we developed RCT-Q curves for each tributary.

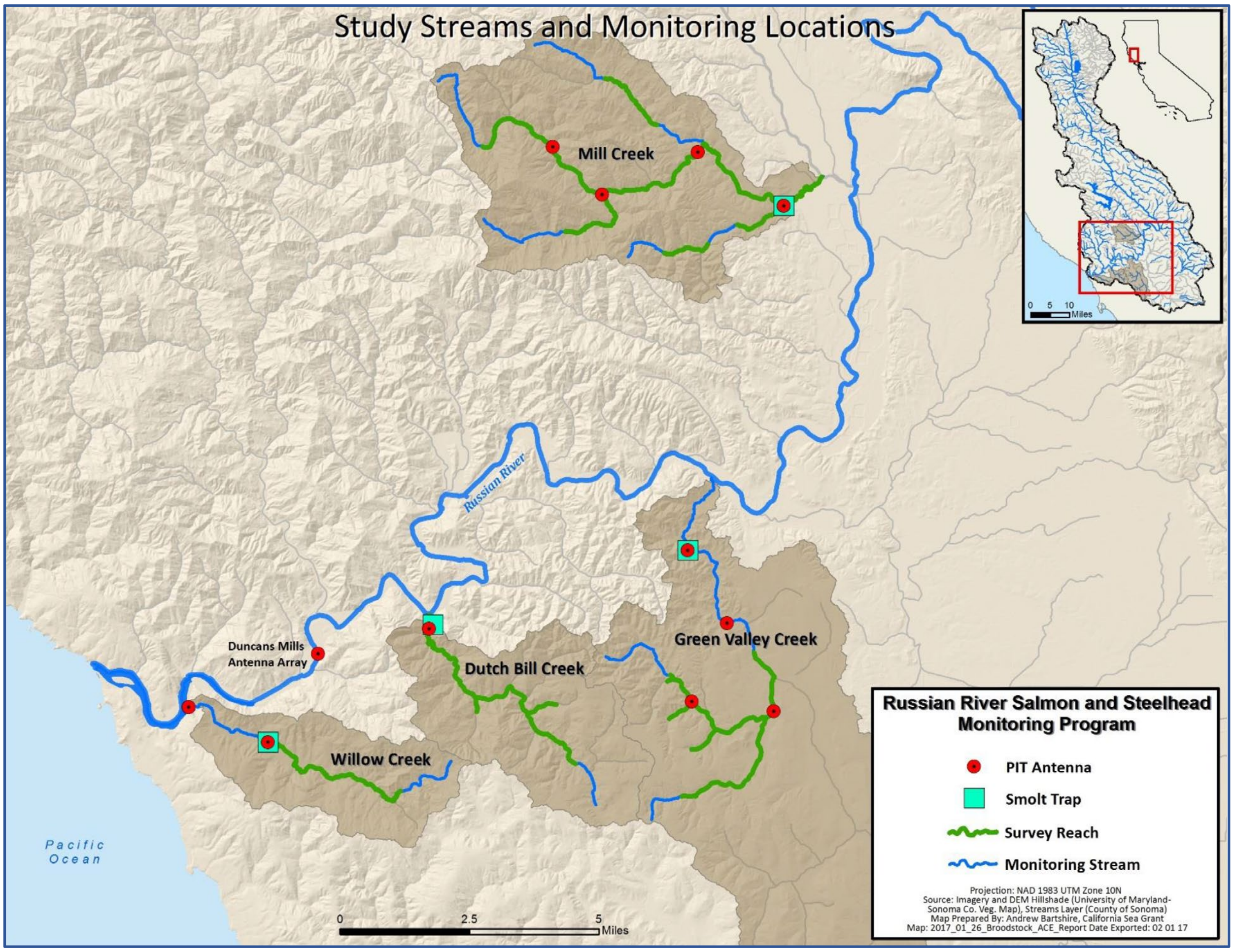

Figure 2: Location of the study streams (UC Cooperative Extension).

Figure 3: Photos showing characteristically different geomorphologies of four study streams.

In October we collected geomorphic data in all five streams. Figure 3 displays some of their geomorphic distinctions. We measured longitudinal and cross section profiles using an automatic level. Cross sections intersected RCT measurement locations and included the active channel heights, bank-full heights, and three points between the RCT and bank edge of both channel sides. Active channel elevation was determined based on the upper elevation of the scoured channel and height of unvegetated lateral bars. We took five distance and depth measurements for each longitudinal profile including: riffle RCT immediately upstream, maximum depth immediately upstream, RCT of interest, maximum pool depth immediately downstream, and riffle RCT immediately downstream. We conducted pebble count measurements within each reach by blindly selecting 100 substrate samples within a one square meter quadrat, selecting the first piece of substrate to come in contact with the sampler's fingernail each time. Pebble measurements were counted into bins based on Kondolf (2007) and Wolman (1954) methods. The 84th percentile pebble diameter (D_{84}) was used to characterize site substrate, in accordance with standard practice for stream substrate surveys (Bunte & Abt 2001).

Results

RCT and Outmigration

Coho outmigrations are correlated with water depths in the study streams (Figure 4). January – April 2018 outmigration is associated with deep RCT depths, and May – June 2018 they are associated with shallow depths. Early in the season (January-March), low outmigration counts and low RCT measurements correlate more clearly. Outmigration often begins within hours of the onset of flows from precipitation events, especially earlier in the season. Outmigration becomes less associated with RCT as the season progresses for some tributaries. Large outmigration counts over many sequential days occur in April and early June, during receding flow depths. Outmigration events were recorded at nearly zero RCT depth in Porter Creek, but stopped in mid-June in Mill Creek, during RCT depths over 12cm.

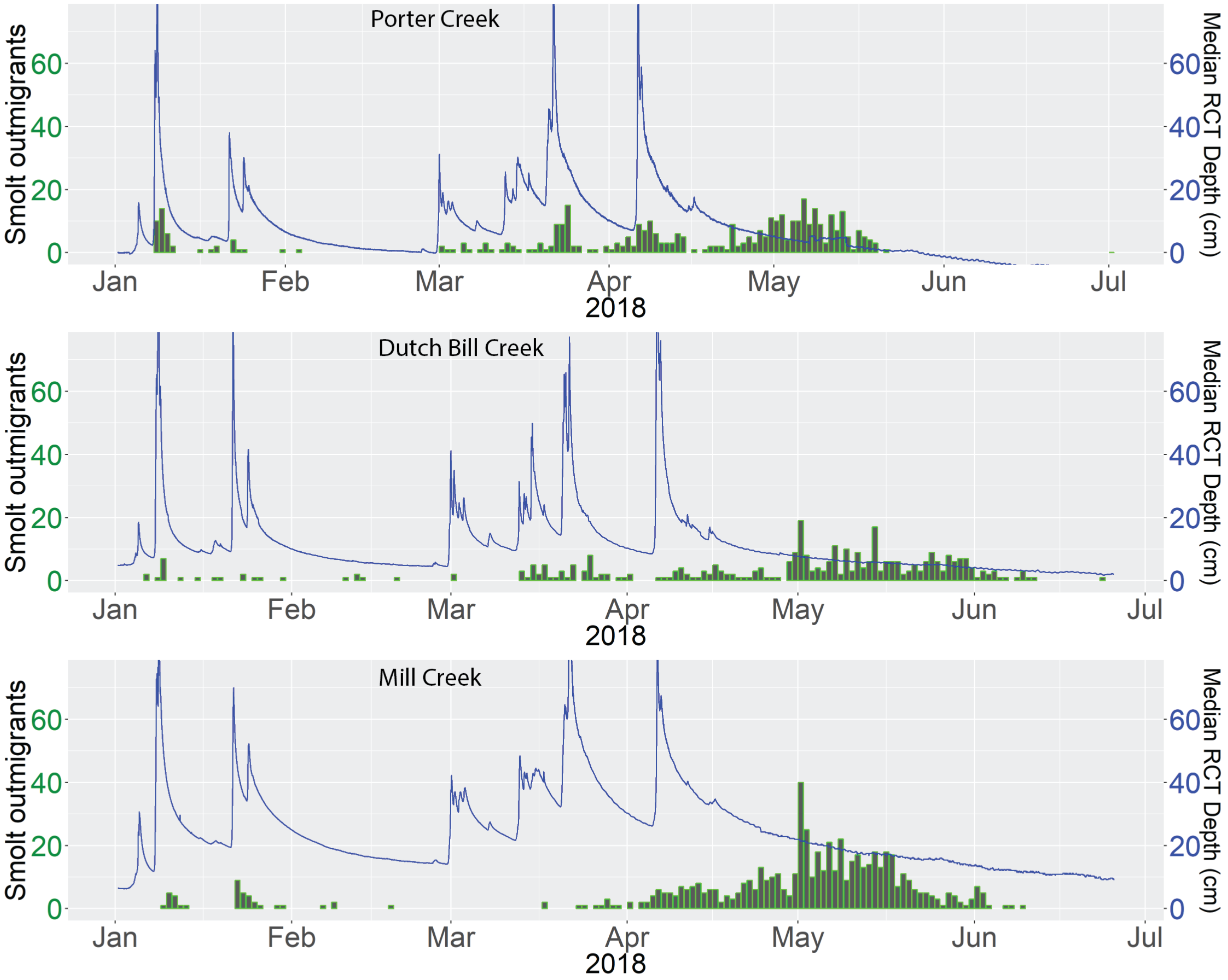

Figure 4: Smolt outmigration frequency and interpolated RCT (riffle crest thalweg) depth for three study streams.

RCT-Q relationships

The five reaches of the study streams each have unique RCT-Q relationships (Figure 5). These curves demonstrate how channel form influences the RCT depth to discharge relationship. Flows required to reach 12cm RCT depths, the standard set by the Department of Fish and Wildlife for outmigration (Woodward 2012), vary by a factor of eight among streams.

Exponents vary from 1.8 to 3.9 among the five RCT-Q curves. Generally, exponents are positively correlated with depth-to-discharge ratios. Coefficients varied by two orders of magnitude between streams, ranging from 0.00011 to 0.1. Curve coefficient values generally correlate negatively with depth-to-discharge ratios.

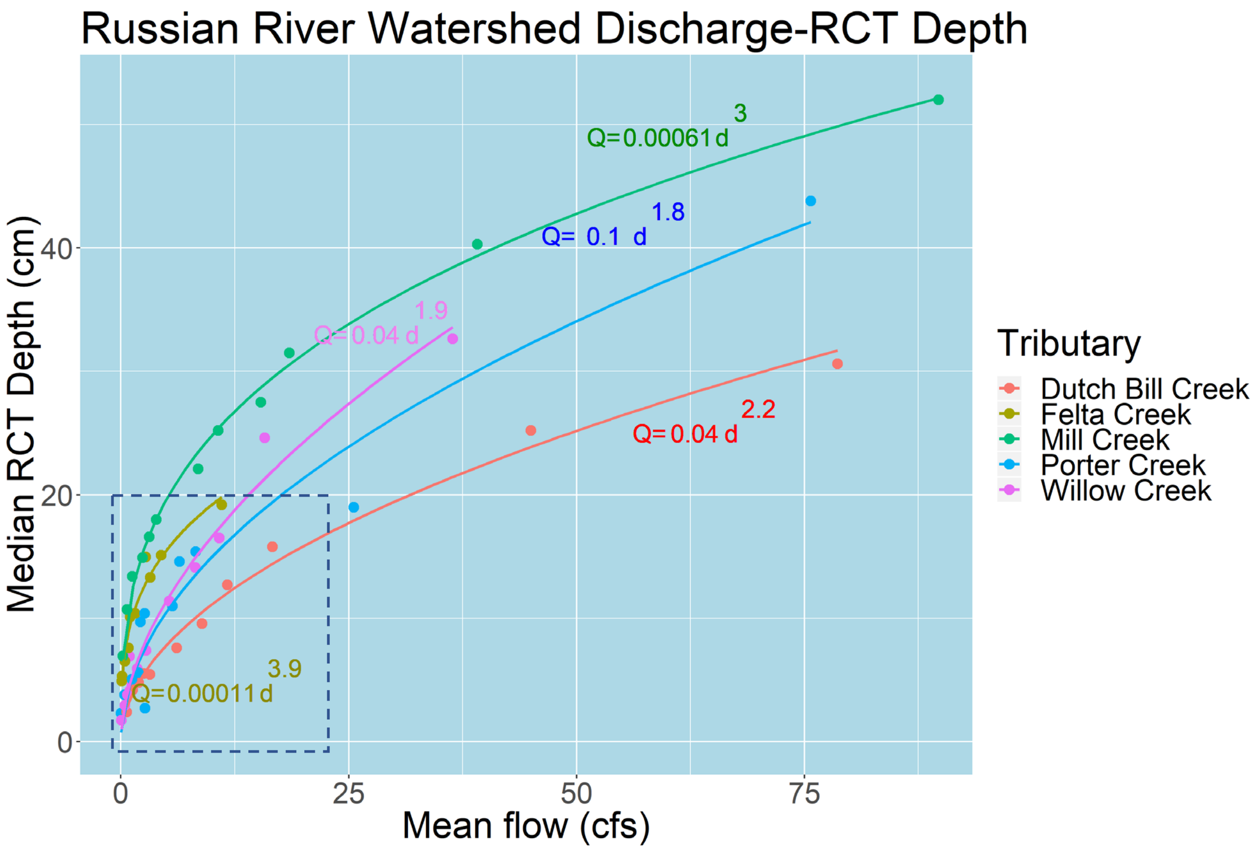

Figure 5a: Median RCTd of 12 sites per stream plotted vs. discharge. Dashed box represented in Figure 5b.

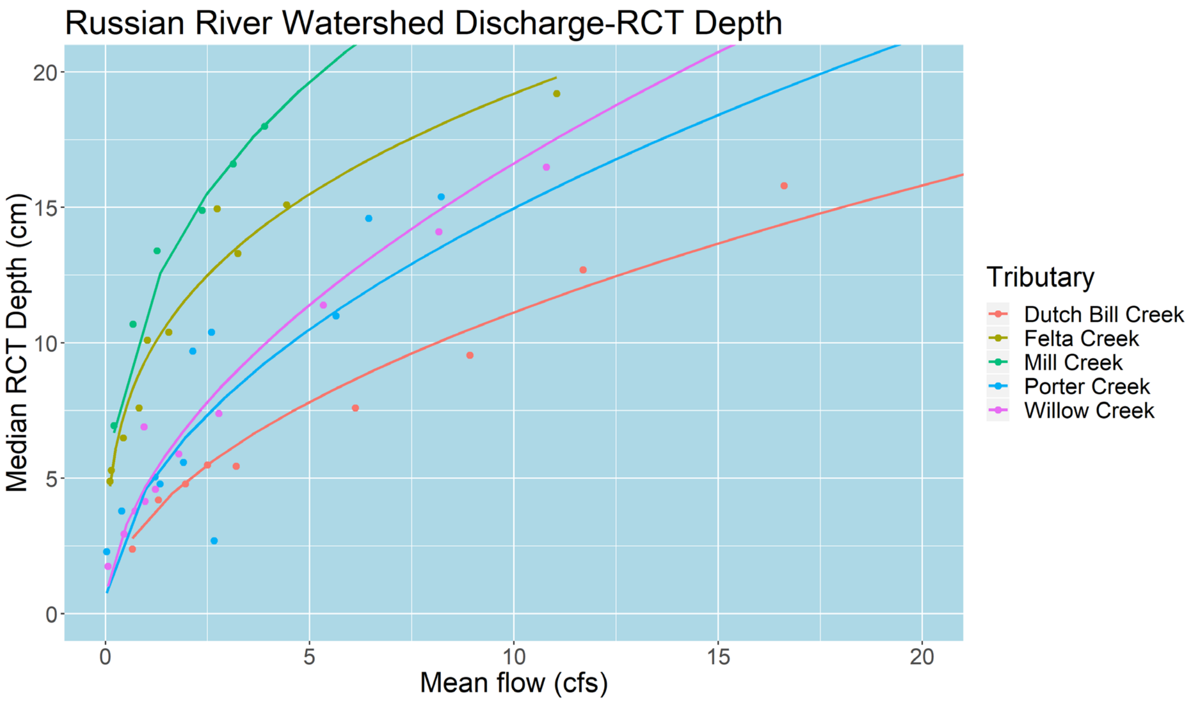

Figure 5b: Zoomed into the dashed box of Figure 5a.

Geomorphic controls on rating curves

Channel cross sections (Figure 6) and longitudinal profiles (Figure 7) can be visually differentiated between streams. Exponents from the RCT-Q curves have: i) a positive correlation with particle size (Figures 8 and 9), ii) a negative correlation with active channel width (Figure 10), iii) a positive correlation with width-to-depth ratios for Porter and Felta Creeks (Figure 11), iv) and a positive correlation with slope for Mill and Willow Creeks (Figure 12).

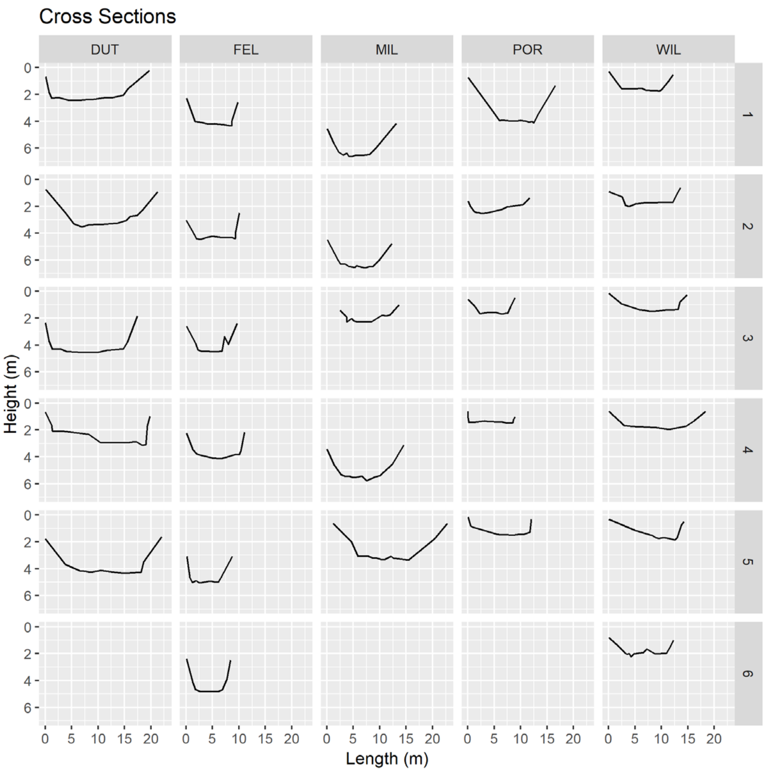

Figure 6: Cross sections at 5-6 RCTd measurement sites per stream. The upper-most elevations represent bank-full levels.

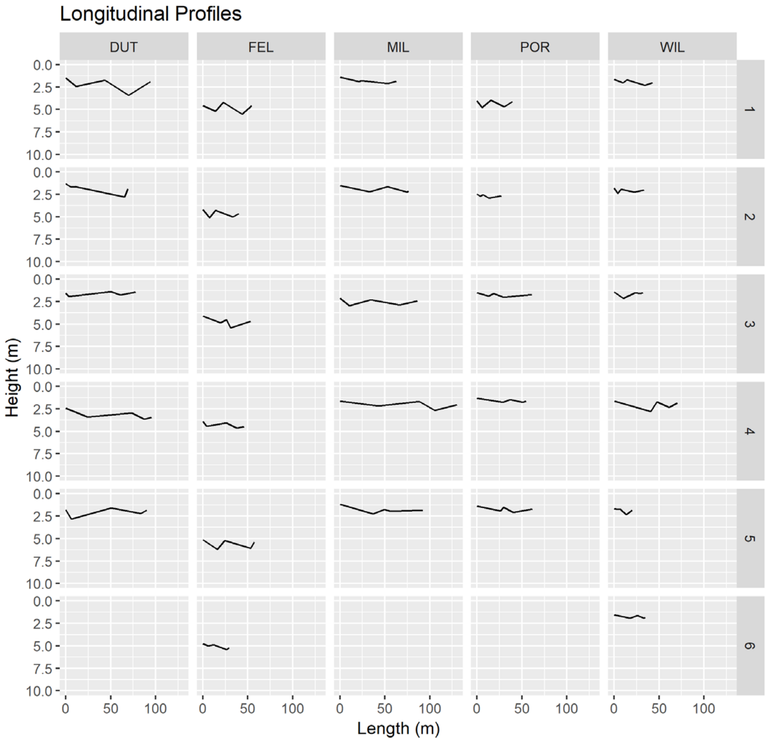

Figure 7: Longitudinal profiles in streams. Five points of elevation, from left to right are: 1) upper RCT, 2) upper pool, 3) middle RCT, 4) lower pool, and 5) lower RCT.

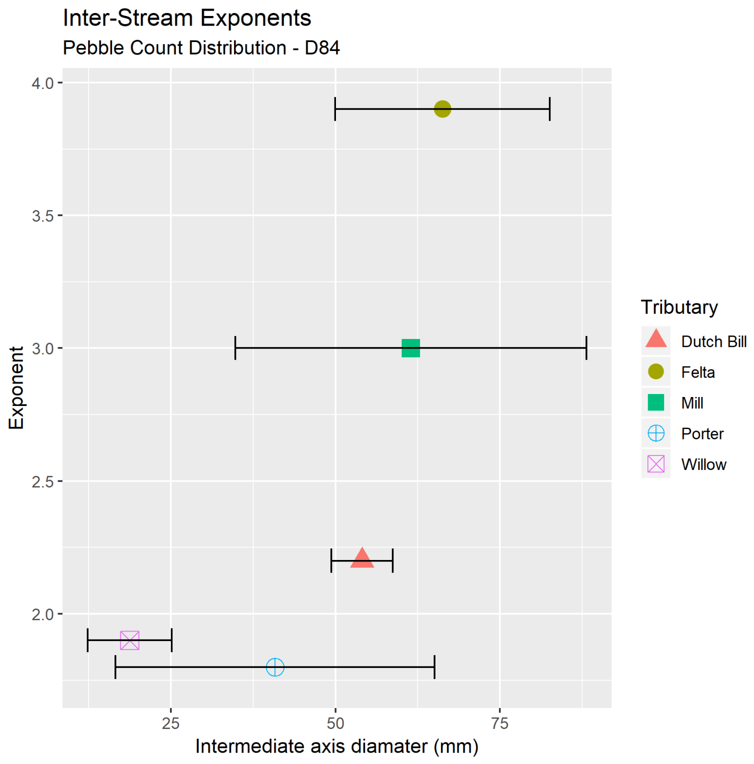

Figure 8: Active channel width vs. exponents of stream power-law functions.

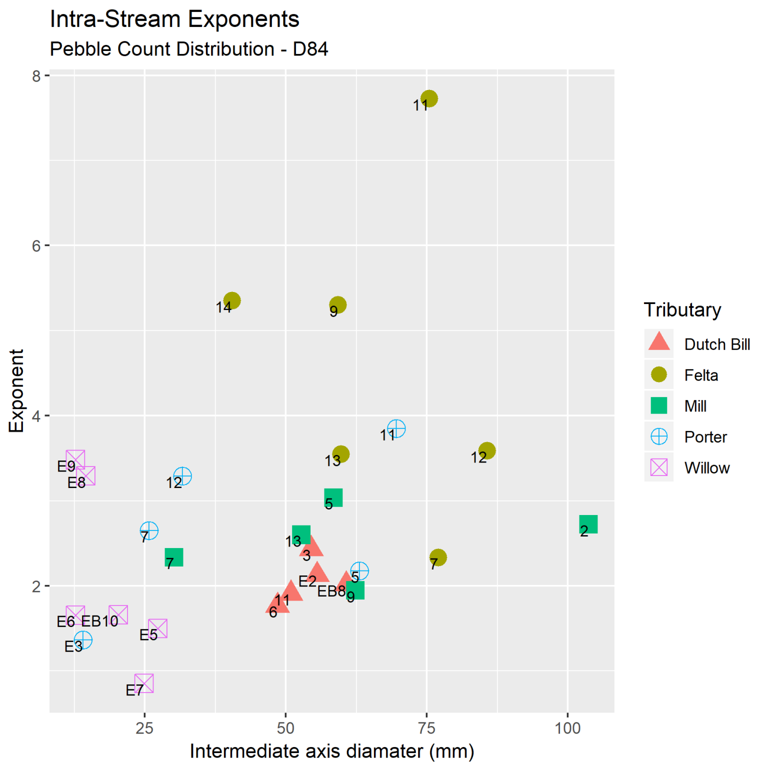

Figure 9***:*** Active channel width-to-depth ratio vs. exponents of stream power-law functions.

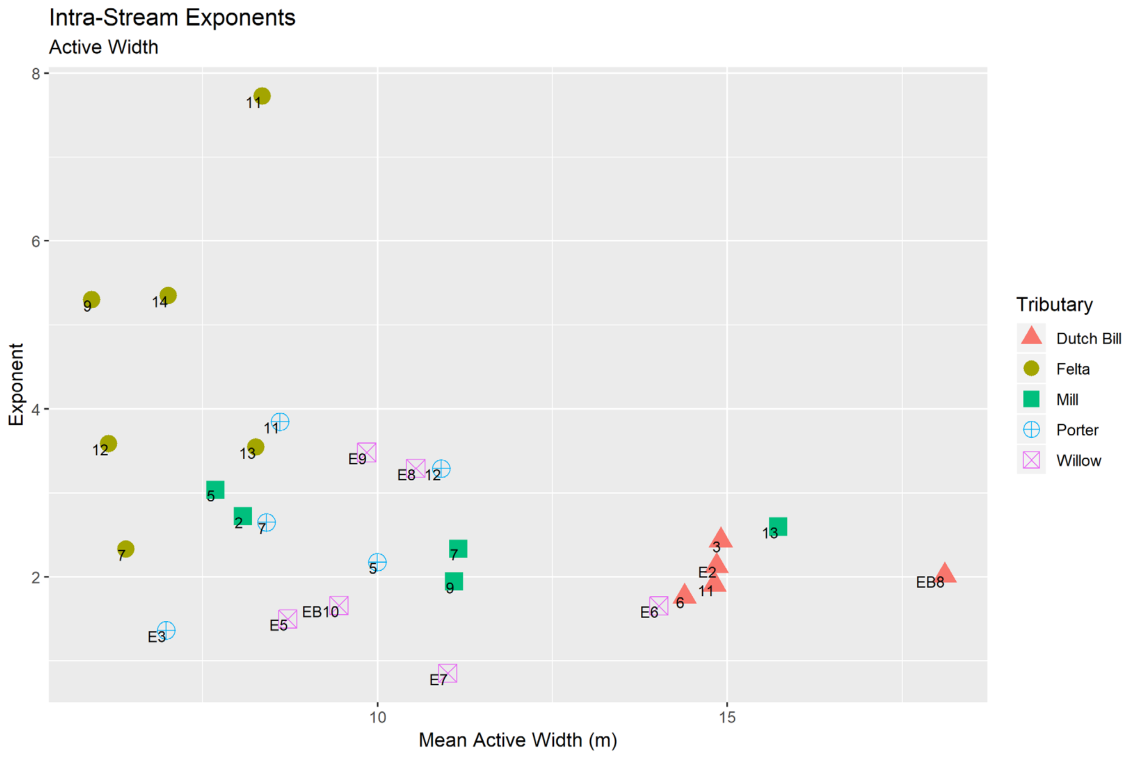

Figure 10: Active channel width vs. exponents of stream power-law functions.

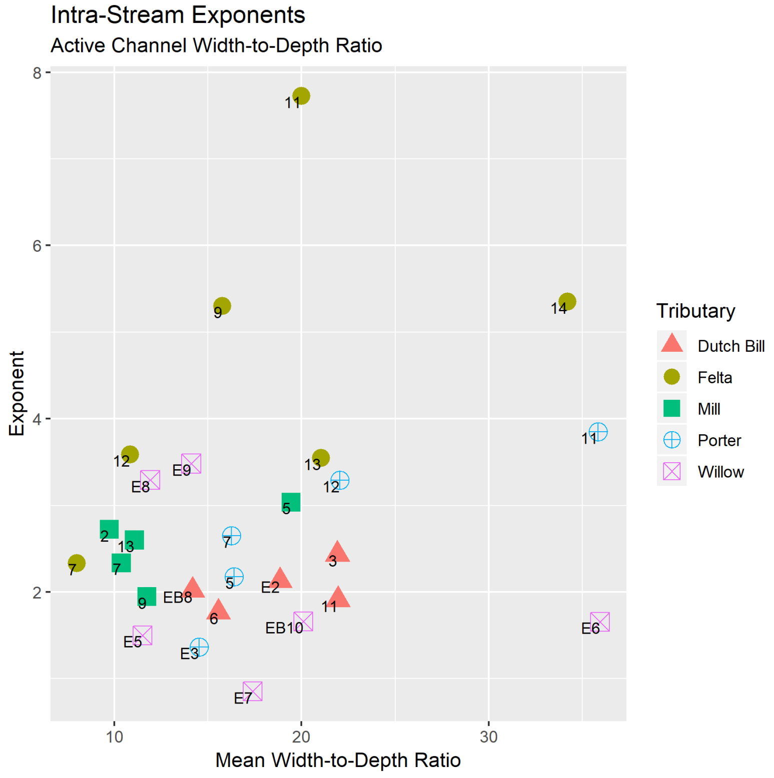

Figure 11: Active channel width-to-depth ratio vs. exponents of stream power-law functions.

Discussion

Before April, most outmigration occurs around the peak streamflows, caused by precipitation events (Figure 4). This may be due to high water velocity actively flushing smolt downstream rather than altering outmigration behavior, if undercut banks and flood refuge are absent. Coho outmigration occurred to a lesser extent during falling limbs of precipitation events during this time, which could indicate that some coho may outmigrate once the danger of peak flow has passed, or that receding flows may still be high enough to flush some smolts downstream.

The relationship between RCT depths and outmigration differed in the latter half of the spring. After April, high numbers of outmigrants were recorded at RCT depths below those suggested by the literature, 0.2-0.3m (Woodard 2012). Late season disregard for flow depth suggests that outmigration in this time may be driven by other seasonal variables, including photoperiod, temperature, and food availability. Still, outmigration ceased at Porter Creek when RCT measurements dropped to zero, highlighting connectivity's importance for outmigration potential.

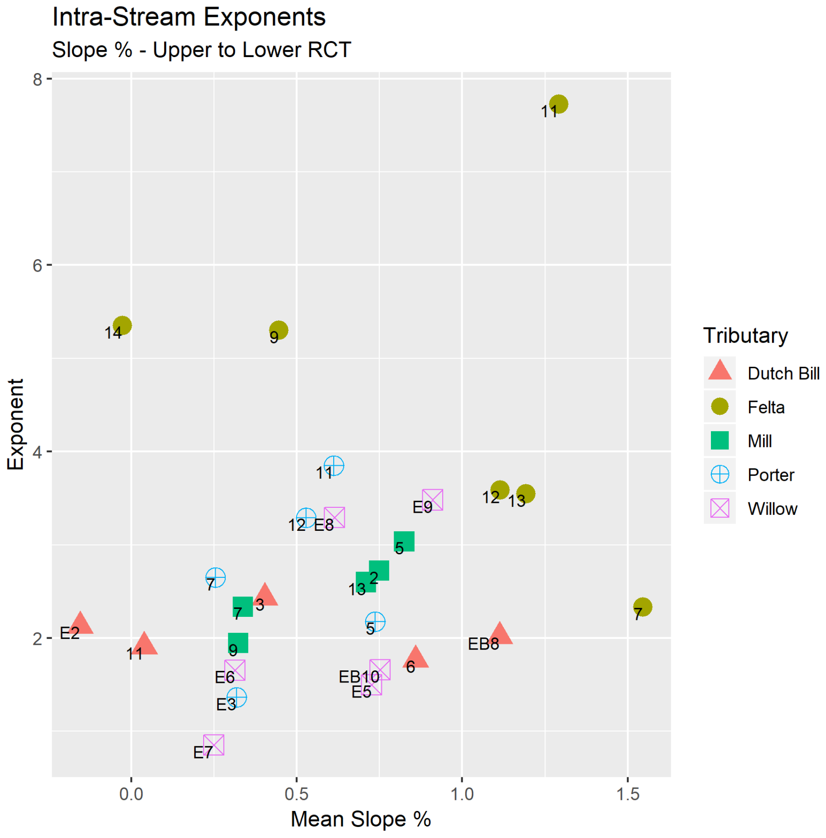

Figure 12: Gradient (from RCT above the RCT of interest to RCT below) vs. exponents of stream power-law functions.

The concentration of late-season migrations at low RCT values may demonstrate ability of the juveniles to wait until the late spring to grow as much as possible (increasing survival rates) before traveling downstream—the analogous concept has been suggested for smolts growing in lagoons before final marine entry (Satterthwaite et al. 2012). A second reason for late-season outmigration regardless of RCT is that shifts in temperature and photoperiod may be more readily perceived by coho than water depth as an indicator of seasonal change and risk of drought. Coho may thus wait, as photoperiod lengthens and associated water temperature increases as the season progresses (McCormick et al. 2000). Outmigration timing may be driven by or associated with habitat or biologic changes not addressed in this paper.

Our data closely fit power-law curves by regression, supporting the use of power-law forms for RCT-Q curves (Figure 5) to determine minimum instream flow magnitudes or maximum allowable flow diversion requirements to maintain desirable RCT depths that facilitate outmigration. All exponent values except that for Felta Creek fit within the range of 1.5-3.7 given in Mierau et al. (2017). High exponent values reflect RCT being less responsive to flow volume; low exponent values reflect RCT being more responsive to flow volume. Because of hydraulic geometry relationships, a low sensitivity for depth-to-flow necessitates higher sensitivity in width-to-flow and/or velocity-to-flow (Leopold et al. 1992). We note that, following equations such as Manning's or Darcy-Weisbach, used for finding water velocity, gradient and velocity are positively correlated (Yochum et al. 2012). Felta Creek has a steep gradient, high D_{84} values, and a low width-to-depth ratio, which distinguish it as a more chute-like than the other tributaries. Felta Creek's very high exponent could suggest that high flow is accommodated by increased velocity, rather than by becoming deeper (or wider, due to narrow banks). Porter Creek is also quite narrow, but it has the highest sensitivity in depth-to-flow (i.e. lowest exponent) and the lowest channel gradient. Given Porter Creek's low gradient, high flow may be accommodated by water level becoming deeper rather than through increased velocity.

Our chosen variables of investigation (i.e. slope, grain size, discharge, bank geometry, flow, and RCT) covary, which complicates the relationship between discharge and RCT. For instance, larger substrate like cobble and boulders will slow water velocity via a higher friction coefficient, but large boulders are also typically found in high-gradient reaches, and gradient is associated with increased velocity. The exact nature of each stream's RCT-Q curve depends on specific channel geometry, which is not completely represented by the width-to-depth ratio.

We see a positive correlation between D_{84} and exponent value, Willow Creek being the only exception. This correlation indicates that streams with coarser particles may not get much deeper in response to higher flows. However, we note that our RCT-Q curves are not sorted (low-to-high flow) by exponent value (Figure 5b). For high RCT values, the exponent will dominate over the coefficient when calculating flow values, but for our relatively low plotted depths, the coefficient and exponent values need to both be considered as key aspects of the RCT-Q curve relationship.

Our findings have management implications that should be considered in streams where human intervention is deemed necessary to restore coho populations. Inter-stream variability in RCT-Q relationships and observed outmigration timing suggests variables other than flow are necessary to consider for management, and that channel geometry needs to be considered in flow management decisions. Seasonal variation in outmigration predictors is apparent, and conditions for outmigration—on the basis of streamflow or otherwise—may change from month-to-month.

Future research should differentiate passive vs. active movement (i.e. smolts actively outmigrating versus being swept downstream) in early season outmigration to improve data that may be otherwise inaccurate. Also necessary is further investigation into survivorship during outmigration as has been done by Michel (2018) for Sacramento River chinook salmon. Lastly, RCT-Q relationships have complicated associations with geomorphic metrics that require more nuanced examination. Particularly, our finding that the exponent in RCT-Q relationships is positively correlated with D_{84} does not yet have a full explanation. This relationship is potentially valuable to managers navigating decisions around stream-appropriate flow release from dams and the nature of diversions in unregulated streams that can be made, while still supporting coho populations across their lifecycles. A caveat of our findings is that the Mediterranean climate of our study may make these results unique compared to Northwest United States populations. Much work is still needed to understand coho outmigration predictors, and we support efforts examining seasonality, hydrodynamic forces, and geomorphology in this endeavor.

Conclusion

Coho salmon populations face tremendous uncertainty due to anthropogenic alterations such as dams, increasing human water demands, and climate change. Their future abundance will depend upon researchers, managers, and the public advancing management to meet ecologically optimal conditions. Inter- and intra-stream variability of Q-RCTd relationships, coupled with outmigration observations imply that absolute depth thresholds of 12 cm for outmigration should be re-addressed for many California streams. Q-RCTd relationship variability may be partially explained by geomorphic factors that could be useful for managers to measure in order to properly balance human-ecological needs of water. Seasonality may also affect outmigration-hydrological relationships. Additionally, the relative importance of season against flow depth is an interesting area of future outmigration research. We support future research of coho outmigration drivers to be paired with research investigating physical limitations of outmigration. Both drivers and connectivity control the success of outmigration and thus must be reviewed together.

Acknowledgements

The authors would like to thank numerous individuals for their assistance with fieldwork and feedback on the research. They include: Lucy Andrews, Andrew Barshire, Stephanie Carlson, Keane Flynn, Celso Garcia, Ted Grantham, Allie Howell, Chippie Kislik, Matt Kondolf, Robin Lopez, Pablo Lozano, Hana Moidu, Mariska Obedzinski, Sean Perez, Sarah Nossamna Pierce, Albert Ruhi, Gabe Rossi, Elizabeth Ruiz, Rachael Ryna, Wes Slaughter, Sylvia Targ, and Ross Vander Vorste.

References cited

Ainley, D., W Sydeman, and J. Norton. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. Marine Ecology Progress Series 118:69–79.

Barlaup, B.T., Rund, H., Norman, E.S., Stranzl, S., Mahlum, S., Vollset, K.W. 2018. Out of sync: monitoring the time of sea entry of wild and hatchery salmon *Salmo salar* smolt using floating passive-integrated transponder antennae. Journal of Fish Biology 93 (3): 455-464.

Beechie, T., Buhle, E., Ruckelshaus, M., Fullerton, A., Holsinger, L. 2006. Hydrologic regime and the conservation of salmon life history diversity. Biological Conservation 130: 560-572.

Braun, D.C., Moore, J.W., Candy, J., Bailey, R.E. 2015. Population diversity in salmon: linkages among response, genetic and life history diversity. Ecography 38: 001-012.

Brown, L.R., Moyle, P.B., Yoshiyama, R.M. 1994. Historical Decline and Current Status of Coho Salmon in California. North American Journal of Fisheries Management 14: 237-261.

Buffington, J.M., Lisle, T.E., Woodsmith, R.D., Hilton, S. 2002. Controls on the size and occurrence of pools in coarse-grained forest rivers. River Research and Applications 18: 507-531.

Bunte, K., Abt, S. R. 2001. Sampling surface and subsurface particle-size distributions in wadable gravel-and cobble-bed streams for analyses in sediment transport, hydraulics, and streambed monitoring. Gen. Tech. Rep. RMRS-GTR-74. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 428 p., 74.

Carlson, S.M., Satterthwaite, W.H. 2011. Weakened portfolio effect in a collapsed salmon population complex. Canadian Journal of Fisheries and Aquatic Sciences 68: 1579-1589.

Carr-Harris, C.N., Moore, J.W., Gottesfeld, A.S., Gordon, J.A., Shepert, W.M., Henry, J.D.J. Jr., Russell, H.J., Helin, W.N.B., Doolan, D.J., Beacham, T.D. 2018. Transactions of the American Fisheries Society 147: 775-790.

Grantham, T.E. 2013. Use of hydraulic modelling to assess passage flow connectivity for salmon in streams. River Research and Applications 29: 250-267.

Grau, E. G., Dickhoff, W. W., Nishioka, R. S., Bern, H. A., & Folmar, L. C. (1981). Lunar phasing of the thyroxine surge preparatory to seaward migration of salmonid fish. Science 211, 607-609.

Gregory, R.S., Levings, C.D. 1998. Turbidity Reduces Predation on Migrating Juvenile Pacific Salmon. Transactions of the American Fisheries Society 127: 275-285.

Hayes, S., Bond, B., Hanson, C., Freund, E., Smith, J., Anderson, E., Amman, A., MacFarlane, B. 2008. Steelhead growth in a small central California watershed: upstream and estuarine rearing patterns. Transactions of the American Fisheries Society 137: 114-128.

Hilborn, R., Quinn, T.P., Schindler, D.E., Rogers, D.E. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences 100(11): 6564-6568.

Johnson, A.L. 2016. A landscape approach to determining and predicting juvenile coho salmon (Oncorhynchus kisutch) movement timing and growth patterns prior to ocean entry. Portland State University Thesis.

Kondolf, G.M., Piégay, H., eds. 2016. Tools in Fluvial Geomorphology. John Wiley & Sons, Hoboken, NJ.

Kondolf , G.M. 1997. Application of the Pebble Count Notes on Purpose, Method, and Variants. Journal of the American Water Resources Association 33:79–87.

Leopold, L.B., Maddock, T. Jr. 1953. The hydraulic geometry of stream channels and some physiographic implications. Geological Survey Professional Paper 252, U.S. Government Printing Office.

Leopold, L.B., Wolman, M.G., Miller, J.P. 1992. Fluvial Processes in Geomorphology. Dover Publications, New York, NY.

Lestelle, L.C. 2007. Coho salmon (Oncorhynchus kisutch) life history patterns in the Pacific Northwest and California. U.S. Bureau of Reclamation.

Lisi, P.J., Schindler, D.E., Bentley, K.T., Pess, G.R. 2013. Association between geomorphic attributes of watersheds, water temperature, and salmon spawn timing in Alaskan streams. Geomorphology 185: 78-86.

McCormick, S.D., Moriyama, S., Björnsson, B.T. 2000. Low temperature limits photoperiod control of smolting in Atlantic salmon through endocrine mechanisms. American Journal of Physiology, Regulatory, Integrative, and Comparative Physiology 278: 1352-1361.

Michel, C.J. 2018. Decoupling outmigration from marine survival indicates outsized influence of streamflow on cohort success for California's Chinook salmon populations. Canadian Journal of Fisheries and Aquatic Sciences *in print*.

Mierau, D.W., Trush, W.J., Rossi, G.J., Carah, J.K., Clifford, M.W., Howard, J.K. 2017. Managing diversions in unregulated streams using a modified percent-of-flow approach. Freshwater Biology 00: 1-17.

Montgomery, D.R., Beamer, E.M., Pess, G.R., Quinn, T.P. 1999. Channel type and salmonid spawning distribution and abundance. Canadian Journal of Fisheries and Aquatic Sciences 56: 377-387.

Montgomery, D.R., Buffington, J.M. 1997. Channel-reach morphology in mountain drainage basins. Geological Society of America Bulletin 109 (5): 596-611.

Moser, M.L., Olson, A.F., Quinn, T.P. 1991. Riverine and estuary migratory behavior of coho salmon (oncorhynchus kisutch) smolts. Canadian Journal of Fisheries and Aquatic Sciences 48: 1670-1678.

Moyle, P.B. 2002. Inland Fishes of California: Revised and Expanded. University of California Press.

Riddell, B.E., Leggett, W.C. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile atlantic salmon (salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 38: 308-320.

Roni, P., Bennett, T., Holland, R., Pess, G., Hanson, K., Moses, R., McHenry, M., Ehinger, W., Walter, J. 2012. Factors affecting migration timing, growth, and survival of juvenile coho salmon in two coastal Washington watersheds. Transactions of the American Fisheries Society 141: 890-906.

Satterthwaite, W.H., Hayes, S.A., Merz, J.E., Sogard, S.M., Frechette, D.M., Mangel, M. 2012. State-dependent migration timing and use of multiple habitat types in anadromous salmonids. Transactions of the American Fisheries Society 141: 781-794.

Schindler, D.E., R. Hilborn, B. Chasco, C.P. Boatright, T.P. Quinn, L.A. Rogers, and M.S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–612.

Schindler, D. E., J. B. Armstrong, and T.E. Reed. 2015. The portfolio concept in ecology and evolution. Frontiers in Ecology and the Environment 13:257–263.

Spence, B.C., Dick, E.J. 2014. Geographic variation in environmental factors regulating outmigration timing of coho salmon (oncorhynchus kisutch) smolts. Canadian Journal of Fisheries and Aquatic Sciences 71: 56-69.

Thompson, K. E. 1972: Determining streamflows for fish life. Proceedings of the instream flow requirements workshop, Pacific Northwest River Basins Commission, Portland, Oregon : 31-50.

Solomon, D.J. 1978. Some observations on salmon smolt migration in a chalkstream. Journal of Fish Biology 12: 571-574.

Waples, R.S., Gustafson, R.G., Weitkamp, L.A., Myers, J.M., Johnson, O.W., Busby, P.J., Hard, J.J., Bryant, G.J., Waknitz, F.W., Neely, K., Teel, D., Grant, W.S., Winans, G.A., Phelps, S., Marshall, A., Baker, B.M. 2001. Characterizing diversity in salmon from the Pacific Northwest. Journal of Fish Biology 59: 1-41.

Wolman, M.G. 1954. A method of sampling coarse river-bed material. Transactions, American Geophysical Union 35:951.

Woodard, M.W. 2012. Standard Operating Procedure for Critical Riffle Analysis for Fish Passage in California. California Department of Fish and Game Instream Flow Program Standard Operating Procedure DFG-IFP-001.

Yochum, S.E., Bledsoe, B.P., David, G.C.L., Wohl, E. 2012. Velocity prediction in high-gradient channels. Journal of Hydrology 424-425: 84-98.

Appendix I

Table 1: Key articles on predictors of juvenile salmonid outmigration timing.

Article Name	Author(s)	Year	Journal	Outmigration Timing Predictors	Species	Geographic Scale	Site(s)
Out of Sync: monitoring the time of sea entry of wild and hatchery…	Barlaup et al.	2018	J. Fish Biol.	lake along path, hatchery	Atlantic	Stream, Watershed	Vosso River (Norway)
Hydrologic regime and the conservation of salmon life history…	Beechie et al.	2006	Biol. Cons.	hydrology, temperature	Chinook	Regional	Puget Sound (WA)
Population diversity in salmon: linkages among response, genetic …	Braun et al.	2016	Ecography		Chinook	Watershed	Fraser River (BC)
Weakened portfolio effect in a collapsed salmon population…	Carlson & Satterthwaite	2011	Can. J. Fish. Aquat. Sci.		Chinook	Stream, Watershed	Central Valley (CA)
Phenological diversity of salmon smolt migration timing within…	Carr-Harris et al.	2018	T. Am. Fish. Soc.	elevation, distance, estuary holding	Sockeye	Watershed	Skeena River (BC)
Turbidity Reduces Predation on Migrating Juvenile Pacific Salmon	Gregory & Levings	1998	T. Am. Fish. Soc.	turbidity	Chinook, Chum, Sockeye	Reach, Stream, Watershed	Harrison & Fraser Rivers (BC)
Biocomplexity and fisheries sustainability	Hilborn et al.	2003	PNAS	flow, predation	Sockeye	Regional	Bristol Bay (AK)
A Landscape Approach to Determining and Predicting Juvenile…	Johnson	2016		gradient, prey availability	Coho	Stream, Watershed	Russian River (CA)
Coho Salmon	Lestelle	2007		connectivity, distance,	Coho, Chinook	Regional	AK, BC, WA,

(oncorhynchus kisutch) Life History Patterns…				temperature, size, hydrology			OR, CA
Association between geomorphic attributes of watersheds…	Lisi et al.	2013	Geomorphology	gradient	Sockeye	Watershed	Wood River (AK)
Low temperature limits photoperiod control of smolting in Atlantic…	McCormick et al.	2000	Am. J. Physiol.-Reg I		Atlantic		(fish reared in lab)
Decoupling outmigration from marine survival indicates outsized…	Michel	2018	Can. J. Fish. Aquat. Sci.	flow	Chinook	Watershed	Sacramento River (CA)
Riverine and estuarine Migratory Behavior of Coho Salmon…	Moser et al.	1991	Can. J. Fish. Aquat. Sci.	temperature, estuary holding	Coho	Stream, Watershed	Chehalis River, Grays Harbor (WA)
Evidence of an Adaptive Basis for Geographic Variation in Body…	Riddell & Leggett	1981	Can. J. Fish. Aquat. Sci.	predation, wintering risk, energetics, prey availability	Atlantic	Stream, Watershed	Miramichi River (NB)
Some observations on salmon smolt migration in a shalkstream	Solomon	1978	J. Fish Biol.	temperature, flow, turbidity	Atlantic	Reach, Stream	Piddle River (UK)
Geographic variation in environmental factors regulating outmigration timing of coho…	Spence & Dick	2014	Can. J. Fish. Aquat. Sci.	photoperiod, temperature, flow, lunar phase	Coho	Stream, Watershed, Species Range	Flynn & Deer Creeks (OR), Sashin Creek (AK), Carnation Creek (BC)
Characterizing diversity in salmon from the Pacific Northwest	Waples et al.	2001	J. Fish Biol.	hatchery	Chum, Pink, Chinook, Sockeye, Coho	Species Range	AK, BC, WA, ID, OR, CA

Sea-to-sea survival of late-run adult steelhead…	Keefer et al.	2017	Can. J. Fish. Aquat. Sci.		(Steelhead trout)	Stream	Columbia River
Effects of smolt release timing and size on the survival…	Irvine et al.	2013	Prog. Oceanogr.		Coho	Watershed	Strait of Georgia
Factors Affecting Migration Timing, Growth, and Survival…	Roni et al.	2012	T. Am. Fish. Soc.	size, distance, depth	Coho	Stream	East Twin & West Twin Riverrs (WA)
Role of Off-Channel Ponds in the Life Cycle of Coho Salmon…	Swales & Levings	1989	Can. J. Fish. Aquat. Sci.	temperature, flow	Coho	Reach	Coldwater River (BC)

Appendix II

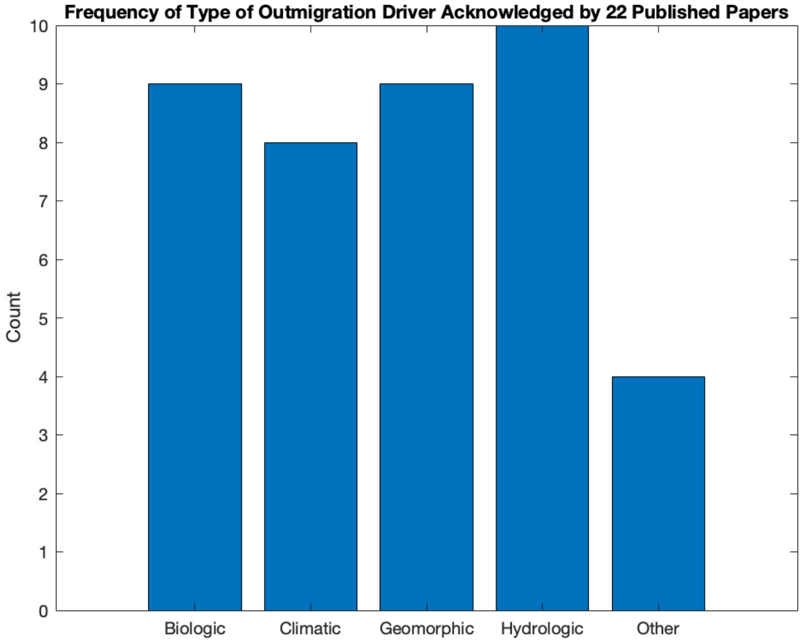

Figure 13: Types of predictors of outmigration timing in existing literature.

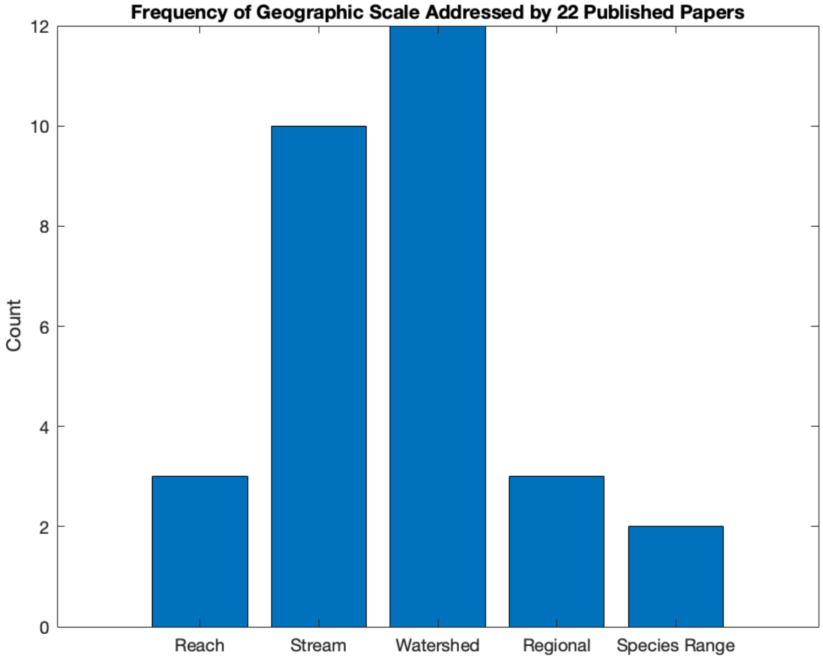

Figure 14*:* Spatial scales of outmigration timing predictors in existing literature. Research papers including multiple scales are counted multiple times.