Food, Phenology, and Flow—How Prey Phenology and Streamflow Dynamics Affect the Behavior, Ecology, and Recovery of Pacific Salmon

By

Gabriel Jacob Rossi

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Mary E. Power, Chair

Professor Stephanie M. Carlson

Adjunct Professor Theodore E. Grantham

Spring 2020

Food, Phenology, and Flow—How Prey Phenology and Streamflow Dynamics Affect the Behavior, Ecology, and Recovery of Pacific Salmon

Copyright 2020

By

Gabriel Jacob Rossi

ABSTRACT

Food, Phenology, and Flow—How Prey Phenology and Streamflow Dynamics Affect the Behavior, Ecology, and Recovery of Pacific Salmon

By

Gabriel Jacob Rossi

Doctor of Philosophy in Integrative Biology

University of California, Berkeley

Professor Mary E. Power, Chair

Pacific salmon (*Oncorhynchus)* are an iconic genus of anadromous fish whose decline over the last century has linked indigenous peoples, government agencies, fishers, advocates, and scientists in the common, albeit messy, cause of salmon recovery. While the history of ecology, and the earliest research on Pacific salmon, is grounded in the understanding that food web and prey dynamics control the abundance and distribution of predators, the last half-century of salmon management has focused primarily on hatchery production and physical habitat suitability. The continued decline of Pacific salmon, after decades of efforts to restore them, has prompted salmon ecologists to remember what Charles Elton (1927) understood nearly a century ago: "*Food is the burning question in animal society, and the whole structure and activities of the community are dependent upon questions of food-supply.*" My dissertation proceeds from the observation that both salmon management and salmon ecology have placed *too little* emphasis on aquatic food webs, animal behavior, and biotic interactions as key drivers of salmon production and resilience—and thus as chief mechanisms of salmon recovery.

This dissertation is comprised of a series of studies and experiments from 2016 to 2019, which explore how the seasonal *interaction* among physical habitat, phenology of salmon prey, and foraging behavior affects juvenile salmon growth and performance. The experiments described here take place near the southern end of the range of Pacific salmon—in Mediterranean streams along the Pacific Coast of California. These streams experience a characteristic recession of streamflow between spring and fall, which is an ideal natural gradient to investigate the dynamic interaction between physical habitat and prey phenology. The studies described here also focus on one species of Pacific salmon—*Oncorhynchus mykiss* (the "steelhead" or "rainbow trout").

My first chapter starts from the observation that *O. mykiss* are typically considered drift foragers that occupy higher velocity habitat than other salmonids. Yet their persistence in Mediterranean coastal streams with seasonally low velocity and drift suggests an underappreciated flexibility in foraging behavior. Using novel 3-D videogrammetry along with measurements of invertebrate drift and stream hydraulics, I quantified the seasonality of foraging behaviors that *O. mykiss* employ during the spring-summer flow recession. I also explored the factors that trigger of foraging mode shifts, which are important for both ecological interactions and salmon management. I found that 80% of *O. mykiss* were drift foraging in May, 2018; while over 70%

used alternative foraging modes by July. Foraging mode was significantly correlated to maximum water velocity and to riffle crest depth. While drift concentration was a poor univariate predictor, the top-ranked statistical models of foraging mode included both hydraulic variables and drift concentration. This study revealed that *O. mykiss* in Mediterranean streams express more diverse foraging behavior than previously suggested in the literature, and that changes in foraging mode could be predicted by simple hydraulic indicators. This study also lead us to speculate that non-drifting prey fluxes, as well as risk aversion, may influence late-summer foraging decisions in Mediterranean coastal streams.

In my second chapter I took advantage of an existing streamflow augmentation project to conduct a novel manipulative experiment to elevate dry-season flow in an intermittent, salmon-bearing stream. Using a *Before-After-Control-Impact* (BACI) study design, I directly measured the responses of *O. mykiss* behavior, their invertebrate prey, physical habitat, and water quality to flow enhancement. I found that elevating mid-summer baseflow for one week caused significant increases in dissolved oxygen, riffle width, depth, velocity, invertebrate drift, and benthic invertebrate standing crop – and these changes were evident at sites more than 1 km downstream from the point of flow augmentation. I also documented consistent behavioral changes indicating that pool-dwelling salmonids were able to exploit the increased prey abundance and improved metabolic environment in the treatment reach after flow augmentation. Counts of foraging salmonids near riffle-pool transition zones doubled, foraging movement remained steady (relative to decreasing movement in the control reach), and the proportion of drift foraging salmonids increased from an average of 26% to an average of 77% after augmentation. Collectively, these results suggest that dry season flow enhancement can significantly improve habitat profitability for salmonids, but that the timing and location of flow augmentation, relative to downstream points of interest, are critical to meeting ecological objectives.

In my third chapter I propose a conceptual model for how stream hydraulics and secondary production interact to affect foraging profitability for juvenile salmon during the streamflow recession in Mediterranean coastal streams. I evaluated the model by comparing two distinct salmonid rearing streams—one perennial, cool, and shaded; the other intermittent, seasonally warm, and sunny. In both streams, I conducted a photon-to-salmon food web study to document the seasonality of hydraulic habitat relative to the phenology of prey biomass for *O. mykiss*. I also estimated the seasonal change in *O. mykiss* growth potential using a drift foraging bioenergetics model. Both streams offered profitable foraging opportunities for *O. mykiss,* but modeled growth potential peaked at least two months earlier in the intermittent stream, where lipid storage measured in mid-July was nearly twice as high. In contrast, modeled and measured early-summer growth was higher in the perennial stream. By late summer, foraging profitability declined in both streams. However, abiotic conditions approached lethal tolerance levels in the intermittent stream, whereas the perennial stream maintained suitable abiotic conditions all summer. Seasonal changes in growth *potential* were explained by the timing of streamflow recession relative to the phenology of prey fluxes. But ecological interactions (especially intraspecific competition) and flexible foraging behavior both appear to have mediated *realized* foraging opportunity. These observations lead me to speculate that juvenile *O. mykiss* life histories should differ among streams, due to the timing of their spring-summer growth potential and to differing late summer survival rates. Collectively, these stream types could contribute to a stabilizing portfolio of juvenile salmonid life histories.

This dissertation is dedicated to my three sons—Maximo, Theodore, and Basil Rossi
And to their mother (with the perfect middle name)—Maya River Liles Rossi

"And the other is Gary Nabhan's idea. In one of his books he says that animals don't go extinct because someone shoots the last one, or a bulldozer scrapes away the last habitat. They go extinct because the web of relationships that sustain them unravels. He then put it in anthropomorphic terms and said, they go extinct because of a lack of ecological companionship."

Jim Lichatowitch (2013)

Far better an approximate answer to the right question, which is often vague, than an exact answer to the wrong question, which can always be made precise.

John Tukey (1962)

Those who wish to succeed must ask the right preliminary questions.

Aristotle (~330 BC)

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

I have so many people to thank for the past five years that my dissertation feels more like a community project than a singular accomplishment of my own. In the course of this pursuit, my mother, Patricia Rossi, passed away and two new babies were added to our family. The single greatest credit for this dissertation is due to my wife, Maya River Liles Rossi, who sacrificed years away from her dream job, bore and raised our sons, and moved our family twice, all while managing to support me intellectually and emotionally with interest, patience, kindness, and love. I don't believe there is anyone else in the world who could have done those things. I am the luckiest man alive. In fact, two of my fellow researchers (Wes and Keane) noticed a theme of "everything working out for the best" in my life and they termed it "Gabe luck." It is an apt description. To Necia Liles—thank you so much for putting up with me (as a son-in-law), my noisy family, and my team of researchers countless times in your wonderful home.

My academic and scientific advisors have been exceptional. Before I came to Berkeley, the fire to "be more excellent" in the study of river ecology was lit by Bill Trush, who has always challenged me to look deeper and understand more. I left an eminent and supportive consulting group, led by Scott McBain, to pursue this research and my time at McBain Associates was formative for me. A fortuitous scientific connection between Bill Trush and Mary Power led me to Berkeley and I could not have fallen into better hands. Bill, you told me I couldn't do better than to work with Mary, and it was the truth. Mary, you have been the best advisor a graduate student could ask for. You have taught me the yin and yang of ecology (blending natural history with quantitative science). You have shown me what an imaginative, deeply knowledgeable scientific mind is capable of when it is not shackled by egotism. But you have also supported me as a friend and colleague. I will be a different scientist because I knew you. I may not ever get *affect* and *effect* straight, but I won't ever forget to "look behind every competitive interaction to find the facilitation hiding in the background." Stephanie Carlson you taught me so much about diversity in ecology, and how to connect ideas from radically different research systems to make better hypotheses. Our kindred passion for salmon ecology fired me up! Ted Grantham you connected me to a whole new study system, and a world of applied ecology. You also have a knack for getting me to think beyond my own research interests so that our work is relevant to a wider audience. Designing research projects with you to address pressing management concerns has been fulfilling work. Eileen Lacy and Wayne Sousa, I will always remember our invigorating reading and discussion sessions from my qualifying exam semester, especially Wayne's great stories about the world behind the scenes of ecological history.

This research project required long, generally intense weeks of field and laboratory work—often in areas beyond my expertise. I could not have done this work on my own, or even with a small group. There are so many people to thank for their involvement with this project, but a few stand out. The invertebrate expertise and tremendous effort of Shelley Pneh was a *sine qua non* for this dissertation. Shelley, I can't thank you enough and I hope we continue to work together. Terrance Wang, Weston Slaughter, and Keane Flynn formed a key group of researchers who contributed in the field and laboratory. Most significantly, you three established an ethos within our group that directly supported this work and led to creative science. Wes and Keane continued to work with me for three years, and the pleasure has been all mine! But many others contributed valuable time and effort into this project—especially Hannah Roodenrijs, Kobie Boslough,

Samuel Larkin, Shannon Mckillop-herr, Garbo Gan, Gunnar Rieth, Kate Stonecypher, Riley Brown, Emily Long, Vicky Fong, Elena Hauser, Paige Griggs, Rebecca Hernandez, Daisy Schadlich, and Isabelle Claire Radis. Thank you all so much for your hard work and support. I appreciate you so much.

I am also so thankful for the group of graduate students and post-docs I've had the pleasure to know and work with during my time at Berkeley. Keith Bouma-Gregson, Philip Georgakakos, and Suzanne Kelson made the Angelo research team a cheerful, welcoming, and stimulating place to work. Our group got along so well and I'm honored to be part of this cohort. I've also benefitted and learned much from other graduate students, post-docs, and colleagues at the Eel River Critical Zone Observatory, especially David Dralle and Jesse Hahm. Special thanks to Angelo Reserve Manager Peter Steel and to Collin Bode for the continued support and technical assistance. Brian Kastle, thanks for carrying on the great work with riffle crests and for joining our field team! Hana Moidu, thanks for going e-fishing with us during your first weeks at Cal. Ross Vander Vorste, thanks for your help in applying good statistics to freshwater ecology. (I haven't forgotten about our pig-hunting plans.)

Several professional colleagues have played pivotal roles in this project, and in my life as well. First and foremost is Darren Mierau. Darren, since my first day at McBain & Trush (2009) you have been lifting me up and pushing me onward as a professional, a scientist, and a steadfast friend. Not only through your work and financial support from California Trout but in all our projects together, you keep the fire burning. Tim Caldwell, we've shared a lot of our journey together, and it's been awesome going through this process with you. I'm looking forward to our next project together. Sarah Kupferberg, you have been a real mentor and wonderful colleague to me; (thanks for putting in a good word all those years ago). Casa de Kupferberg is not only a house of great science but great emotional support, too. Jennifer Carah, you are an inspiration. Jason Neuswanger, your work paved the way for this dissertation (and for others as well). Sean Naman, I've benefited from our many phone calls about fish ecology and bioenergetics. Thanks also to John Nagle, Tyler Hammond and the Gallo Vineyards team on Porter Creek, for supporting our research and for your stewardship of our local salmon. To the California Sea Grant team in Sonoma county—you all are super stars. I especially want to thank Mariska Obedzinksi, Sarah Nossaman Pierce, William Boucher, Andrew Bartshire, and Elizabeth Ruiz. Your passion for conservation and understanding the salmon populations in the Russian River evince a model that should be exported throughout California and the PNW. If we are going to recover salmon—you are showing us the way.

Finally, I want to thank the brotherhood of St. Silouan's Monastery in Sonora California. Your prayers, phone calls, and spiritual support have lifted me up throughout this whole process. You constantly remind me that good science and care for creation are not only compatible, but mutually vital efforts. Thank you to Fr Maximos for reminding me that "piety never dispenses with technique."

I received generous funding for this dissertation from Eel River Critical Zone Observatory (NSF CZO EAR-1331940). Additional funding came from the UC NRS Mildred E. Mathias Award, the Carol Baird Fund for Graduate Field Research, the Institute for the Study of Ecological and Evolutionary Climate Impacts, the Grantham Lab, and generous support from California Trout.

INTRODUCTION

Rivers are "continuous, hierarchical, and heterogeneous" networks – sculpted, and maintained by well-described geomorphic and hydrologic processes (Leopold et al. 1964, Montgomery and Buffington 1997, Fausch et al. 2002). The physical processes that form and maintain river networks also exert a strong effect on spatio-temporal patterns of habitat, disturbance, and primary production – which in turn influence energy flow, biomass and biotic interactions in river food webs (Power and Dietrich 2002). These material and energetic flow paths form the basis ("bottom up") of the river ecosystem. However – biotic interactions between consumers, their conspecifics, and their prey can exert a strong "top down" effect in river food webs – which also influences material and energy flows in the stream environment (Power 1992). Collectively, this interplay of physical, energetic, and biotic forces shape the world that stream dwelling animals inhabit. Despite this, human management of river ecosystems has tended to emphasize the physical controls on habitat and animal populations while neglecting food web and organismal interactions (Vander Zanden et al. 2016).

A half-century of human management of Pacific salmon (*Oncorhynchus)* embodies this disregard for food web dynamics and organismal interactions. While the history of ecology is grounded in the understanding that food and prey dynamics drive animal abundance and distribution (Elton 1927, Lindeman 1941) – and early research into salmon also emphasized this point (Chapman 1966), for decades salmon management has focused primarily on hatchery production and physical habitat (Mobrand et al. 1997, Lichatowich et al. 2018). My dissertation joins others (Cederholm et al. 1999, Power and Rainey 2000, Baxter et al. 2005, Wiplfi and Baxter 2010, Bellmore et al. 2013, Naman et al. 2018, Jeffres et al. 2019 and others) in attempting to refocus a scientific narrative on the food web and biotic interactions that support rearing Pacific salmon. The three research chapters in this dissertation comprise a hierarchical investigation into the effect of interactions among habitat, prey abundance, and behavior, on one species of pacific salmon — *Oncorhynchus mykiss* (the "steelhead" or "rainbow trout").

In 2016 (Chapter 1), I explored the behavioral diversity that *O. mykiss* employ to survive in Elder Creek, a Mediterranean stream with periods of seasonally low velocity and low abundance of drifting aquatic prey. Three observations from this research led directly to hypotheses that I tested in Chapters 2 and 3. First, I observed strong seasonal changes in foraging movement and foraging mode of *O. mykiss* between May and August. Drift foraging in late spring and early summer gave way to search and benthic foraging in later summer. Foraging movement increased between May and July as invertebrate drift waned, but movement declined in August, perhaps in response to increased predator risk as pools shrank. Second, I observed that these foraging mode shifts were predictable from simple hydraulic indicators, which I manipulated in Chapter 2. And third, I noted that streamflow and invertebrate drift in Elder Creek were only weakly correlated across the spring-summer recession – leading me to speculate on how these variables interacted to affect salmon growth (Chapter 3).

My second chapter explores the capacity for human management to modulate physical habitat, prey dynamics, and animal behavior for the benefit of rearing juvenile salmon. I took advantage of an existing summer streamflow augmentation project on Porter Creek to conduct a novel manipulative experiment to elevate dry-season flow in an intermittent, salmon-bearing stream

and directly measure the responses of *O. mykiss* behavior, their invertebrate prey and their physical habitat using a *Before-After Control-Impact* (BACI) study design. I found that 1-week of mid-summer flow augmentation caused significant increases in dissolved oxygen, riffle width, depth and velocity, as well as increased invertebrate drift and benthic invertebrate standing crop. The interaction of these physical and biotic variables allowed pool-dwelling salmonids to exploit the increased prey abundance and the improved metabolic environment in the treatment reach after flow augmentation. However, three years of inter-annual studies on Porter Creek revealed that the effects of augmentation varied seasonally, in response to ambient streamflow and channel characteristics (especially hyporheic conductivity). Collectively these results suggest that dry season flow enhancement is a restoration technique that can significantly improve habitat profitability for foraging salmonids, but that the timing and location of flow augmentation, relative to downstream points of interest, are critical to meeting ecological objectives.

My third chapter integrates lessons from chapters one and two to develop a conceptual model for how stream hydraulics and secondary production interact in Mediterranean streams to affect foraging profitability for juvenile Pacific salmon. Returning to Elder Creek (Chapter 1) and Porter Creek (Chapter 2), I tested the conceptual model in these two, very different salmonid rearing streams. Elder Creek (perennial, shaded, and cool) and Porter Creek (intermittent, sunny, and seasonally warm) both offered profitable foraging opportunities for pool-dwelling *O. mykiss* during the spring and summer of 2018. Yet the timing of peak prey concentration and drift foraging profitability was at least two months earlier in Porter Creek, and Porter Creek's late summer abiotic conditions (drying pools, low dissolved oxygen and high temperature), were also much more severe. I also found that profitability of *O. mykiss* foraging in both streams—while driven by their specific seasonal changes in food and habitat, was strongly mediated by ecological interactions (intraspecific competition) and behavioral flexibility. These observations led me to argue that salmon foraging profitability in Mediterranean streams can be better evaluated by adapting bioenergetics models to account for non-drift related foraging behaviors (e.g. Harvey and Railsback 2014) and the context specific effects of ecological interactions on foraging opportunity (Naman et al. 2019). This dissertation ends by speculating that juvenile *O. mykiss* life histories in these two different (but both regionally common) systems are attuned to the distinct timing of spring growth potential and opportunity for over-summer survival.

The experiments described in this dissertation highlight the importance all aspects of the stream ecosystem—physical habitat, food webs, and biotitic interactions, in supporting rearing Pacific salmon. Each chapter includes a discussion with reference to the other two, linking this integrative research theme throughout my dissertation. Collectively, these chapters emphasize that to understand how any of component of the stream ecosystem (habitat, food web, or biotic interactions) affect salmon, we must understand them *in relation* to one another, since their interaction ultimately drives consumer growth and performance.

Literature Cited

Baxter, C. V., K. D. Fausch, and W. Carl Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones: Prey subsidies link stream and riparian food webs. Freshwater Biology 50:201–220.

Bellmore, J. R., C. V. Baxter, K. Martens, and P. J. Connolly. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. Ecological Applications 23:189–207.
Cederholm, C. J., M. D. Kunze, T. Murota, and A. Sibatani. 1999. Pacific Salmon Carcasses: Essential Contributions of Nutrients and Energy for Aquatic and Terrestrial Ecosystems. Fisheries 24:6–15.
Chapman, D. W. 1966. Food and Space as Regulators of Salmonid Populations in Streams. The American Naturalist 100:345–357.
Elton, C. S. 1927. Animal ecology. Reprinted 2001. University of Chicago Press, Chicago.
Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes. BioScience 52:483.
Harvey, B. C., and S. F. Railsback. 2014. Feeding modes in stream salmonid population models: is drift feeding the whole story? Environmental Biology of Fishes 97:615–625.
Jeffres, C. A., E. J. Holmes, T. R. Sommer, and J. V. E. Katz. 2019. Detrital Food Web Drives Aquatic Ecosystem Productivity in a Managed Floodplain. preprint, Ecology.
Leopold, L.B., Wolman, M.G., Miller, J.P. 1964. Fluvial Processes in Geomorphology. Freeman, San Francisco, CA, 522 pp
Lichatowich, J., R. Williams, B. Bakke, J Myron, D. Bella, B. McMillan, J. Stanford, D. Montgomery, K. Beardslee and N. Gayeski. 2018. Wild Pacific Salmon: A Threatened Legacy. jalich@comcast.net. Expanded July 2018 version, printed by Bemis Printing, St. Helens, OR.
Lindeman, R. L. 1941. Seasonal Food-Cycle Dynamics in a Senescent Lake. American Midland Naturalist 26:636.
Mobrand, L. E., J. A. Lichatowich, L. C. Lestelle, and T. S. Vogel. 1997. An approach to describing ecosystem performance “through the eyes of salmon” 54:10.
Montgomery, D.R., Buffington, J.M. 1997. Channel-reach morphology in mountain drainage basins. Geological Society of America Bulletin 109, 596–611.
Naman, S. M., J. S. Rosenfeld, P. M. Kiffney, and J. S. Richardson. 2018. The energetic consequences of habitat structure for forest stream salmonids. Journal of Animal Ecology 87:1383–1394.
Naman, S. M., R. Ueda, and T. Sato. 2019. Predation risk and resource abundance mediate foraging behaviour and intraspecific resource partitioning among consumers in dominance hierarchies. Oikos 128:1005–1014.
Power, M. E., and W. E. Rainey. 2000. Food webs and resource sheds: towards spatially delimiting trophic interactions. Page 24 Ecological Consequences.
Power, M. E. 1992. Top-Down and Bottom-Up Forces in Food Webs: Do Plants Have Primacy. Ecology 73:733–746.x
Power, M. E., and W. E. Dietrich. 2002. Food webs in river networks. Ecological Research 17:451–471.
Vander Zanden, M.J, J.D. Olden, C. Gratton,T.D. Tunney. 2016. Food web theory and ecological restoration. Pages 301-329 In Foundations of Restoration Ecology Second Edition: Eds. M. A. Palmer, J.B. Zedler, D.A. Falk. Island Press, Washington D.C.
Wipfli, M. S., and C. V. Baxter. 2010. Linking Ecosystems, Food Webs, and Fish Production: Subsidies in Salmonid Watersheds. Fisheries 35:373–387.

CHAPTER 1

Foraging modes and movements of *Oncorhynchus mykiss* as flow and invertebrate drift recede in a California Stream

ABSTRACT

Salmonids frequently adapt their feeding and movement strategies to cope with seasonally fluctuating stream environments. *Oncorhynchus mykiss* tend to drift forage in higher velocity habitat than other salmon, yet their presence in streams with seasonally low velocity and drift suggests more behavioral flexibility. We combined novel video analysis with measurements of invertebrate drift and stream hydraulics to investigate *O. mykiss* foraging behavior and movement during the seasonal recession of a 17 km^2 California stream. From May to July (2016), foraging movement increased as prey concentration and velocity declined; however, movement decreased in August as pools became low and still. In May, 80% of *O. mykiss* were drift foraging, while by July, over 70% used alternative foraging modes. Foraging mode was significantly correlated to maximum velocity and riffle crest depth. While drift concentration was a poor univariate predictor, top ranked models included both hydraulic variables and drift concentration. A drift foraging bioenergetic model was also a poor predictor of foraging mode. We suggest that infall and benthic prey, as well as risk aversion may alter late-summer foraging decisions.

INTRODUCTION

Substantial work has examined the fitness consequences of foraging behavior for juvenile salmonids. Much has focused on the energetics and position choices of drift foraging, where fish hold at stations in the water column, and make short forays to intercept drifting invertebrate prey (Jenkins 1969, Fausch 1984; Hughes and Dill 1990; Nakano et al. 1999a). However, juvenile salmonids forage in other, less studied ways (Harvey and Railsback 2014, Nielsen 1992, Nakano et al. 1999a). Search or cruise foraging salmonids actively move throughout the foraging patch, locating and attacking prey, without maintaining a focal point or even a specific directionality (Tippets and Moyle 1978; Puckett and Dill 1985; Nielsen 1992, Fausch et al. 1997; Rosenfeld and Raeburn 2009; Harvey and Railsback 2014). A foraging mode distinction can also be made between search foragers who focus their efforts on drift in the water column versus on the stream bed (Nakano et al. 1999a). Attacks on the water surface, while common, generally tend to be opportunistic (at least in shaded headwater streams) rather than associated with a sustained foraging "mode."

Relative to most other salmonid species, stream dwelling *Oncorhynchus mykiss* (resident "rainbow trout" and or anadromous "steelhead") are considered to be primarily drift foragers (Nakano et al. 1999b; Van Leeuwen et al. 2011; Rosenfeld et al. 2014). *O. mykiss* tend to prefer habitats with higher velocities and more hydraulic complexity then other salmonids. They choose drift foraging locations in these habitats where adjacent roughness elements afford holding

stations with reduced swimming costs (Tucker and Rasmussen 1999; Van Leeuwen et al. 2011; Rosenfeld et al. 2014). However, the sustained presence of *O. mykiss* in Mediterranean streams (Shapovalov and Taft 1954, Smith and Li 1982) with very low or intermittent summer flow, when drift is minimal (Smith and Li 1982), may require more flexible foraging behavior. Railsback and Harvey (2014) and Caldwell et al. (2018) included a search foraging mode in their energetic models for *O. mykiss* in Mediterranean streams; however, reported observations of search or benthic foraging in lotic *O. mykiss* are rare in the literature.

Tippets and Moyle (1978) report evidence of benthic foraging by adult (but not juvenile) *O. mykiss* in the McCloud River – which they attribute largely to turbidity. Merz (2002) noted that small *O. mykiss* ingested algal material from the benthic mats in the lower Mokulemne River in California. In other salmonids, search and benthic have been more frequently documented, for example in brook trout (*S. fontinalis*), white spotted char (*S. leucomaenis*), cutthroat trout (*O. clarki)*, Coho (*O. kistuch)*, and Atlantic salmon (*Salmo salar*) (Nielsen 1992; Fausch et al. 1997; Nislow et al. 1998, Nakano et al. 1999a, Rosenfeld and Raeburn 2009, Naman et al. 2018). Given the importance of flexible foraging behavior for understanding salmon ecology and management (Dill 1983, Mittelbach et al. 2014, Nakano et al. 1999a), and the comparative lack of research on juvenile *O. mykiss* foraging in Mediterranean streams, or other systems with seasonally low flow and drift, a clearer understanding of seasonal changes in *O. mykiss* foraging behavior during the ecologically critical streamflow recession period is needed (Yarnell et al. 2015).

We investigated how trends in the foraging behavior of juvenile *O. mykiss* shifted with stream hydraulics and the phenology of invertebrate drift during the spring and summer streamflow recession of a 17 km^2 (drainage area) Californian stream with Mediterranean seasonality. The spring and summer streamflow recession is an ecologically significant event in rainfall-dominated streams with Mediterranean seasonality (Yarnell et al. 2015; Dralle et al. 2017). During the recession, streamflow declines following power laws (Dralle et al. 2017) and opportunities for foraging, movement, and growth of salmonids change rapidly (Hayes et al. 2008). The seasonal recession also provides a continuously changing context of hydraulic and biotic conditions, which is useful for a natural experiment to investigate the seasonality and drivers of *O. mykiss* foraging behavior and movement.

The purpose of this study was both to quantify the seasonal variation in *O. mykiss* foraging behavior over the spring-summer recession and to investigate the relative importance of pool hydraulics and drifting prey concentration in driving seasonal variation in foraging behavior. We expected drifting prey concentration would decline with streamflow during the seasonal recession. We hypothesized that the declines in water velocity and drifting prey concentration would: (1) lead *O. mykiss* to increase their within-pool foraging movement to maintain prey encounter rates, which would (2) increase the proportion of search foraging fish relative to drift foragers. We further hypothesized that (3) a seasonal decline in the energetic profitability of drift foraging—computed as the net rate of energy intake (NREI)—would determine the timing of shifts from drift foraging to search foraging better than hydraulic variables (e.g. depth, velocity) or drift concentration since NREI models are based on mechanistic relationships between hydraulics and drifting prey (Hughes and Dill 1990).

METHODS

This study was conducted in Elder Creek, a 16.7 km^2 tributary of the upper South Fork Eel River in Northern California (39.7181° N, 123.6527° W). We studied the first 4 km of Elder Creek above its confluence with the South Fork Eel River. The stream has a coarse bed dominated by cobbles and boulders. Gradients range from 2% - 5% in riffles, averaging 2.4% over the 4 km whole study reach (McBain and Trush 2000). The South Fork Eel River basin, including Elder Creek, has a Mediterranean climate, with > 90 % of the annual rainfall occurring from November through April (Mierau et al. 2018). Elder Creek experiences the characteristic Mediterranean flow recession between April and October (Dralle et al. 2015), with typical summer low flows from 0.015 to 0.03 m3·s-1 and rarely dropping below that range. Nevertheless, unlike many small Mediterranean streams, Elder Creek maintains perennial flow over much of its course, even during prolonged drought (Lovill et al. 2018). The perennial flow of this small basin in an otherwise Mediterranean climate is largely due to the thick critical zone, of its watershed, which is underlain by water-holding argillite shales in the Northern California Coastal belt (Rempe and Dietrich 2018; Lovill et al. 2018). Perennial flow in Elder Creek supports continuous (although seasonally varying) production and drift of benthic invertebrates.

Site-Selection and Hydraulic Measurements

Habitat units (riffle-pool sequences) were selected for study based on two primary criteria: (1) the site was a riffle-pool sequence that supported multiple age classes of foraging *O. mykiss*, and (2) the site had suitable morphology for filming videos, which were shot perpendicular to flow. Thirty sites meeting these two criteria were identified within our study reach, and seven were selected, based on their favorability for filming. To evaluate the relationship between invertebrate drift and foraging behavior, we focused video recording on the head of each pool (hereafter pool head patch), where fish were most likely to intercept drifting invertebrates during the summer low flow period (Smith and Li 1982, Harvey et al. 2006, Van Leeuwen et al. 2011).

Sampling began on May 18th, 2016 and ended on August 16th, 2016. Fish behavior, invertebrate drift, and hydraulic measurements were taken on: May 26-27th, June 18-20th, July 5-6th, July 26-27th, and August 15-16th. Streamflows in Elder Creek declined during the study period from 0.15 $m^3 \cdot s^{-1}$ on May 18th to 0.02 $m^3 \cdot s^{-1}$ on August 17th 2016 (Fig. S1). Streamflow and water temperature were retrieved from USGS gaging station 11475560 "Elder Creek near Branscomb CA," which is 0.6 km upstream from the Elder Creek's confluence with the SF Eel River. Water temperature ranged from 9.8 °C on May 23rd to 19.8 °C on July 29th 2016.

At each study site, three cross-stream transects were established in the pool head patch – one where the riffle and invertebrate drift enters the pool from the riffle upstream, a second bisecting the focal area for video analysis, and a third over the maximum depth of the pool – which marked the downstream boundary of our designated 'pool head patch' (Fig. 1, Table 1). Depth and velocity were measured at 0.5-m increments along each cross section. Velocity was measured at 0.6 depth with a SonTek Flow Tracker (ADV series) acoustic doppler velocity profiler. Volume was calculated between each cross section on each survey date, using the average end method (Taube 2000). A stage meter was installed in each pool, and pool stage was measured every two weeks. Depth of flow was also measured where the thalweg bisects the downstream riffle crest of each pool at the 'riffle crest thalweg (RCT)' (Hilton and Lisle 1993;

Mierau et al. 2018). The hydraulic relationship between this riffle crest depth and streamflow is sensitive to channel morphology (Clifford et al. 2002; Emery et al. 2003), and has been shown to be primary control on upstream pool depth and velocities (Lisle 1987; Pasternack et al. 2008). In this study we used RCT depth and maximum velocity as indicators of seasonal change in pool hydraulics (Pasternack et al. 2008, Chiu and Tung 2002), and as an independent variable to predict changes in fish behavior and movement.

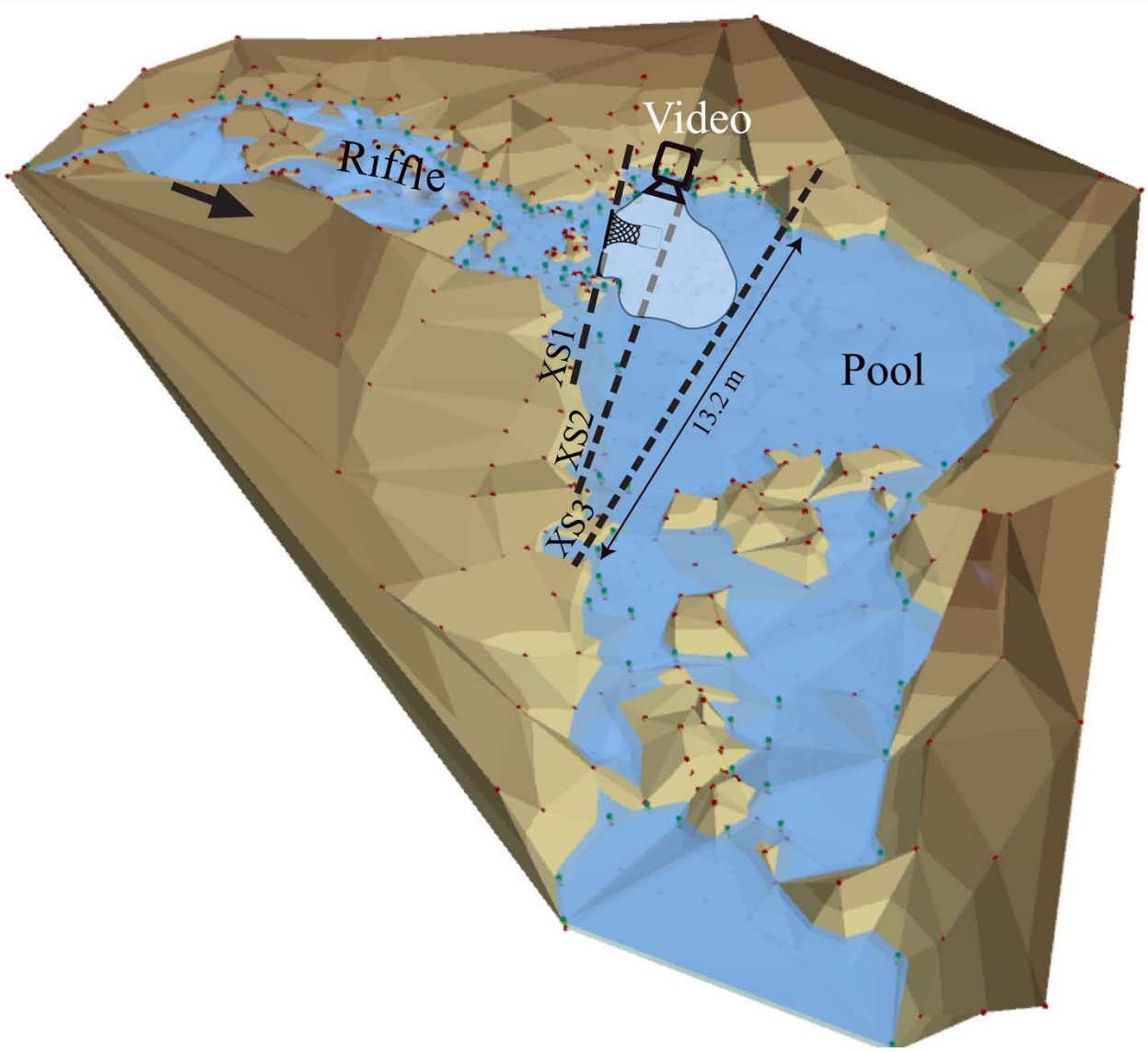


Figure 1. A topographic map of a riffle-pool replicate in Elder Creek showing transects, video pin location where the cameras were anchored and invertebrate drift net location. The light blue match represents the approximate area that was filmed. The area between XS 1 and XS 3 is the "pool head patch."

Table 1. Operational definitions for habitat, hydraulic, invertebrate, and fish variables.

Terms and Variables*	Operational Definition	Units
Pool head patch	The head of the pool – from where the upstream riffle enters the pool to the maximum pool depth (Fig. 1)	m^3
Whole pool	The entire pool from where the upstream riffle enters the pool to the downstream riffle crest	m^3
Drift $Flux_{Numbers}$	# of invertebrates caught, per hour, in thalweg drift net	$\#\cdot hr^{-1}$
Drift $Flux_{Mass}$	Mass of invertebrates caught, per hour, in thalweg drift net	$mg\cdot hr^{-1}$
Drift $Concentration_{Numbers}$ *	# of invertebrates per volume	$\#\cdot m^{-3}$
Drift $Concentration_{Mass}$ *	Mass of invertebrates per volume	$mg\cdot m^{-3}$
Q *	Streamflow	$m^3\cdot s^{-1}$
Temp *	Water Temperature	^oC
Max Depth XS_i	The maximum depth measured on cross section i	m
Max Depth *	Maximum depth at XS 3 (e.g. max pool depth)	m
Max Velocity XS_i *	The maximum velocity measured on section_i	$m\cdot s^{-1}$
Avg Velocity XS_i	The average velocity measured on section_i	$m\cdot s^{-1}$
RCT_i *	Riffle crest depth measurement taken at downstream hydraulic control	cm
Foraging movement	The distance that foraging *O. mykiss* (in the pool head patch) traveled per unit time e.g. microhabitat movement	$mm\ s^{-1}$
Pool head patch counts	The number of *O. mykiss* observed in video scans at the head of the pool	Individuals
Whole pool counts	The number of *O. mykiss* observed during whole pool snorkel counts	Individuals
Pool head patch density*	The number of *O. mykiss* observed in video scans at the head of the pool, divided by pool head patch volume	$Indiv.\cdot m^{-3}$

* Denotes predictor variables used in statistical analysis.

Analysis of Fish Behavior

Video of fish behavior in the pool head patch was used to track individuals through time and space (Neuswanger et al. 2016), and to take behavioral scan samples over short, fixed time intervals (Altmann 1974). Videos of fish behavior were collected with stereo-pairs of mounted GoPro cameras (model: HERO 4 Black, recorded at 30 frames per second with 1080p resolution) installed at monumented stations in each pool (Fig. 2, Fig. S2). Recordings lasted approximately 30 minutes and were collected between 4pm and 6pm every evening during each of 5 monthly survey events. Camera angle and distance from the ground were kept as constant as possible between sampling events to sample a consistent volume of the pool head patch throughout the study period.

Fish Position and Movement

Individual *O. mykiss* were tracked on the pool head patch video using the open source software VidSync, which allows the user to triangulate a 3-D position, in relative space, using known lines of sight from two or more cameras (Neuswanger et al. 2016). We followed the video correction

and calibration procedure described in Neuswanger et al. (2016). The primary output data from the Vidsync analysis were 3-D positions and times of measured behaviors (e.g., foraging maneuvers) or attributes (e.g., body length), organized by object (e.g., fish ID) and event (type of measurement) (Fig. 2).

Using VidSync software, we tracked the locations of 151 fish, with a minimum of five 3-second observations in each of 4 study pools throughout the spring and summer of 2016. Videos from the other 3 of our 7 study pools were unsuitable for VidSync analysis because camera placement on two or more dates did not provide adequate overlapping views that encompassed the focal foraging areas in each pool. For each surveyed video, we selected the 3-minute clip with the highest counts of *O. mykiss* in the video frame. Within this 3-minute clip, we tracked the nose-point location of each individual fish every 3 seconds. The maximum number of location data points for a focal individual was n=60 (180 seconds/3 seconds per data point), although most fish were tracked for fewer than 60 locations because fish would leave the field of view. A minimum of n=5 samples were used to develop movement data. To test the accuracy of length estimates from VidSync, we measured the length of a known object within our field of view n=5 times for each video. Errors ranged from >1% to 6%, which are higher than reported by Neuswanger et al. (2016), but still achieves a level of precision much greater than snorkeling or bankside estimates.

Fish Behavior Scans

Foraging mode and foraging types were defined based on common literature descriptions (Table 2), and assigned in video scans. When viewing videos for analyses, we allowed at least three minutes after the camera was placed in the pool for fish to resume their normal behavior. To determine a fish's foraging mode, a reviewer watched the animal in motion for a ten-second video interval, which we determined to be adequate time to discern foraging mode, but less than expected for fish behavior and density to change. Video reviewers sampled the first ten-second interval for every 30 seconds of video, counting the number of animals that were engaged in specific foraging modes during the scan. Only one foraging mode was assigned per fish, per 10-second scan, based on their dominant behavior. Other behavioral events such as surface strikes, attacks, or nips, (Table 2), were also counted and summed within each scan. Fifteen 10-second scans was the minimum subsample size (26 scans was the maximum) included in this study.

The maximum number of *O. mykiss* observed in any 10-second scan was used to estimate pool head patch abundance. Pool head patch density was estimated by dividing fish abundance by the volume of the pool head patch (defined as the volume upstream of XS-3 in Fig. 1). In addition to video, each pool was also snorkeled three times during the summer (May 26th, June 21st, and August 17th, 2016) to compare trends in pool head patch abundance and density with estimated abundance and density of *O. mykiss* in the whole pool. The snorkeler entered below the downstream riffle crest of each pool and moved upstream slowly and carefully, face forward. Given the small size of most study pools, much of the pool volume could frequently be observed from the downstream riffle crest. Fish were only counted once they were downstream of the observer to minimized double counting. All salmonids observed during snorkel surveys were identified to species and binned in one of five size classes to estimate age ($\leq$30mm ~ fry, 30 to 80mm ~ young of year, 80 to 120 mm ~ 1 year old; 120 to 200 mm ~ 2+ year old).

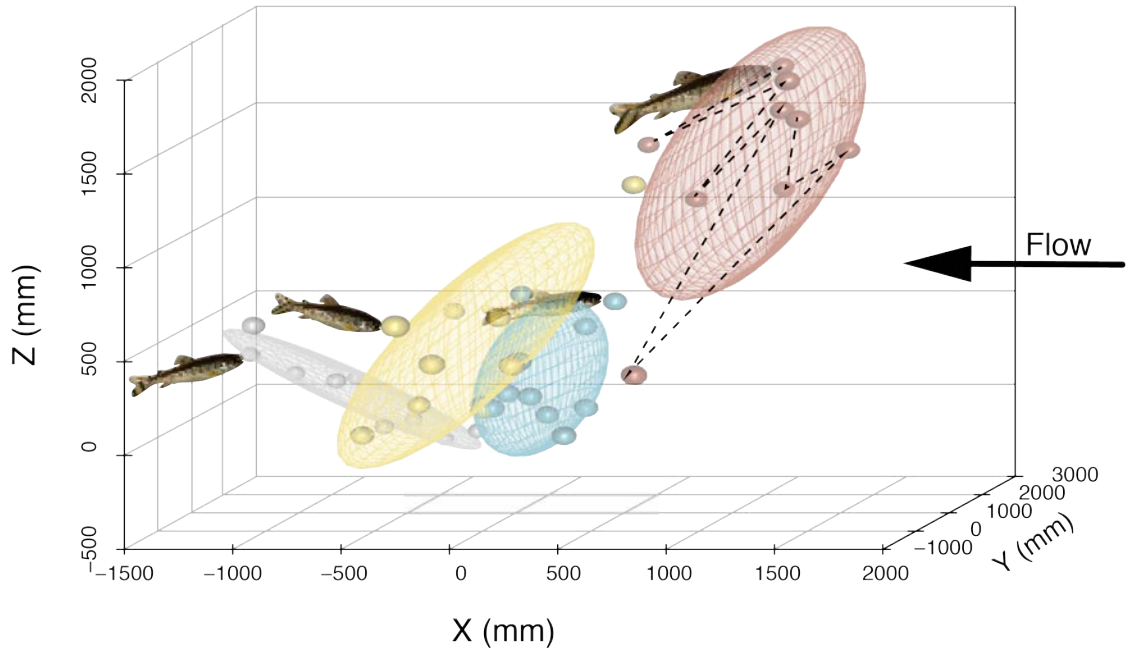


Figure 2. A schematic of 3D fish location data from VidSync for four *O. mykiss* in an Elder Creek pool during 30-seconds of a VidSync survey. For each X, Y, Z, location (shown as colored spheres) a fish ID, timestamp, and qualitative behavior are defined. An example of foraging movement path (30 seconds) for distance/time analysis is shown with the dashed line as the dominant fish (red) engages in a foray-return pattern of drift foraging. For illustrative purposes best-fit ellipses are fit over 3D occupied volumes using the R package "rgl".

Table 2. Definition of Foraging Behaviors Used in Video Scan Samples

Foraging Mode	**Definition**
Drift Foraging	Fish holds focal points in the water column and makes short forays to intercept drift, with only occasional attacks on benthic prey near their focal points (Nakano et al. 1999a).
Benthic Foraging	Fish primarily cruise over larger areas of stream-bed and capture benthic prey by making forceful attacks at the substrate (Nakano et al. 1999a).
Search Foraging	Fish undertake continuous undirected swimming, foraging was not associated with a focal point, and fish consumed drift, falling, or benthic prey (adapted from Neilsen 1992).
Behavioral Event	**Definition**
Surface Strike	A fish swims towards the surface and either attempts to or successfully bites an item floating on or just under the water surface (Suttle et al. 2004).
Attacks	A fish makes a rapid, aggressive darting approach toward another fish without making direct contact ("attacks" in Neilsen 1992).
Nips	A fish rapidly approached another fish and gives it a bite (Neilsen 1992).

Invertebrate Drift

Immediately after our video collection was completed, drift was sampled for 2 hours (+/- 10 minutes) between 5pm and 7pm, when diel peak drift of common invertebrates (especially *Baetids* and *Chironomids*) has been reported (Waters 1972, Statzner & Mogel 1985, Schreiber 1995 cited in Svendsen et al. 2004). Invertebrate drift was collected at each of the seven study pools during each of the five primary sampling events between May and August 2016. Thirty-five samples of drift were collected (one at each of seven sites on each of five sampling events) using a circular drift net (30 cm diameter mouth aperture, 500-µm mesh). The drift net was installed just below the water surface along the most upstream cross section at the head of the pool (Fig. 1); cross-stream position of the net was adjusted on each occasion to capture the region of highest velocity at each sampled streamflow. Drift samples were elutriated through 500-µm mesh and preserved in ethanol. In the laboratory, drift samples were sorted and invertebrates identified to family or genus (Merritt et al. 2008) under 10X magnification. Each invertebrate was measured to the nearest 0.5mm under a dissecting scope and biomass (mg dry mass) was estimated from published length to dry mass relationships (Benke et al. 1999; Sabo et al. 2002). Drift flux ($mg \cdot hr^{-1}$) was computed by summing the mass of drifting invertebrates captured in the drift net and dividing the total mass by the duration of the drift sample. Drift concentration ($mg \cdot m^{-3}$) was computed by dividing drift flux by the discharge through the drift net ($m^3 \cdot sec^{-1}$).

Net Rate of Energy Intake

We estimated seasonal trends in drift foraging profitability in the five video-study pools with a simplified drift foraging bioenergetic model (Caldwell et al. 2018). The energetics equations for the model are based on Rosenfeld and Taylor (2009) and Hayes et al. (2000). The model uses drift concentration, discharge rate through the foraging volume, fish size, and prey size to quantify gross energetic intake rate – a product of capture probability, drift concentration, and discharge through foraging volume; and energy expenditures based on swimming costs – a function of fish size and focal point velocity (Caldwell et al. 2018, Rosenfeld and Taylor 2009). Water temperature was incorporated into the swimming costs (following Rosenfeld and Taylor 2009); however, we assumed a constant energy assimilation efficiency of 0.6 (Tucker and Rasmussen 1999). The fish focal point velocity (measured at 0.6 depth) was measured at the thalweg station on cross section 1 at the head of each pool (Fig. 1). The net rate of energetic intake (NREI, joules $\cdot$ $second^{-1}$) is the net energy acquired by juvenile fish for growth (gross energy intake – swimming and metabolic costs). The model was run for each date and site combination in the summer of 2016, for a total of 25 model runs (5 sites × 5 dates).

Since our intent was simply to track the phenology of drift foraging profitability, rather than estimate size and habitat-specific NREI, we modeled NREI for a single 100mm drift forager (approximately the mean size of *O. mykiss* observed in the pool head patch over the summer) at a single foraging location in the channel thalweg at the head of the pool. We chose to model this location to represent the most profitable drift foraging position in the pool. We typically observed that this position was occupied by the dominant foraging fish, and numerous previous studies have shown the head of the pool to be preferred by drift foraging *O. mykiss* (Harvey et al. 2006, Smith and Li 1982 Van Leeuwen et al. 2011). While we could have modeled NREI at multiple downstream locations, this would introduce uncertainty because of the need to scale drift concentration down from our measurement location (the head of the pool) to downstream

and edge-water locations, accounting for upstream consumption and settling of drift. While these issues are surmountable with adequate sampling (e.g. following methods in Hayes et al. 2007), our intent was to determine how well drift foraging NREI predicted the timing of behavioral shift to search foraging – and thus we considered the head of the pool a conservative estimate of drift foraging profitability. In addition, Caldwell et al. (2018) noted that NREI for different size classes of drift foragers, and foraging locations downstream from the head of the pool locations, followed a similar seasonal pattern over the hydrograph recession, although the magnitudes differed.

Statistical Analysis

The drivers of *O. mykiss* foraging mode were evaluated using generalized linear mixed effects models in R version 3.5.1. Dependent variables were the relative proportions of foraging modes (drift, search and benthic) across five pools and five sampled dates. The movement of foraging fish followed a non-linear pattern across the study period, so we chose to analyze movement with descriptive statistics rather than mixed effects models. We separated the predictor variables (Table 1) *a priori* into four categories: pool hydraulics variables, drifting prey variables, combined variables (prey + hydraulics), and NREI (which integrates hydraulics and prey mechanistically). We organized the models this way to provide heuristic value – since frequently stream ecologists and managers cannot measure or compute all of these variables.

- **Pool Hydraulics:** Streamflow; Velocity; RCT depth;
- **Drifting Prey:** Drift Concentration$_{Numbers}$; Drift Concentration$_{Mass}$
- **Hydraulics + Prey:** Combinations of each non-colinear variable above.
- **NREI:** Computed Net Rate of Energy Intake for a 100mm drift foraging *O. mykiss*

Within each category, we built models by separating colinear terms (using an arbitrary threshold of 0.5 Pearson coefficient). This process resulted in twelve models for predicting each foraging mode – for a total of 36 models. We also controlled for fish density in the pool head patch and water temperature by including them as fixed effects in each model.

Because our dependent variables were proportions, we used generalized linear mixed effects models from the GLMM package in R (glmer command). A binomial distribution with logit link function was assigned, and weights were determined based on the total behavioral observations of each scan sample (Bolker et al. 2009). Our study used a crossed sampling design in which each pool was sampled on multiple dates, multiple pools were sampled on each date, and there was more than one observation per date-pool combination. Therefore, random effects were assigned for: “study site,” “date”, and “date nested within site” (Bolker et al. 2009).

All models were ranked using Akaike information criterion modified for small sample sizes (AICc), as well model weights which represent the relative likelihood of a model being selected (Burnham and Anderson 2004). In addition we evaluated the marginal r^2 (proportion of variance explained by the fixed effects) and conditional r^2 (proportion of variance explained by both fixed and random effects) values for a generalized linear mixed effects model, calculated using the r.squaredGLMM function in the MuMIN package in R (Nakagawa et al. 2014). The results of these statistical models were evaluated against established theory of salmonid foraging behavior to interpret our findings.

RESULTS

Seasonal Trends in Hydraulics, Food Flux, and Fish Abundance in Elder Creek Pools

The hydraulic variables (pool maximum depth, velocity, RCT depth, and pool volume) all declined with streamflow and date in all pools between May and August (Fig. 3A - 3D). Streamflow, RCT depth, and maximum velocity declined exponentially, but pool volume and maximum pool depth declined at a slow, near constant rate (Fig. 3A - 3D). The average flux of individual drifting invertebrates ($\#\cdot hr^{-1}$) was highest in May and June, while average concentration of individual drifting invertebrates ($\#\cdot m^{-3}$) peaked in early July at most sites (Fig. 3E and 3G). However, the flux and concentration of drifting invertebrate biomass ($mg\cdot hr^{-1}$ and $mg\cdot m^{-3}$, respectively) were highest in May by a wide margin (Fig. 3F and 3H). The average length of drifting invertebrates steadily declined from April to August, with the largest invertebrates drifting in May. Although 120 unique taxa of drifting invertebrates were identified, four taxa – *Simuliidae, Brachycentridae, Baetidae*, and *Chironomidae* -- made up 79% of the individual invertebrates in the drift. *Micrasem*a (a small cased *Brachycentrid* caddisfly) alone made of 38% of all individuals counted.

O. mykiss counted during snorkeling observations in Elder Creek pools increased by almost an order of magnitude between May (26 fish observed in seven pools), and August (218 fish observed in seven pools) (Fig. S3). Increases of pool head patch densities were more modest but still close to three-fold between May (mean density = 0.032 *individuals/*m^3; mean video counts= 4.6 *individuals* /scan) and July (mean density = 0.082 *individuals /*m^3; mean video counts 9.8 *individuals* /scan) (Fig. 4D and Fig. S4). Pool head patch density peaked in late July and declined slightly between late July and August (Fig. 4D). Pool head patch counts and pool-wide counts from the snorkel surveys followed similar trajectories, although counts increased faster over the summer in snorkel observations of the whole pool than in video scans of the pool head patch (Fig. S4*).*

Seasonal Patterns of O. mykiss Foraging Movement

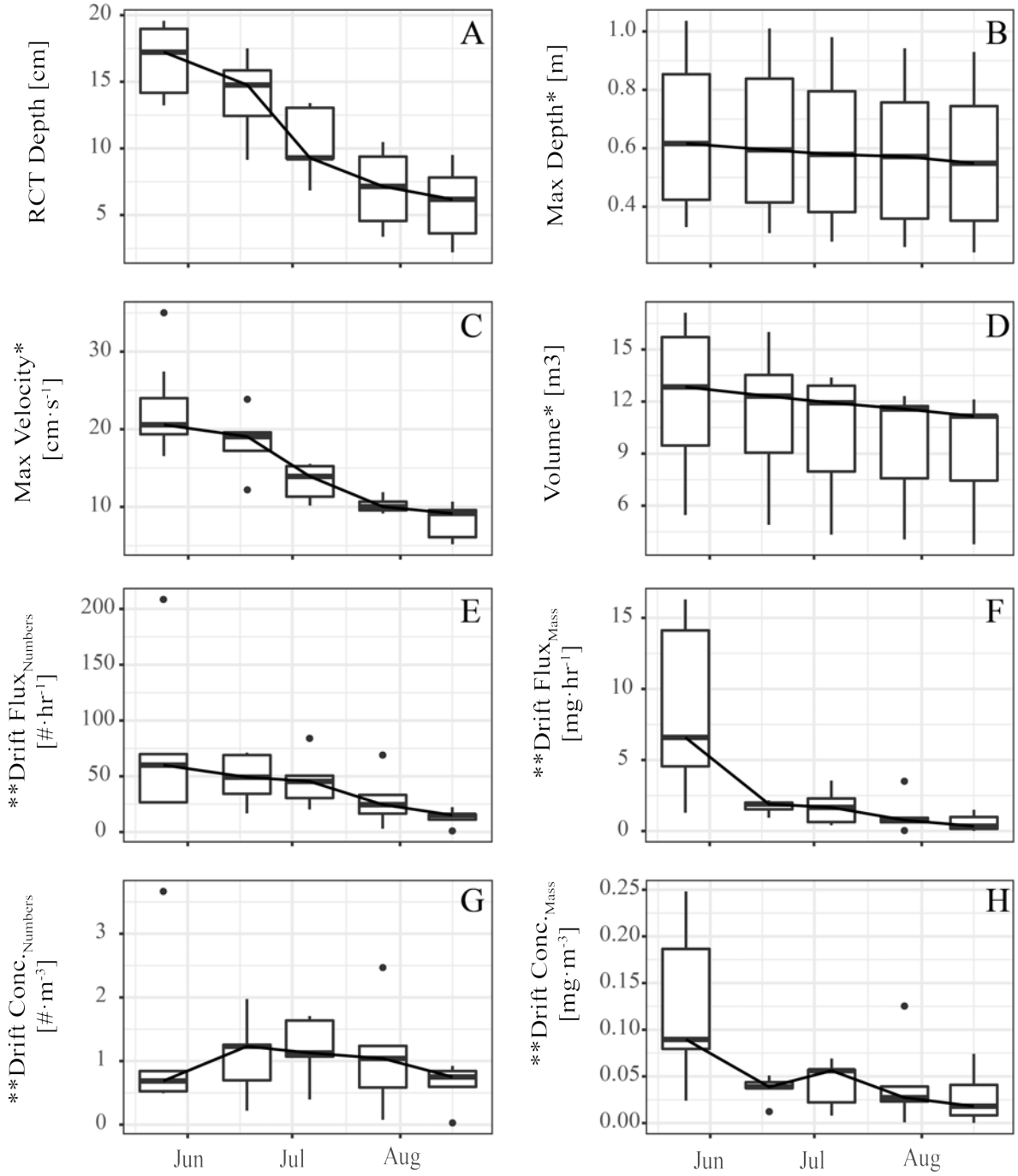
Fish movement per time was lowest in May (mean = 35 $mm\cdot s^{-1}$) and steadily increased to a peak in late July (mean = 81 $mm\cdot s^{-1}$), but later declined between late July and August (mean = 45 $mm\cdot s^{-1}$) (Fig. 4C). Peak movement was observed in early July in almost all sites. During the pre-peak movement period (May to early July), drift foraging was the most common behavior of *O. mykiss* in all study pools. During this period most observed fish foraged within small focal volumes, moving short distances (typically 3 to 6 cm) to capture prey. Between May and early July, movement increased with density in the pool head patch, and with decreasing pool velocity and RCT depth. Between early July and August, search foraging was the dominant behavior and fish tended to occupy larger volumes than they did in May. Movement per time, however, decreased by half between late July and August, as pools became low and still, and both hydraulic variables and drift concentration were near their late-summer nadir (Fig. 3G - 3H).

Seasonal Patterns of O. mykiss Foraging Mode in Elder Creek Pools

A total of 654 scan samples were completed over 25 videos from five pools, and 3,104 occurrences of a foraging behavior were identified (Table S1). Drift foraging (49%) and search foraging (39%) were most common, but attacks on the benthos accounted for another 12% (Fig. 4A - 4B). Strong seasonal trends were observed in the proportion of drift, search, and benthic

foraging *O. mykiss* in Elder Creek pools from May to August in 2016 (Fig. 4A – 4B, and Fig.5). In May, an average of 80% of *O. mykiss* in the pool head patch were drift foraging. Drift foraging decreased as search foraging increased, with the proportion of search foragers exceeding drift foragers by mid-July. By August, 63% of observed *O. mykiss* were search foraging and 13% of were benthic foraging (Fig. 5).

In reduced models, hydraulic indicator variables were the strongest predictors of the proportion of fish that were drift and search foragers. Maximum velocity and riffle crest depth, independent of invertebrate drift data, had significant, positive correlations to the proportion of drift foragers and negative correlations to the proportion of search foragers (Table 3A - B). In reduced (prey only) models, drift concentration alone was a weak predictor of foraging mode. However, the top statistical models for predicting the proportion of drift and search foragers combined both hydraulics and drift concentration and both variables had highly significant *p-values* (Table 3A - B). Benthic foraging was poorly predicted by any of the combined mixed effects models (Table 3C). In univariate regression, maximum water temperature and riffle crest depth were each significantly correlated to the proportion of benthic foragers. However, the failure of mixed effects models to predict benthic foraging suggests that we may not have measured the variables that best predict benthic foraging.



* Measured in the pool head patch

** Entering thalweg drift net at the head of the pool (located on XS1)

Figure 3. Seasonal trends (May and August 2016) in A. riffle crest depth, B. maximum pool depth, C. velocity, and D. volume; E, F; invertebrate drift flux and G, H. invertebrate drift concentration for Elder Creek pools. Median values for each date connected with straight lines.

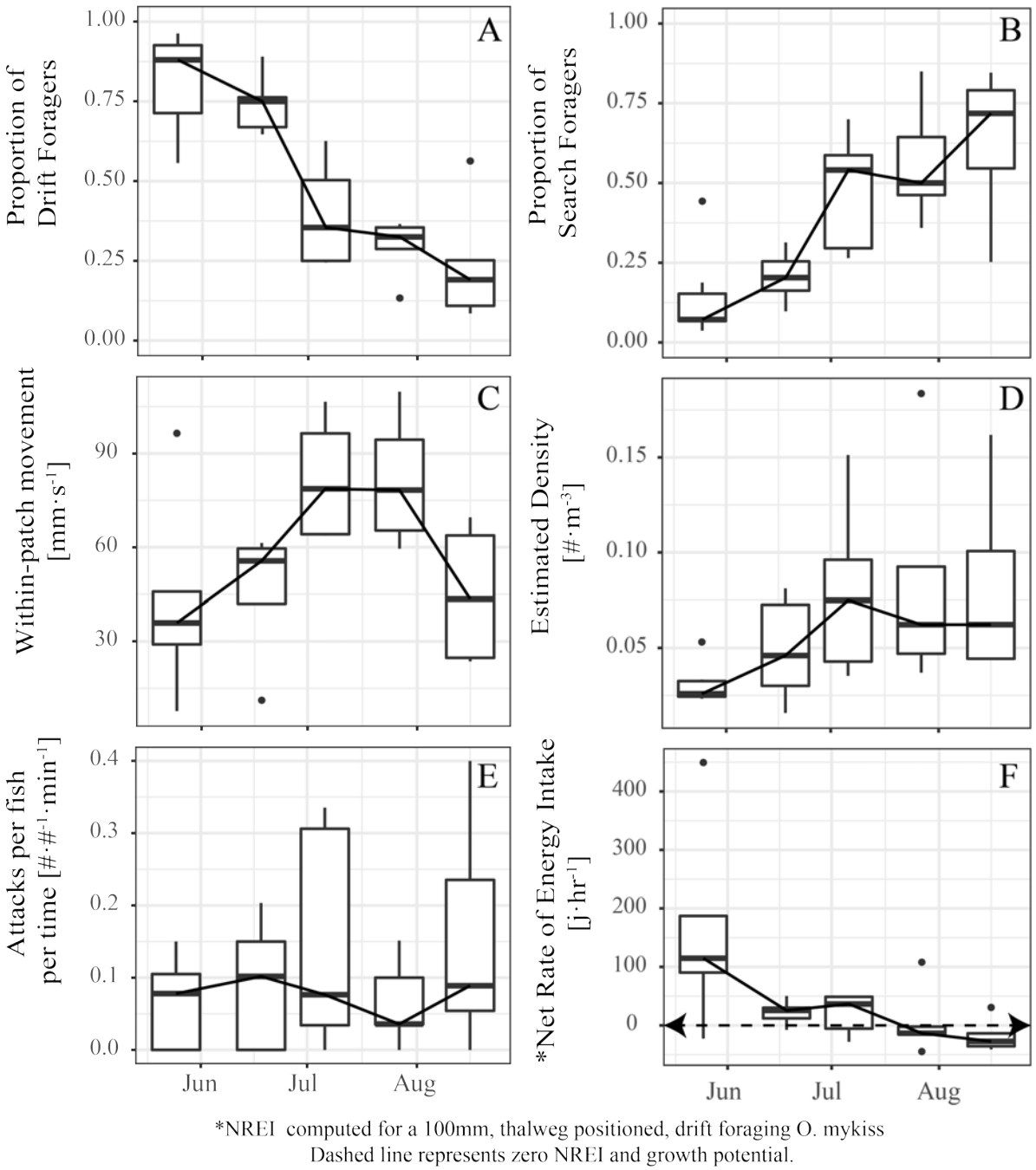


Figure 4. The seasonal phenology of (A, B) *O. mykiss* foraging mode, C. foraging movement, D. density and E. aggression in the pool head patch, as well as F, computed Net Rate of Energy Intake for a 100mm drift foraging *O. mykiss* in each pool. Median values for each date are connected with straight lines.

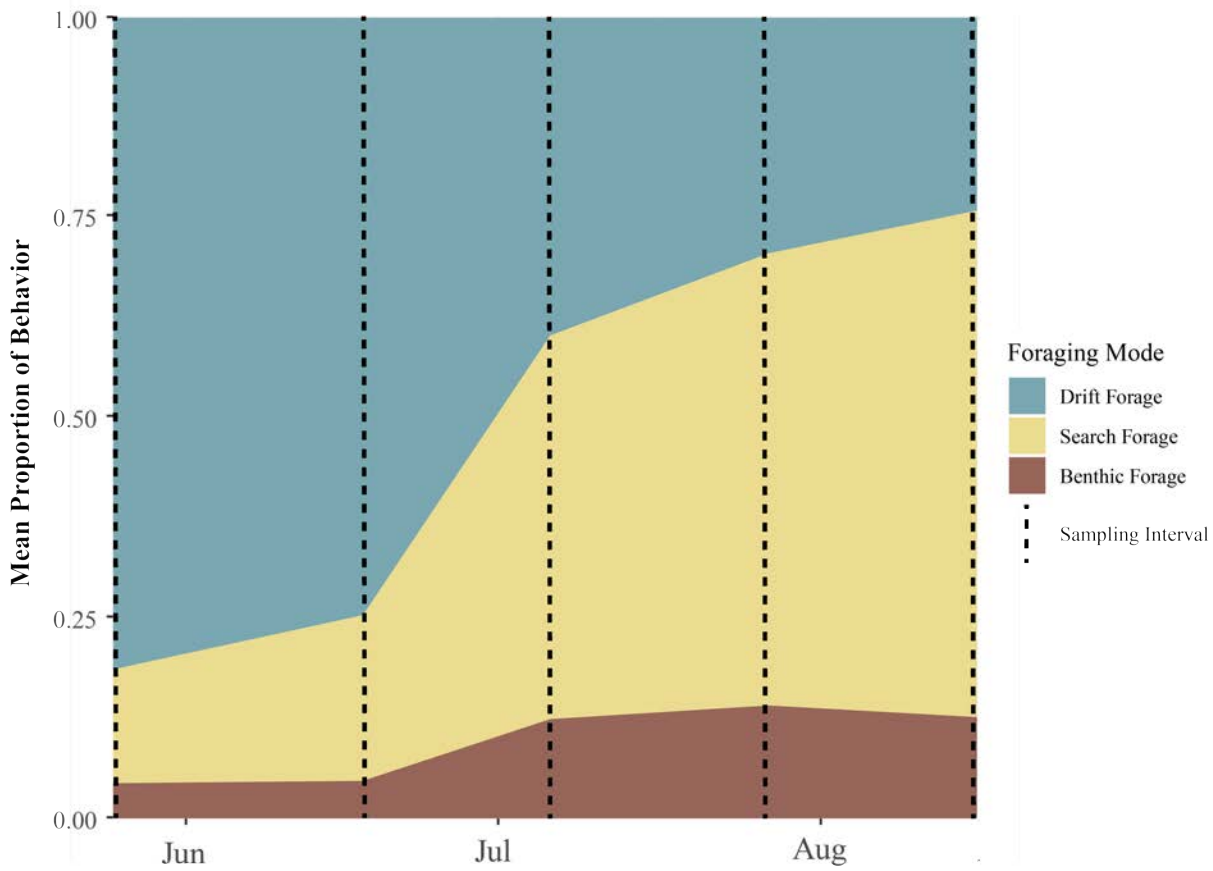


Figure 5. Seasonal patterns in the cumulative proportions of drift, search, and benthic foraging *O. mykiss*, aggregated across five study pools in Elder Creek.

Figure 6. The author's father (left) and brothers (center) congratulating the author (right) on his original research – overlooking the Mad River valley in Arcata, California.

Table 3. The results of generalized linear mixed effects models for predicting the proportion of (A) drift, (B) search, and (C) benthic foraging *O. mykiss* across five sites. The variables included in highest ranked models from each category (Hydraulics, Prey, Hydraulics + Prey, and NREI) are shown in the second column. The delta AICc, model weights, and adjusted r^2 values are shown on the right. The parameter coefficients, standard error and *p-values* of the single highest ranked model (in bold) are shown in the second row of each foraging mode category.

A. Proportion of Drift Foragers				
Ranked Models	Variables in Ranked Models	Delta AICc	Weights*	r^2 m/c**
Hydraulic + Prey	**RCT_i + Drift Concentration$_{Mass}$**	**0**	**0.95**	**0.30 / 0.34**
Hydraulic	RCT_i,	5.8	0.05	0.28 / 0.34
Prey	Drift Concentration$_{Numbers}$	15.5	0	0.25/.40
NREI	NREI (j×hr^{-1})	16.5	0	0.24/0.39
Parameter Coefficients in Hydraulic + Prey Model	*Parameter*	*Coefficient*	*Std. Error*	*Pr(>|z|)*
	RCT_i	8.24	1.34	*7.00E-10*
	Drift Concentration$_{Mass}$	10.82	3.16	*6.20E-04*
	Density in Pool Head Patch	-0.09	0.17	0.6
	Maximum Daily Temperature	0.04	0.12	0.75
B. Proportion of Search Foragers				
Ranked Models	Variables in Ranked Models	Delta AICc	Weights*	r^2 m/c**
Hydraulic + Prey	**RCT_i + Drift Concentration$_{Mass}$**	**0**	**0.91**	**0.27 / 0.34**
Hydraulic	Max Velocity	4.7	0.08	0.28 / 0.37
Prey	Drift Concentration$_{Mass}$	11.8	0	0.20/.37
NREI	NREI (j×hr^{-1})	13.7	0	0.18/0.36
Parameter Coefficients in Hydraulic + Prey Model	*Parameter*	*Coefficient*	*Std. Error*	*Pr(>|z|)*
	RCT_i	-8.98	1.76	*3.29E-07*
	Drift Concentration$_{Mass}$	-19.09	4.86	*8.55E-05*
	Density in Pool Head Patch	0.20	0.15	0.16
	Maximum Daily Temperature	-0.19	0.14	0.19
C. Proportion of Benthic Foragers				
Ranked Models	Variables in Ranked Models	Delta AICc	Weights*	r^2 m/c**
Hydraulic Model	Q	0	0.3	0.10 / 0.26
Prey Concentration	Drift Concentration$_{Numbers}$	0.12	0.28	0.10 / 0.25
Drift Foraging NREI	NREI (j×hr-1)	0.19	0.27	0.11/ 0.27
Hydraulic + Prey	Max Velocity + DriftConc$_{Num}$	1.48	0.14	0.11 / 0.27
Parameter Coefficients in Hydraulic Model	*Parameter*	*Coefficient*	*Std. Error*	*Pr(>|z|)*
	Q	-0.138	0.241	0.568
	Density in Pool Head Patch	0.125	0.215	0.561
	Maximum Daily Temperature	0.218	0.153	0.155

***** AIC weights represent the represent the relative likelihood of a model being selected and are computed as: Weights $= \exp(-1/2\Delta i(AIC))\sum Kk=1\exp(-1/2\Delta k(AIC))$

** This is the marginal r^2 and conditional r^2 following Nakagawa et al. (2014).

DISCUSSION

The Phenology and Drivers of Foraging Movement

Between May and late July, foraging movement increased as expected while drift concentration and velocity both declined; however, we observed a decrease in foraging movement between late July and August at the lowest velocities and drift concentrations (Fig. 4C). Salmonid movement in other studies has been shown to peak at intermediate velocities (Steingrímsson and Grant 2011). Piccolo et al. (2008) found that drift foraging *O. mykiss* could maintain ~95% of their prey capture success rate at velocities between 0.26 and 0.42 $m \cdot s^{-1}$, but capture success declined at lower and higher velocities. Declining prey encounter rates are a major driver of movement in foraging animals (Holling 1959) and explicitly for salmonids (Fausch and White 1981). However, habitat contraction and reduced cover can increase predator avoidance behavior, which also reduces the movement of foraging salmonids (Dill 1983, Brown 1988, Harvey and White 2017, Naman et al. 2019). We observed that surface turbulence, an important source of cover from avian and terrestrial predators, (Allouche and Gaudin 2001), extended far into pools in May, but was absent from most pools by August when fish were much more visible from above. We also noted that fish would take longer to return to normal foraging after we installed the cameras in August.

Our data (showing declining prey concentration and increasing movement rates between May and July) support the hypothesis that a decrease in drifting prey encounter rates increased foraging movement earlier in the recession. But our anecdotal observations suggest that predator avoidance and fear, relative to declining profitability of search foraging, may have reduced movement, as we observed between late July and August. Body size – which has been shown to be a strong determinant of behavior, was not measured in VidSync during this study (however it was in Chapter 3 of this dissertation) and thus not correlated to foraging mode. It is likely that body size effects both foraging choice and risk aversion (Brown 1988, Naman et al. 2019). Including size specific foraging data in future VidSync work and incorporating manipulative experiments, like those done by Harvey and White (2017), or Naman et al. (2019) would further resolve the tradeoffs between prey concentration, predation risk, and foraging movement in *O. mykiss* over the seasonal recession period.

The Phenology and Drivers of Foraging Mode

As expected, *O. mykiss* switched from drift to search foraging as decreasing water velocity and drifting prey increased fish movement during the hydrograph recession. Our mixed effects models suggest that hydraulic indicators (RCT depth and maximum pool velocity) were much stronger univariate predictors of drift and search foraging than the concentration of drifting invertebrate prey. Initially this observation was surprising, because foraging mode shifts have been induced rapidly by experimental reduction of invertebrate drift (Nislow et al. 1998, Fausch et al. 1997). However, while velocity and food concentration interact to mediate the *profitability* of foraging (Fausch 1984; Hughes and Dill 1990), the short-term behavioral response of foraging salmonids to the changes in the physical environment may not completely reflect profitability or fitness. Many fish have been shown to use a spatial sampling process guided by physical cues to develop reliable knowledge of habitat conditions (Johnson and Rice 2014). Gowan (2007) found that velocity was the primary cue for drift foraging in *O. clarki* and that dominant fish would not abandon their foraging mode even when food availability was artificially subsidized in a low risk

adjacent habitat. When velocity was manipulated; however, fish adapted their behavior and found prey subsidies. While drift concentration was a poor *univariate* predictor of foraging behavior in our study, it was a significant variable in the top ranked models to predict drift and search foraging (Table 3A and 3B). This suggests that 1) drift concentrating has an additive effect together with hydraulics on fish foraging response and 2) that prey (as expected) is an important factor in foraging decisions. However, we found no significant interaction terms between hydraulics and prey (across the entire summer) and we suspect that the way food and hydraulics *together* influence behavior may vary as other factors like predation risk and intraspecific competition change seasonally (Harvey and White 2017).

Benthic foraging was less frequently observed then search foraging – peaking in late July when it accounted for just over 13% of all foraging observations. Across all pools, we observed over 300 direct attacks on benthic prey, mostly by small young of year *O. mykiss*. Naman et al. (2018) working in British Columbia and Neilson (1992) working in Washington State also observed very few attacks on the benthos by juvenile salmonids. Merz (2002), working near the southern end of the range of *O. mykiss* observed juveniles scraping the substrate with their sides and mouths, dislodging algae, which was either ingested by them or other trout close by. We observed a similar behavior in Elder Creek, where juvenile O. mykiss would forcefully roll and slap the benthos with their side, before immediately turning to consume any dislodged prey. The increased counts of benthic foraging we observed in late summer may be associated with both the seasonal decline of hydraulically-mediated drift *and* the increasing secondary production on the stream benthos during the streamflow recession in Mediterranean streams. Although we did not sample benthic invertebrate standing crop or renewal rates in pools during this study, we did observe that benthic standing crops in Elder Creek pools peaked a month or more after peak drift flux in 2017 and 2018 (see Chapter 3 Fig. 6C). Waxing abundance of benthic prey, particularly in late summer when drifting prey are waning, may underlie the observed increase in benthic foraging in July (Fig. S4).

Foraging Mode and NREI

The statistical associations between hydraulics and prey in top ranked mixed effects models (for drift and search foraging) suggests that an energetics approach which mechanistically integrates these variables, would be a better predictor of foraging mode shifts. However the energetics model underperformed in this regard. There are several possible explanations for the weaker response of behavior to NREI, and they suggest some useful hypotheses and assumptions that need to be modified about fish behavior and prey fluxes in streams with seasonally low flow and invertebrate drift.

The simplest explanation is that NREI may be a poor predictor of realized energy intake (Hughes et al. 2003), due to possible differences between prey capture and gross energy intake parameters used in the NREI model and those experienced by fish in Elder Creek. Drift sampling with passive nets may also significantly under sample the concentration of small drifting taxa (Williams 1985) which would affect realized gross energy intake. Given the preponderance of 1mm (and smaller) *Brachycentridae* in our drift samples, this explanation is plausible. Our NREI model also assumed no variation in prey assimilation efficiency with temperature which may have biased our results and it is possible that incorporating this interaction could improve the NREI – behavior linkage. However, summer temperatures in Elder Creek were generally

between 10 and 19 C and average daily temperature remained below 16.5 C all year. Within this range assimilation efficiency is expected to change less then 10% (Brockson and Bugge 1972).

Another possible explanation is the weak correlation between hydraulics and drift concentration – and the possible primacy of hydraulics as a cue for *O. mykiss* foraging behavior (Gowan 2007). The streamflow recession is not strictly coupled to photoperiod or terrestrial carbon fluxes that drive secondary production of invertebrates. Thus there may be significant interannual and perhaps intra-annual noise in the relationship between hydraulic cues that fish respond to and the food production they are ultimately seeking. While streamflow tends to begin recessing in early spring when day-length begins to increase – understanding more precisely the interactions and seasonal offsets of these two drivers (hydraulics and secondary production) is an important consideration for future bioenergetic and food web modeling efforts that span seasonal scales.

A third explanation for why our NREI model had relatively poor association with foraging mode is that the foraging cues, provided by the complex 3-D hydraulic environment that fish experience, were not reflected in the single focal point velocity used in the NREI model. RCT depth and pool max velocity, serving as hydraulic indicators (rather than important *in situ* measurements), may have better reflected the shifting *hydraulic state* of the pool (Pasternack et al. 2008, Chiu and Tung 2002) than NREI.

Finally, a fourth possible explanation that our study did not evaluate is the role that invertebrates from non-drifting sources (e.g. benthos and infall of aquatic and terrestrial prey) played in the energetic tradeoffs between drift, search, and benthic foraging. The increase of benthic and search foraging in late summer may not only reflect declining drift profitability but potentially increasing availability of benthic standing crop and infall of aquatic and terrestrial prey (see Chapter 3 Fig. 6). Future efforts to incorporate benthic foraging into NREI models (as Railsback and Harvey (2014) and Caldwell et al. (2018) did with search foraging) would benefit energetics and behavior modeling in streams with seasonally low flow and drift.

CONCLUSION

The seasonal streamflow recession, common in Mediterranean coastal streams, exerts strong effects on stream hydraulics and invertebrate prey concentration, which in turn affect the foraging behavior of lotic predators such as *O. mykiss.* In Elder Creek, we observed strong seasonal changes in foraging movement and foraging mode of *O. mykiss* between May and August. Foraging movement increased between May and July as invertebrate drift waned, but movement declined in August, perhaps in response to increased predator risk as pools shrank. Our study reports significantly more search and benthic foraging of juvenile *O. mykiss* then commonly described for this species. Statistical models indicated that *O. mykiss* foraging mode was most strongly associated with pool maximum velocity and riffle crest depth; and drift concentration was a poor univariate predictor of foraging mode. However, the concentration of invertebrate drift had large significant additive effect to pool hydraulics in our top-ranked statistical models. In addition, we expected a drift foraging NREI model to be a better predictor of foraging mode then simple hydraulic indicators, but it was not. Behavioral theory strongly suggests that prey availability and capture success rates (which are elements of the NREI model) should drive consumer movement patterns and foraging mode. Therefore, we pose several post-

hoc hypotheses, based on our data, as to why drift foraging NREI was a poor predictor of foraging mode: (1) the weak correlation between hydraulics and drift concentration and the possible primacy of hydraulics as a sampling cue for *O. mykiss;* (2) the complex 3-dimensional hydraulics of the pool that likely modulated prey capture success and energy expenditure in ways that are not well described by the NREI model; and, (3) seasonal changes in the importance of other prey sources (besides upstream drift) including infall of terrestrial and aquatic aerial prey, or increasingly available benthic prey. Taken together, the interacting physical and biotic gradients across the seasonal streamflow recession evince more diversity of juvenile *O. mykiss* foraging behavior than previously reported for this species.

Acknowledgments
This study was co-authored by Mary Power, Jason Neuswanger, Shelley Pneh, and Timothy Caldwell. We thank Ted Grantham and Stephanie Carlson for their reviews and comments, which improved this study. We thank Peter Steel, the reserve manager at the UC Angelo Coast Range Reserve, for logistical support of this research. We are deeply grateful to Terrance Wang for his tireless assistance with field work and Vidsync analysis, as well as Garbo Gan who spent long hours sorting, counting and identify stream invertebrates. This work was funded in part by a National Science Foundation CZO EAR-1331940, Eel River Critical Zone Observatory. GJ Rossi was also supported during this study by research funds from California Trout and the UC Natural Reserve System Mildred E. Mathias Award.

Literature Cited
Allouche, S., and P. Gaudin. 2001. Effects of avian predation threat, water flow and cover on growth and habitat use by chub, Leuciscus cephalus, in an experimental stream. Oikos 94:481–492.

Altmann, J. 1974. Observational Study of Behavior: Sampling Methods. Behaviour 49(3/4): 227–267.

Benke, A.C., Huryn, A.D., Smock, L.A., and Wallace, J.B. 1999. Length-Mass Relationships for Freshwater Macroinvertebrates in North America with Particular Reference to the Southeastern United States. Journal of the North American Benthological Society 18(3): 308–343. doi:10.2307/1468447.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., and White, J.-S.S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24(3): 127–135. doi:10.1016/j.tree.2008.10.008.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22:37–47.

Burnham, K.P., and Anderson, D.R. (Editors). 2004. Model Selection and Multimodel Inference. Springer New York, New York, NY. doi:10.1007/b97636.

Caldwell, T.J., Rossi, G.J., Henery, R.E., and Chandra, S. 2018. Decreased streamflow impacts fish movement and energetics through reductions to invertebrate drift body size and abundance: Reduced streamflow changes drift, fish behavior and fish energetics. River Research and Applications 34(8): 965–976. doi:10.1002/rra.3340.

Clifford, N.J., Soar, P.J., Emery, J.C., Gurnell, A.M., and Petts, G.E. 2002. Sustaining water-related ecosystems— the role of in-stream bedform design in river channel rehabilitation. Fourth International Conference on FRIEND. IAHS Publication, 274, 407–416.

Dill, L.M. 1983. Adaptive Flexibility in the Foraging Behavior of Fishes. Canadian Journal of Fisheries and Aquatic Sciences 40(4): 398–408. doi:10.1139/f83-058.

Dralle, D.N., Karst, N.J., Charalampous, K., Veenstra, A., and Thompson, S.E. 2017. Event-scale power law recession analysis: quantifying methodological uncertainty. Hydrology and Earth System Sciences 21(1): 65–81. doi:10.5194/hess-21-65-2017.

Emery, J.C., Gurnell, A.M., Clifford, N.J., Petts, G.E., Morrissey, I.P., and Soar, P.J. 2003. Classifying the hydraulic performance of riffle-pool bedforms for habitat assessment and river rehabilitation design. River Research and Applications 19(5–6): 533–549. doi:10.1002/rra.744.

Fausch, K. D., and R. J. White. 1981. Competition Between Brook Trout (Salvelinus fontinalis) and Brown Trout (Salmo trutta) for Positions in a Michigan Stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220–1227.

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. doi:10.1139/z84-067.

Fausch, K.D., Nakano, S., and Khano, S. 1997. Experimentally induced foraging mode shift by sympatric chairs in a Japanese mountain stream. Behavioral Ecology 8(4): 414-420.

Gowan, C. 2007. Short-term cues used by foraging trout in a California stream. Environmental Biology of Fishes 78:317–331.

Harvey, B.C., and Railsback, S.F. 2014. Feeding modes in stream salmonid population models: is drift feeding the whole story? Environmental Biology of Fishes 97(5): 615–625. doi:10.1007/s10641-013-0186-7.

Harvey, B. C., and J. L. White. 2017. Axes of fear for stream fish: water depth and distance to cover. Environmental Biology of Fishes 100:565–573.

Hayes, J.W., Goodwin, E., Shearer, K.A., Hay, J., and Kelly, L. 2016. Can Weighted Useable Area Predict Flow Requirements of Drift-Feeding Salmonids? Comparison with a Net Rate of Energy Intake Model Incorporating Drift–Flow Processes. Transactions of the American Fisheries Society 145(3): 589–609. doi:10.1080/00028487.2015.1121923.

Hayes, J.W., Stark, J.D., and Shearer, K.A. 2000. Development and Test of a Whole-Lifetime Foraging and Bioenergetics Growth Model for Drift-Feeding Brown Trout. Transactions of the American Fisheries Society 129(2): 315–332. doi:10.1577/1548-8659(2000)129<0315:DATOAW>2.0.CO;2.

Hayes, S.A., Bond, M.H., Hanson, C.V., Freund, E.V., Smith, J.J., Anderson, E.C., Ammann, A.J., and MacFarlane, R.B. 2008. Steelhead Growth in a Small Central California Watershed: Upstream and Estuarine Rearing Patterns. Transactions of the American Fisheries Society 137(1): 114–128. doi:10.1577/T07-043.1.

Hill, J., and Grossman, G.D. 1993. An Energetic Model of Microhabitat Use for Rainbow Trout and Rosyside Dace. Ecology 74(3): 685–698. doi:10.2307/1940796.

Holling, C. S. 1959. The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly. The Canadian Entomologist 91:293–320.

Hughes, N.F., and Dill, L.M. 1990. Position Choice by Drift-Feeding Salmonids: Model and Test for Arctic Grayling (Thymallus arcticus) in Subarctic Mountain Streams, Interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47(10): 2039–2048. doi:10.1139/f90-228.

Hughes, N. F., J. W. Hayes, K. A. Shearer, and R. G. Young. 2003. Testing a model of drift-feeding using three-dimensional videography of wild brown trout, *Salmo trutta* , in a New Zealand river. Canadian Journal of Fisheries and Aquatic Sciences 60:1462–1476.

Jenkins, T. M. 1969. Social Structure, Position Choice and Micro-distribution of Two Trout Species (Salmo trutta and Salmo gairdneri) Resident in Mountain Streams. Animal Behaviour Monographs 2:55–123.

Larranaga, N., Valdimarsson, S.K., Linnansaari, T., and Steingrímsson, S.Ó. 2018. Diel activity and foraging mode of juvenile Arctic charr in fluctuating water flow. River Research and Applications 34(4): 348–356. doi:10.1002/rra.3256.

Ligon, F.K., Nakamoto, R.J., Harvey, B.C., and Baker, P.F. 2016. Use of streambed substrate as refuge by steelhead or rainbow trout Oncorhynchus mykiss during simulated freshets: use of substrate by o. mykiss during freshets. Journal of Fish Biology 88(4): 1475–1485. doi:10.1111/jfb.12925.

Lisle, T.E. 1987. Using "residual depths" to monitor pool depths independently of discharge. U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. doi:10.2737/PSW-RN-394.

Lovill, S.M., Hahm, W.J., and Dietrich, W.E. 2018. Drainage from the Critical Zone: Lithologic Controls on the Persistence and Spatial Extent of Wetted Channels during the Summer Dry Season. Water Resources Research 54(8): 5702–5726. doi:10.1029/2017WR021903.

Merritt, R.W., Cummins, K.W. and Berg, M.B., Eds. 2008. Aquatic Insects of North America. 4th Edition, Kendall/Hunt, Dubuque.

Mierau, D.W., Trush, W.J., Rossi, G.J., Carah, J.K., Clifford, M.O., and Howard, J.K. 2018. Managing diversions in unregulated streams using a modified percent-of-flow approach. Freshwater Biology 63(8): 752–768. doi:10.1111/fwb.12985.

Mittelbach, G. G., N. G. Ballew, and M. K. Kjelvik. 2014. Fish behavioral types and their ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 71:927–944.

Nakagawa, S., and Schielzeth, H. 2013. A general and simple method for obtaining R 2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4(2): 133–142. doi:10.1111/j.2041-210x.2012.00261.x.

Nakano, S., Fausch, K.D., and Kitano, S. 1999a. Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. Journal of Animal Ecology 68(6): 1079–1092. doi:10.1046/j.1365-2656.1999.00355.x.

Nakano, S., Kawaguchi, Y., Taniguchi, Y., Miyasaka, H., Shibata, Y., Urabe, H., and Kuhara, N. 1999b. Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in northern Japan: Terrestrial invertebrate feeding by fish. Ecological Research 14(4): 351–360. doi:10.1046/j.1440-1703.1999.00315.x.

Naman, S.M., Rosenfeld, J.S., Third, L.C., and Richardson, J.S. 2017. Habitat-specific production of aquatic and terrestrial invertebrate drift in small forest streams: implications for drift-feeding fish. Canadian Journal of Fisheries and Aquatic Sciences 74(8): 1208–1217. doi:10.1139/cjfas-2016-0406.

Naman, S. M., R. Ueda, and T. Sato. 2019. Predation risk and resource abundance mediate foraging behaviour and intraspecific resource partitioning among consumers in dominance hierarchies. Oikos 128:1005–1014.

Nislow, K.H., Folt, C., and Seandel, M. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. 55: 12.

Pasternack, G.B., Bounrisavong, M.K., and Parikh, K.K. 2008. Backwater control on riffle–pool hydraulics, fish habitat quality, and sediment transport regime in gravel-bed rivers. Journal of Hydrology 357(1–2): 125–139. doi:10.1016/j.jhydrol.2008.05.014.

Piccolo, J.J., Hughes, N.F., and Bryant, M.D. 2008. Development of net energy intake models for drift-feeding juvenile coho salmon and steelhead. Environmental Biology of Fishes 83(3): 259–267. doi:10.1007/s10641-008-9330-1.

Puckett, K.J., and Dill, L.M. 1985. he Energetics of Feeding Territoriality in Juvenile Coho Salmon (Oncorhynchus Kisutch). Behaviour. Available from https://doi.org/10.1163/156853985X00398.

Rempe, D.M., and Dietrich, W.E. 2018. Direct observations of rock moisture, a hidden component of the hydrologic cycle. Proceedings of the National Academy of Sciences 115(11): 2664–2669. doi:10.1073/pnas.1800141115.

Rosenfeld, J.S., Bouwes, N., Wall, C.E., and Naman, S.M. 2014. Successes, failures, and opportunities in the practical application of drift-foraging models. Environmental Biology of Fishes 97(5): 551–574. doi:10.1007/s10641-013-0195-6.

Rosenfeld, J.S., and Raeburn, E. 2009. Effects of habitat and internal prey subsidies on juvenile coho salmon growth: implications for stream productive capacity. Ecology of Freshwater Fish 18(4): 572–584. doi:10.1111/j.1600-0633.2009.00372.x.

Rosenfeld, J.S., and Taylor, J. 2009. Prey abundance, channel structure and the allometry of growth rate potential for juvenile trout. Fisheries Management and Ecology 16(3): 202–218. doi:10.1111/j.1365-2400.2009.00656.x.

Sabo, J.L., Bastow, J.L., and Power, M.E. 2002. Length–mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society 21(2): 336–343. doi:10.2307/1468420.

Smith, J.J., and Li, H.W. 1982. Energetic factors influencing foraging tactics of juvenile steelhead trout, Salmo gairdneri. Pages 173-180 in (ed.) D. L. G. Noakes, D. G. Lindquist, G. S. Helfman, and J. A. Ward. Predators and Prey in Fishes. The Hague, Netherlands. ISBN 90 6193 922 8.

Steingrímsson, S.Ó., and Grant, J.W.A. 2011. Shape of Single and Multiple Central-Place Territories in a Stream-Dwelling Fish: Territory Shape in Stream Fish. Ethology 117(12): 1170–1177. doi:10.1111/j.1439-0310.2011.01976.x.

Suttle, K.B., Power, M.E., Levine, J.M., and McNeely, C. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. Ecological Applications 14(4): 969–974. doi:10.1890/03-5190.

Svendsen, C.R., Quinn, T., and Kolbe, D. 2004. Review of Macroinvertebrate Drift. Wildlife Research Program, Environmental and Safety Division, Seattle City Light: 92.

Taube, Clarence.M. 2000. Instructions for winter lake mapping. Chapter 12 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.Taube, Clarence M. 2000. : 6.

Tippets, W.E., and Moyle, P.B. 1978. Epibenthic Feeding by Rainbow Trout (*Salmo gairdneri*) in the McCloud River, California. The Journal of Animal Ecology 47(2): 549. doi:10.2307/3800.

Tucker, S., and Rasmussen, J.B. 1999. Using ^{137}Cs to measure and compare bioenergetic budgets of juvenile Atlantic salmon (Salmo salar) and brook trout (*Salvelinus*

fontinalis) in the field. Canadian Journal of Fisheries and Aquatic Sciences 56(5): 875–887. doi:10.1139/f99-025.

Van Leeuwen, T.E., Rosenfeld, J.S., and Richards, J.G. 2011. Adaptive trade-offs in juvenile salmonid metabolism associated with habitat partitioning between coho salmon and steelhead trout in coastal streams: Adaptive trade-offs of juvenile salmonids. Journal of Animal Ecology 80(5): 1012–1023. doi:10.1111/j.1365-2656.2011.01841.x.

Yarnell, S.M., Petts, G.E., Schmidt, J.C., Whipple, A.A., Beller, E.E., Dahm, C.N., Goodwin, P., and Viers, J.H. 2015. Functional Flows in Modified Riverscapes: Hydrographs, Habitats and Opportunities. BioScience 65(10): 963–972. doi:10.1093

SUPPLEMENTAL MATERIALS

Table S1. Frequency of observed fish behaviors by sampling period.

Sample Period	Counts of Observations				Proportion of Observations			
	Drift	**Search**	**Benthic**	**Shelter**	**Drift**	**Search**	**Benthic**	**Shelter**
May	346	57	6	23	80%	14%	1%	5%
June	525	126	47	4	75%	18%	7%	>1%
early-July	277	284	83	4	43%	44%	13%	>1%
late July	218	357	115	9	31%	51%	16%	2%
August	143	392	82	6	23%	63%	13%	1%
Total	**1509**	**1216**	**333**	**46**	**49%**	**39%**	**11%**	**1%**

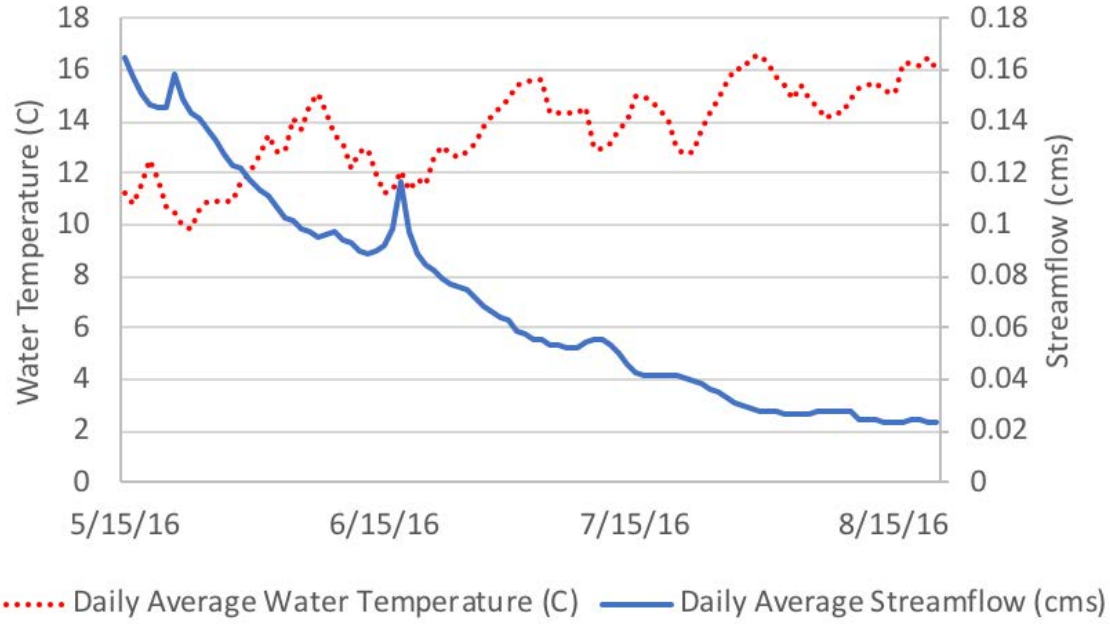


Figure S1. Daily average streamflow and water temperature measured at USGS gaging station 11475560 in Elder Creek.

Figure S2. Image showing the typical camera placement and approximate field of view for video analysis of fish behavior in one of the Elder Creek riffle:pool units used in this study. The stereo-camera mount is seen in white PVC on the right, and attached to a stationary video monitoring rebar pin which was left in place for the duration of the study.

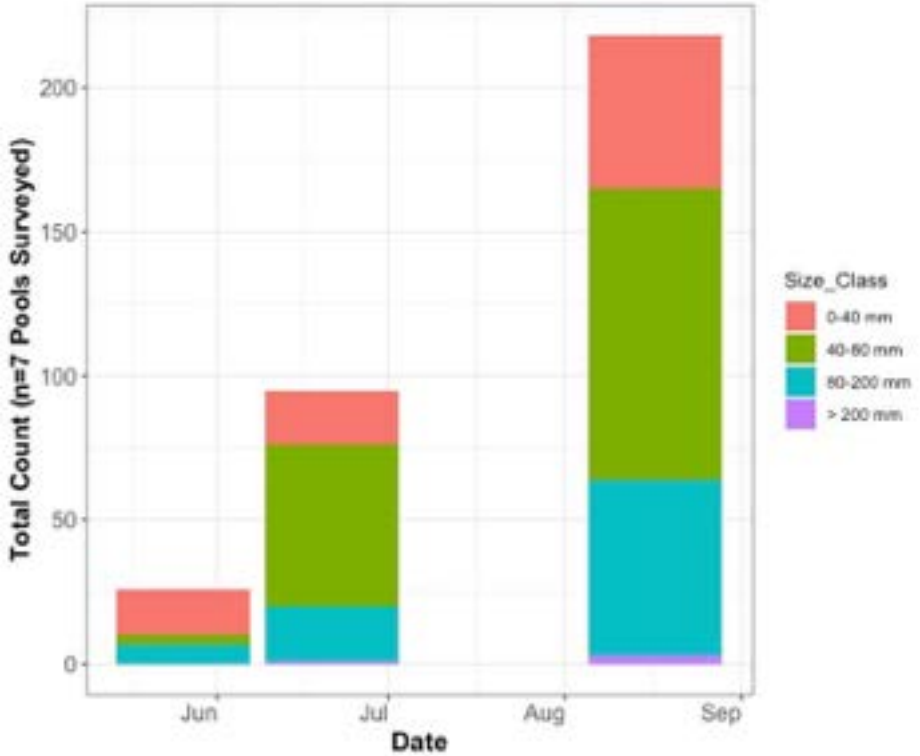


Figure S3. Total counts of O. mykiss from seven Elder Creek pools snorkeled on three dates during the summer of 2016. Counts are apportioned into four size classes which are intended to reflect age: 0-40 mm = fry, 40-80mm = older young of year, 80-200 mm = 1-3 year old juveniles, >200 mm = adult (residents). No anadromous smolts were observed during our study.

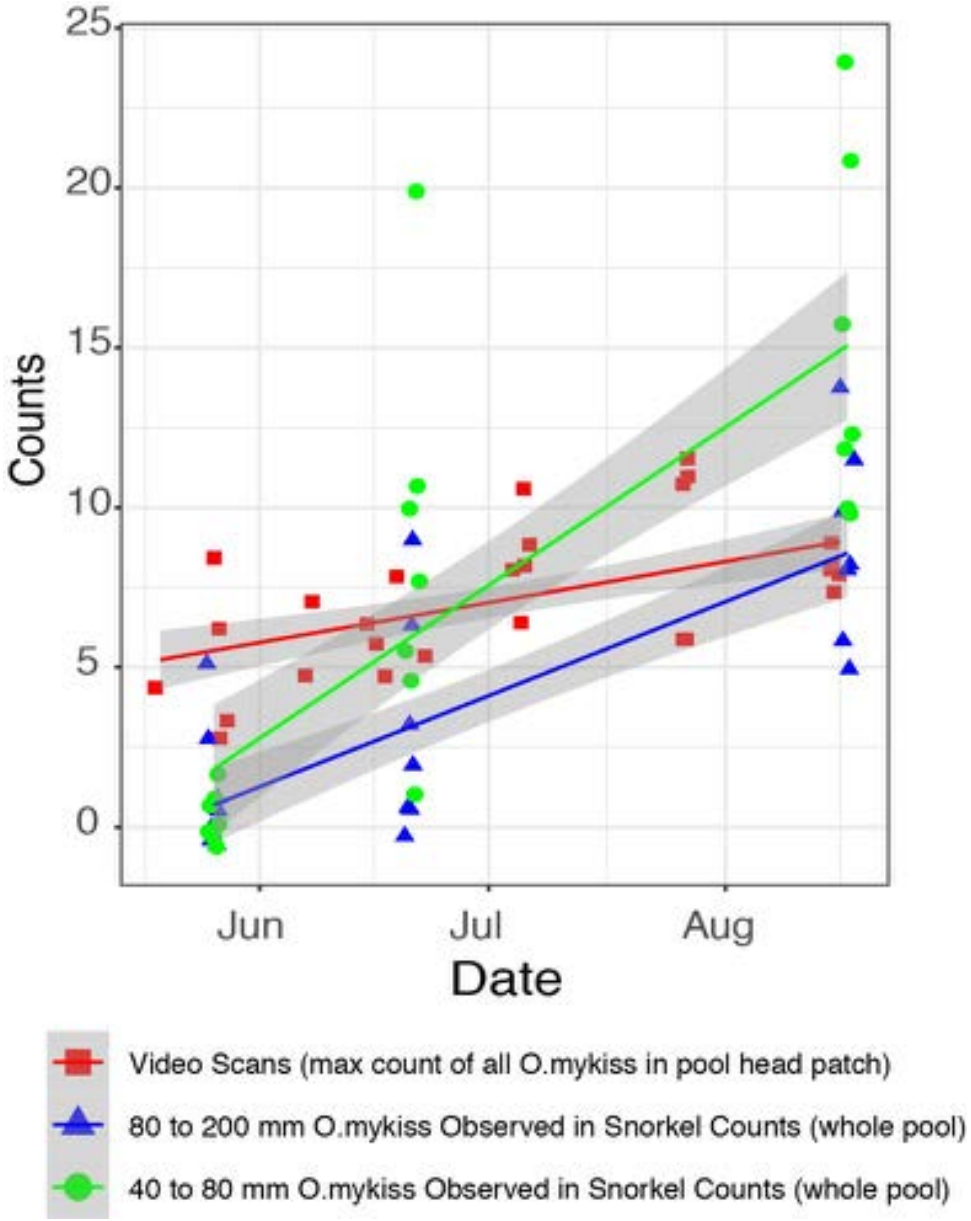


Figure S4. Total counts of YOY and 1+ steelhead from snorkel surveys, compared to counts from video scans in the pool head patch..

Chapter 1 – 2 Transition

Observations from Chapter 1 led directly to hypotheses that I tested in Chapter 2. For example, the sensitivity of *O. mykiss* foraging mode to hydraulic variables that I observed in Chapter 1, led me to consider how foraging behavior and profitability would respond to human manipulation of flow and stream hydraulics. In addition, in Elder Creek (Chapter 1) I observed strong declines in drifting prey in early summer; however in later summer drift concentration declined at nearly stable rate. I knew from past experience that Elder Creek represented a more stable, and perennial class of Mediterranean stream then was common on the California coast, and I wondered how these trends in behavior and invertebrate flux would translate to a drier, intermittent stream.

The impacts from anthropogenic streamflow diversion on salmon physical habitat have been well documented in the literature. However, the ways that flow alteration affect salmon behavior and food flux have been less studied, particularly in the type of small, unregulated, Mediterranean streams I focus on in this dissertation. For several year prior to my dissertation (starting around 2014), flow augmentation from off channel ponds has been implemented opportunistically, as a restoration strategy for salmonids in intermittent tributaries of the Russian River basin, (Deitch and Dolman 2017, Ruiz et al. 2019); however the ecological effects of flow enhancement had yet to be evaluated through peer-reviewed scientific studies. Through a collaboration between California Sea Grant in Sonoma County, Gallo Vineyards, Trout Unlimited, and UC Berkeley, I was able to study the effects of flow alteration on salmonid behavior, invertebrate dynamics, and stream habitat in Porter Creek (tributary to the Russian River) using the E&J Gallo vineyard flow enhancement infrastructure. Those studies (from 2017 to 2019) led directly to the research, data, and analysis presented in Chapter 2.

.

CHAPTER 2

Flow augmentation influences salmonid foraging behavior, invertebrates, water quality and habitat in a California stream

ABSTRACT

Efforts to restore and protect streamflow in salmon and trout-bearing streams have been underway for decades in the Western United States. The ecological impacts from anthropogenic streamflow impairment are well documented, but the effects of flow enhancement in small, unregulated streams has been difficult to quantify. This is primarily due to the challenge of measuring (and attributing) flow responses to management actions, especially in decentralized water management systems that are affected by many points of flow alteration. A related challenge is measuring habitat and biotic responses over incremental changes in flow, while controlling for other environmental factors. Here we conducted a flow augmentation experiment by releasing water from a small storage pond to elevate dry-season flow in an intermittent, salmon-bearing stream. We directly measured the responses of seventeen physical and ecological variables to controlled changes in streamflow, using a "*before-after-control-impact*" (BACI) study design. Following augmentation, we documented significant increases in wetted habitat connectivity, riffle depth and velocity, dissolved oxygen, invertebrate drift and invertebrate standing crop. In contrast, effects on water temperature and pool volume were negligible. Using 3-D videogrammetry to monitor fish foraging behavior and movement, we found that juvenile salmonids, and one non-salmonid, shifted from search foraging to drift foraging when flows were elevated. Counts of foraging salmonids doubled after augmentation, and fish sustained their movement (relative to declining movement in a control reach), although occupied foraging volumes did not change significantly. Inter-annual wetted habitat surveys suggests that the effects of flow augmentation varied in relation to ambient streamflow and channel characteristics. While the ecological effects of flow enhancement remain difficult to generalize, these experiments provide empirical support that dry season flow augmentation in small, unregulated streams can improve habitat conditions and foraging profitability for juvenile salmonids.

INTRODUCTION

Small streams make up 70% - 80% of river networks in the United States and are critical habitat for rearing salmon and trout (Wohl 2017, Wigington et al. 2006, Boughton et al. 2009, Hwan and Carlson 2016). In the western United States, small and intermittent streams exhibit patterns of seasonal growth opportunity for rearing Pacific salmon (*Oncorhynchus)* that are distinct from larger, more perennial systems and can be highly productive (Wigington et al. 2006, Ebersole et al. 2006, Boughton et al. 2009). However, a growing body of research from California has consistently found that salmonids rearing in small and intermittent streams are highly sensitive to low flow conditions during the dry season (Harvey et al. 2006; Boughton et al. 2009; Grantham et al. 2012; Obedzinski et al. 2018; Hwan et al. 2018; Sloat and Osterback 2012; Woelfle-Erskine et al. 2017). Collectively, these studies show that salmon and trout in many small and

intermittent streams live on a "metabolic knife's edge"– where only a few days of hydraulic disconnection, a few available calories, a slight change in dissolved oxygen levels, or few degrees of temperature may separate profitable from unfavorable habitat conditions (Vander Vorste et al. 2020). There is general consensus that water diversions during the dry season can compound the stressors associated with seasonally low streamflow, potentially tipping the balance to stressful or even lethal environments for juvenile salmonids (Deitch et al. 2009, Grantham et al. 2012, Power et al. 2015, Obedzinski et al. 2018).

Efforts to restore streamflow to impaired streams have been underway for several decades in California (Grantham et al. 2014) and throughout the Western US (Kendy et al. 2018). Yet, while the impacts of flow diversion on juvenile salmon and other focal species are well documented (Jeffres and Moyle 2012, Grantham et al. 2012, Deitch and Dolman 2017), the reciprocal effects of flow *enhancement* have been challenging to quantify, particularly for small and unregulated streams (Deitch et al. 2009, Harvey et al. 2014). These challenges arise from at least three primary sources: (1) the difficulty in measuring small, incremental changes in streamflow, habitat, and biotic variables at very low flows (Deitch et al. 2009, Harmel et al. 2006, Power et al. 1988); (2) the decentralized and cumulative effects of many small points of diversion (Mierau et al. 2018, Deitch and Dolman 2017), which make it difficult to establish a specific spatial "treatment" or a suitable "control" to evaluate the effects of flow restoration (Connell 1974, Underwood 2009); and (3) the complex and/or localized relationships between streamflow and habitat or biotic responses (Obedzinski et al. 2018, Walters 2014). Thus, while streamflow alteration has consistently been shown to have significant negative ecological impacts (Poff and Zimmerman 2010, Carlisle et al. 2019), the expected beneficial effects of flow restoration on stream-rearing salmonids and other stream biota have largely been inferred or modeled (Harvey et al. 2014, Deitch et al. 2009).

In this study we took advantage of a streamflow augmentation project on Porter Creek, a small, intermittent salmon-bearing stream in Northern California, to conduct a novel manipulative experiment designed to overcome many of the challenges with evaluating the effects of flow enhancement (see Table S1 for definitions for streamflow "augmentation," "enhancement" and "restoration"). Our study specifically targeted response variables relevant to summer rearing salmonids and was not intended as a broad analysis of the ecological effect, merits or tradeoffs of flow augmentation as a recovery strategy. Flow augmentation offers clear benefits to testing the effect of changes in streamflow on biota and habitat, including a treatment of known location and magnitude; and well-defined "control" (upstream of augmentation) and "impact" (downstream of augmentation) reaches. Our primary objective was to directly measure physical and biotic responses to a flow alteration of known proximity and magnitude. A secondary objective was to consider the spatial (downstream) and temporal (inter-annual) effects of augmentation on habitat connectivity and streamflow.

To address these objectives, our study included, (1) monitoring of streamflow and wetted habitat in response to different levels of dry season flow augmentation in 2017, 2018, and 2019; and (2) a short duration (1-week) but higher resolution "before after control impact" (BACI) augmentation experiment during the summer of 2018 to quantify ecological responses to elevated summer streamflow. Combining data from continuous loggers, standard habitat and food web measurements with novel videogrammetry techniques, we measured how flow

augmentation affected dissolved oxygen, water temperature, hydraulic habitat, invertebrate drift and benthic invertebrate standing crop, as well as salmonid foraging behavior, movement and occupied volume. For the multi-year wetted habitat monitoring, we hypothesized that (H1) augmentation would increase streamflow and hydraulic connectivity and that (H2) the effects of augmentation would diminish over space and time (downstream from the point of augmentation and as the dry season progressed). For the short-duration BACI experiment, we hypothesized that augmenting flow would: (H3) increase dissolved oxygen (by reducing biochemical cycling rates due to increased water velocity and decreased flow residence time), (H4) decrease water temperature (due to mixing effects and increased thermal mass of flow), (H5) increase invertebrate drift, and (H6) have a minimal effect on benthic invertebrate standing crop, since the 1-week duration of augmentation would be too short relative to invertebrate life cycles to support increased production. We also hypothesized, based on results of Fausch et al. (1997) and Fausch (1984), that increased invertebrate drift and water velocity from augmentation would (H7) increase the proportion of drift foraging behavior and (H8) decrease the proportion of search foraging behavior in pool dwelling fishes.

Study location and project history

Porter Creek is a tributary to the Russian River in Sonoma County, California (Fig. 1). The 19.4 km^2 watershed is located in California's Coast Range and flows approximately 11.4 km west to east into the Russian River, near the town of Healdsburg. The watershed is entirely privately owned, and managed for timber, livestock and wine-grape production, with extensive vineyard planting on terraces in the lower 2.3 km of the stream. The watershed's geology is primarily composed of Franciscan complex mélange, although the southern slopes and upper watershed are a mix of mélange and coastal belt shales (Jennings 1977, California Geological Survey, Geologic Data Map No. 2). The Franciscan mélange geology is regionally associated with sparse deciduous oak and annual grass savanna and limited subsurface storage capacity to support summer streamflow (Hahm et al. 2019).

Streamflow patterns in Porter Creek are characterized by Mediterranean hydrology. More than 90% of the annual rainfall typically occurs from November through April, resulting in flashy winter flows followed by a steady streamflow recession after the last spring freshets (Deitch et al. 2009). Except in the wettest years, Porter Creek, like many Mediterranean streams, becomes intermittent for much of its length by mid or late summer. As flows recede the riffles dry first, leaving isolated pools, followed by the contraction of wetted pool habitat, and in some stream reaches, complete channel drying by late-summer.

Porter Creek supports both wild and hatchery-stocked Coho salmon (*Oncorhynchus kisutch),* and wild steelhead trout (*Oncorhynchus mykiss*). The creek also supports native non-salmonid fish, amphibians and reptiles in Porter Creek including: California roach (*Hesperoleucus symmetricus*), prickly sculpin (*Cottus asper*), riffle sculpin (*Cottus gulosus)*, California pike-minnow(*Ptychocheilus grandis*), three-spined stickleback (*Gasterosteus aculeatus*), Sacramento sucker (*Catostomus occidentalis)*, Pacific Giant Salamanders (*Dicamptodon sp.*), rough-skinned newt (*Taricha granulosa*), Pacific tree frog (*Pseudacris regilla*), Foothill yellow legged frogs (*Rana boylii*), Western rattlesnakes (*Crotalus oreganus*), Western pond turtles (*Clemmys marmorata),* and garter snake (*Thamnophis spp*. A number of non-native fish were also observed.

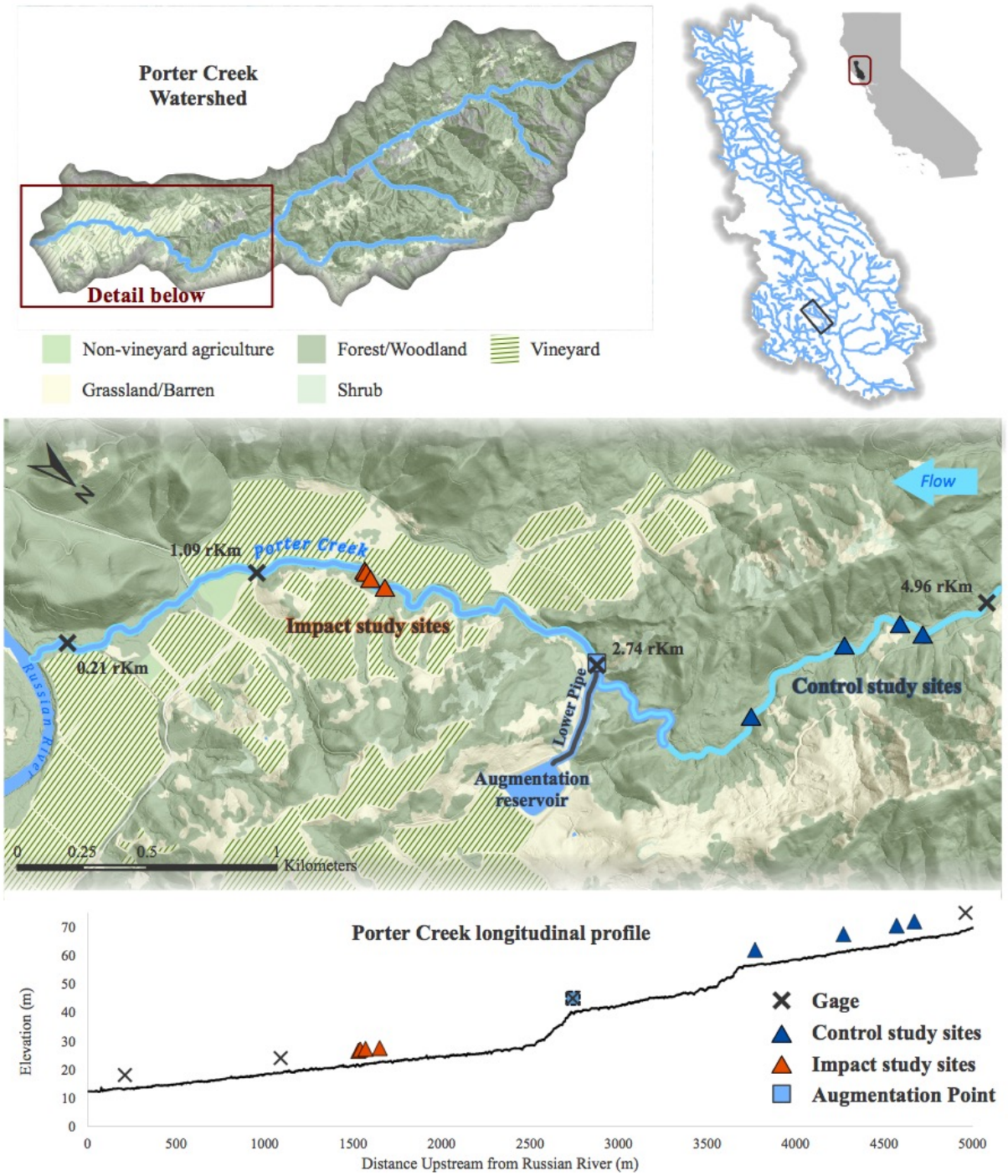


Figure 1. Porter Creek location, and study reach (top) and detailed study area (middle) showing the gaging sites, riffle-pool study sites, off-channel pond and augmentation pipe (dark blue line). Vineyard land use is shown with diagonal lines. The longitudinal profile (bottom) shows the relative location of gaging stations, augmentation points, and the "control" and "impact" study sites.

Russian River salmonid populations, particularly Coho salmon, have experienced rapid declines over the last century, with fewer than 10 adult Coho salmon observed returning each year by the early 2000s. These declines led to state and federal endangered species listings (NMFS 2012) and prompted a multi-agency conservation hatchery effort designed to raise and release juvenile Coho salmon in key Russian River tributaries (NMFS 2012, Obedzinski et al. 2018). Porter Creek was listed in NMFS Coho Salmon Recovery Plan as a priority stream for salmonid restoration and streamflow improvement (NMFS 2012) and has received planted fish from the conservation hatchery most years since 2010.

The 2012 - 2016 California drought was the driest period in California history since modern record-keeping began (Hanak et al. 2015) and precipitated a number of recovery actions for these imperiled salmonid species. In 2014, the primary vineyard landowner on Porter Creek entered into a voluntary drought agreement with state management agencies to release water stored in an off-stream reservoir into the stream channel in order to maintain suitable rearing conditions for juvenile salmon and to facilitate passage of out-migrating smolts (Fig. 1). The storage reservoir is filled with water pumped from shallow wells along the Russian River, upstream of the confluence with Porter Creek. The reservoir elevation is above the augmentation structure and water is gravity fed into the plumbing array, through a series of butterfly valves, and downslope to one of two possible augmentation points in Porter Creek (Fig. 1). A programmable controller regulates flow releases from the reservoir (Fig. S1) and allows an operator to set the start date and duration of specific augmentation levels. The completed streamflow augmentation system can release up to 61000 $m^3$of stored water into the creek each year, at a rate of up to 26 L/s (0.9 ft^3/s).

METHODS

2017 - 2019 Streamflow and Wetted Habitat Monitoring

Streamflow Gaging

In-Situ Level TROLL 500 pressure transducers were deployed in Porter Creek at the augmentation outlet and three additional downstream locations (Fig. 1). Each gage recorded water stage every 15 min for the duration of the study period. In addition, staff plates were installed to detect pressure transducer drift and other factors that may alter the relationship between stage and streamflow. Streamflow was measured at approximately monthly intervals using a U.S. Geological Survey Price Pygmy Current Meter, following protocols adapted from the CDFW Standard Operating Procedures for Discharge Measurements in Wadeable Streams (CDFW 2013). Stage-discharge relationships were developed at each location following standard U.S. Geological Survey protocols (Rantz 1982). In addition, continuous streamflow was estimated in the control reach, by correcting the gage at river kilometer (rkm) 2.7 km using summer (May-August) discharge measurements taken at a control study site (rkm 4.0). This rating curve was only developed for flows under 142 L/s.

Streamflow Augmentation

Streamflow augmentation occurred in Porter Creek during the summers of 2017, 2018, and 2019, depending on water availability, resource agency objectives, and scheduling with the vineyard landowner. The objective each year was to start augmentation when ambient streamflow approached disconnectivity and test the capacity of different augmentation levels to re-wet the

channel or alter hydraulic connectivity. In 2017, three levels of augmentation were tested as "pulse flow" treatments of 6.9 L/s, 13.9 L/s, and 24.6 L/s, over 7-days intervals each (Fig. 2). We repeated this release schedule in early summer (June 13 to July 5) and late summer (July 18 to August 20) after which augmentation was set at a 6.9 L/s "maintenance flow" to support summer salmonid survival until October 1 ("III" in Fig. 2). In 2018, we tested the same three levels of pulse flow treatments; however, the experiment was only conducted once – June 30 to July 15th, after which augmentation was set at 6.9 L/s until October 1 (Fig. 2). The 24.6 L/s pulse flow treatment in 2018 (Fig. 2) was also used for the BACI experiment (described below). In 2019, Porter Creek experienced a large May freshet and ambient streamflow never approached disconnectivity therefore, a single maintenance flow augmentation treatment of 13.9 L/s was implemented, starting on July 15 and continuing through October 1 (Fig. 2).

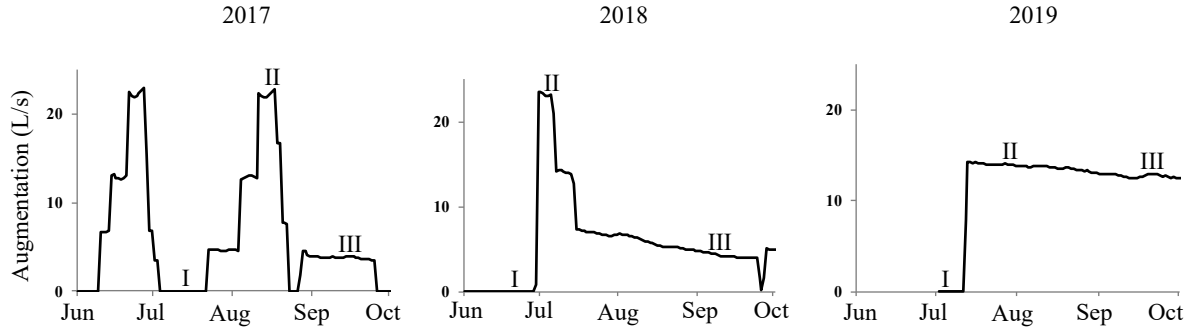


Figure 2. Porter Creek summer augmentation releases for 2017, 2018, and 2019. Wetted habitat surveys occurred before augmentation (I), after 1 week of peak augmentation (II), and during maintenance flow (III). The BACI experiment was conducted between I (Before) and II (After during peak augmentation) in 2018.

Wetted Habitat Mapping

Each year from 2017 to 2019, wetted habitat mapping was conducted at three times: (1) prior to augmentation ("I" in Fig. 2), (2) during peak augmentation ("II" in Fig. 2) and (3) during maintenance flows ("III" in Fig. 2) . Surveys began at the confluence with the Russian River and continued upstream 2.7 km to the augmentation point (Fig. 1). The spatial extent of "wet" (flowing stream), "intermittent" (dry riffles, but wet pools), and "dry" (dry riffles and pools) channel was mapped on each survey using the mobile ArcCollector application with a handheld GPS unit (BadElf, accuracy 5m to 10m). Summary statistics describing the proportion "wet," "intermittent," and "dry," channel from rkm 0 to rkm 2.7 were computed for each surveyed interval and related to augmentation level and ambient streamflow.

2018 BACI Study

Study Site Selection and Streamflow Augmentation

In the summer of 2018, a BACI experiment was conducted to measure the effect of streamflow augmentation on pool-scale dissolved oxygen, water temperature, depth, velocity, wetted width, pool volume, invertebrate prey, salmonid foraging behavior, movement, and occupied volume. Eight riffle-pool habitat units were selected as study site "replicates" (Fig. 3) – four in the control reach (upstream of augmentation) and four in the impact reach (downstream of augmentation). The riffle-pool unit is a ubiquitous geomorphic feature in alluvial streams with slopes between

0.5% and 2% (Leopold and Wolman 1957) and provides a discrete habitat unit for evaluating juvenile salmonid rearing and foraging during the low-flow period (Mathews at al. 1995; Naman et al. 2018). Study site selection was constrained by landowner access and confinement in the upper reaches of Porter Creek and was, therefore, not random. For filming videos, we selected reaches with similar slope and geomorphic characteristics that supported foraging salmonids. Study sites with simple hydraulic controls were also prioritized so that we could develop robust rating curves at the downstream riffle crest. Data was collected "before" and "after" the maximum augmentation value of approximately 24.6 L/s, which began the evening of June 30 and continued through the evening of July 7. "Before" sampling took place on June 29 and 30 of 2018 and "After" sampling took place on July 6 and 7 of 2018.

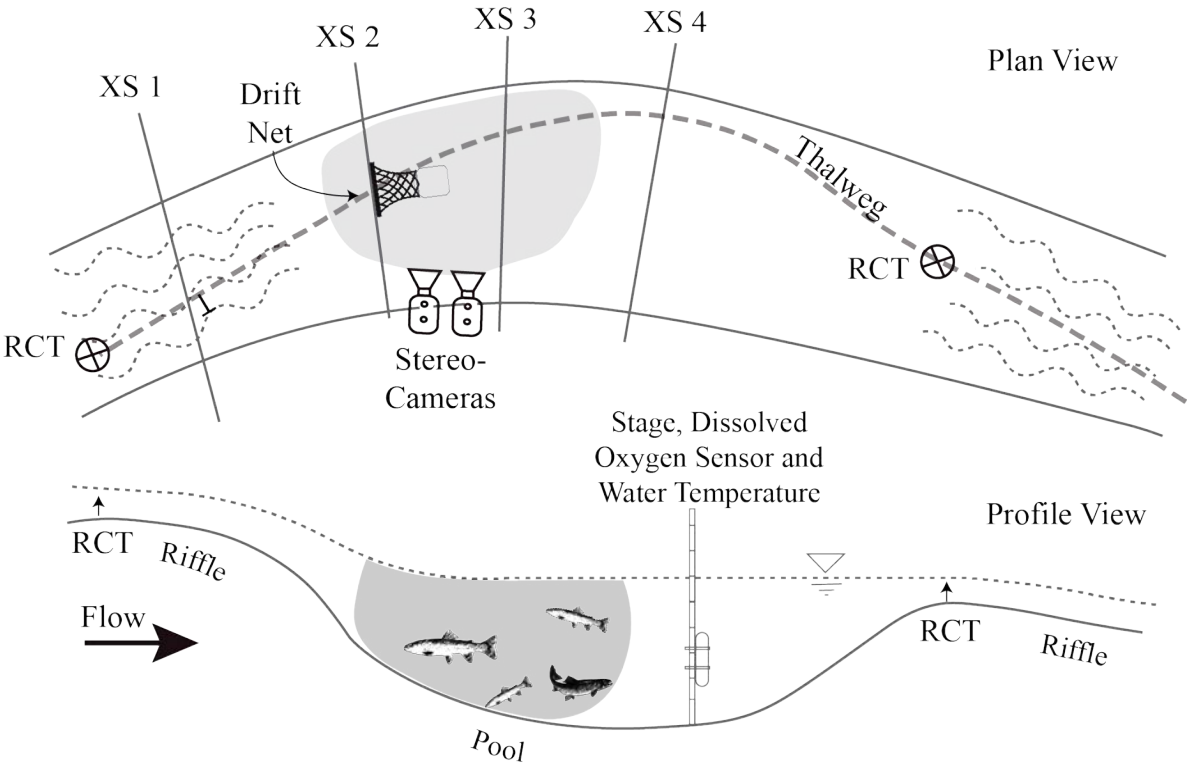


Figure 3. Schematic of site-scale measurement locations for hydraulic habitat, water quality, stream invertebrate, and salmonid behavior monitoring replicated at each study site in Fig. 1.

Hydraulic Habitat Measurements

At each study site, we installed a cross-stream transect midway through the upstream riffle, and three cross-stream transects in the downstream pool – one where the riffle enters the pool, a second bisecting the focal area for video analysis, and a third over the maximum depth of the pool (Fig. 3). Depth and velocity were measured at 0.25-m intervals along each cross section the day before augmentation and after 1 week of augmentation. Velocity was measured with a Marsh-McBirney Flo-Mate 2000 Electromagnetic Flow Meter. Wetted width of each transect was measured. In addition, depth of flow was measured where the thalweg bisects the downstream riffle crest of each pool, a point known as the 'riffle crest thalweg' (RCT) (Mierau et al. 2018; Rossi et al. 2020 in review). Volume was also calculated between each cross section, and estimated for the whole pool, on each survey date, using the average end method (Taube 2000).

Water Quality Monitoring
We measured dissolved oxygen and stream temperature using continuous HOBO U26 data loggers in one control site (rkm 3.7) and one impact site (rkm 1.6) during the BACI experiment. The dissolved oxygen loggers were calibrated prior to deployment, and the output data was corrected using HOBOware Pro's Dissolved Oxygen Assistant software. Calibration measurements were taken using a handheld YSI Pro20 in each pool.

Invertebrate Sampling
To estimate the effect of streamflow augmentation on stream invertebrate assemblage, and on prey abundance for salmonids, we sampled invertebrate drift entering each pool, and benthic invertebrate standing crop on cobbles in the riffle and pool of each study site. Invertebrate drift was sampled for 2 hours (+/- 10 minutes) the day before and 1 week after augmentation. Sampling took place between 16:00 and 19:00. Drift was collected in nets with a 50 cm x 20 cm mouth aperture and 500-µm mesh. The drift net was installed just below the water surface along the cross section two (XS2) at the head of the pool (Fig. 3). Cross-stream position of the net was adjusted on each occasion in order to capture the region of highest velocity at each sampled streamflow.

Benthic invertebrate standing crop was measured on 3 riffle cobbles and 3 pool cobbles of each study site the day before augmentation and after 1-week of augmentation. Stones to be used for benthic sampling were collected from the stream bed in each habitat type using the step-toe procedure (Harrelson et al. 1994); however, we only retained stones in the coarse gravel to cobble size class (46mm to 256mm b-axis). To reduce loss of epibenthic prey, aquarium nets were held directly downstream of each stone as it was dislodged. All invertebrates on the stone surface and in the aquarium net were removed by hand, and by washing and elutriating through 500-µm mesh. The stones' dimensions (a- and b-axes) and shapes were recorded and the surface area of each stone was computed.

All invertebrate samples (drift and standing crop) were preserved in labeled 50ml centrifuge tubes and filled in the field with ethanol. In the laboratory, drift and benthic samples were sorted and invertebrates identified to family or genus (Merritt et al. 2008) under 10X magnification. Each invertebrate was measured to the nearest 0.5mm under a dissecting scope and biomass (mg dry mass) was estimated from published length to dry mass relationships (Benke et al. 1999; Sabo et al. 2002). In addition, we categorized invertebrates into qualitative binary status as "vulnerable" or "invulnerable" for young-of-year salmonids (age-1+ and older parr were extremely rare in our study) using gape limitation (Brodeur 1991), and the armored status of each invertebrate taxa (Sabo et al. 2002).

Videogrammetry
Fish behavior and foraging movements were monitored by underwater video recordings. Videos were collected with stereo-pairs of mounted GoPro cameras (HERO 4 Black, recorded at 30 frames per second with 1080p resolution) installed at monumented stations at the head of each pool (Fig. 3). We chose the head of the pool because the first point of entry for invertebrate drift from the riffle is a preferred foraging location for pool dwelling salmonids (Harvey et al. 2006). Recordings lasted approximately 30 minutes and were collected between 16:00 and 18:00 one

day before augmentation and on one day after one week of augmentation in each pool. Camera angle and distance from the ground were kept as constant as possible between sampling events to sample a consistent volume of the pool throughout the study period.

Video from one study site in the control reach and one study site in the impact reach was unsuitable for analysis due to insufficient overlap between the left and right cameras and poor camera angles to capture fish behavior, which left 6 total sites (3 control pools and 3 impact pools) available for analysis. Twelve videos (n = 6 sites x 2 events) were analyzed using the videogrammetry program Vidsync (Neuswanger et al. 2016) during the BACI experiment to assess fish foraging behavior and within-pool movement. Vidsync allows the user to triangulate a 3-D position, in relative space, using known lines of sight from two or more cameras. For each video, we followed the video correction and calibration procedure described in Neuswanger et al. (2016).

To analyze the videos, we selected the 10-minute clip with the highest counts of juvenile salmonids in the video frame. Within this 10-minute clip, we used a random number generator to select six 30-second subsamples. In each subsample, we used VidSync software to track the nose-point location of each observed fish on 3-second intervals, and assign a foraging mode at each interval. Foraging modes were defined based on common literature descriptions (Table S2). VidSync output from these analyses included relative X, Y, Z positions of fish, times stamps, foraging mode or aggression attributes and body length. Data for each subsample were organized by object (e.g., fish ID) and event (type of measurement). These data were exported into the statistical software R (version 3.5.1) and scripts were developed to compute fish lengths, distance traveled per time, foraging volume occupied, and as well as counts and proportion of behavioral observations. For statistical analysis only steelhead had sufficient representation in the "control" and "impact" sites to do a BACI analysis; however, "before" and "after" behavioral data are reported for Coho and California Roach.

2018 BACI Statistical Analysis

The effect of augmentation (treatment) on response variables was evaluated using mixed effects models in R version 3.5.1. Seventeen response variables were monitored, including those representing hydraulic habitat (n = 6), water quality (n = 2), benthic invertebrates (n=3), and fish behavior (n= 6) (Table 1). In a BACI experiment, the interaction of "Time" (before or after impact) and "Location" (control or impact sites) is significant "when change occurs at the impact site but not the control site" (e.g. Popescu et al., 2012 ; Smokorowski and Randal 2017). We constructed individual mixed effect models for each response variable with the interaction of "Time" and "Location" as the predictor variable. Models were constructed using the R packages "lme4" for continuous variables and "GLMM" for proportional variables. We included a random effect for "study site" in each model to account for spatial effects that were not due to augmentation, and a second random effect for "subsample" in the Vidsync fish foraging data.

The continuous variables were evaluated using the lmer command in R package lme4:

$$[\text{Variable} \sim \text{Time}^* \text{Location} + (1|\text{Site}) + (1|\text{Subsample})]$$

The proportional data (e.g. proportion of drift foraging fish) were analyzed using the command "glmer" from the R package GLMM with binomial distributions, and weights assigned based on the counts (Bolker 2009):

[Variable ~ Time* Location + (1|Site) +(1|Subsample), family = "binomial", weights = count]

For the continuous data we scaled the model coefficients by subtracting the mean and dividing the standard deviation of each dataset from each measured point. This allowed us to report a scaled effect size from augmentation in units of standard deviations. We also reported the 95% confidence interval and significance (*p-value*) from each model. For the binomially distributed data we reported effect size as an odds ratio (the relative change due to augmentation as a multiplicative factor between the control and impact sites) and also reported the 95% confidence interval and significance.

RESULTS

Interannual (2017 - 2019) Augmentation Monitoring

Streamflow

This study spanned a wide range of hydrologic variability in both magnitude and timing. 2017 was a very wet water year –1479 mm of precipitation; however, summer hydrology was normal with only 7 mm precipitation falling after April. 2018 was a dry year – 615 mm of precipitation with only 3 mm falling after April; and 2019 was a normal/wet water year –1218 mm of total precipitation, with an extremely wet summer (58mm of precipitation after April) (CDEC 2020). These inter-annual differences in precipitation were reflected in summer stream flow conditions at Porter Creek. In 2017, ambient streamflows at the augmentation outlet (rkm 2.7) were 50 L/s at the beginning of June and receded to 5 L/s by July and zero by early October (Fig. 3). Summer conditions in 2018 were drier, with flows at rkm 2.7 falling from 22 L/s in June to zero by mid-July. The May rain in 2019 maintained streamflows over 40 L/s throughout the month of June 2019 and 20 L/s through mid-July and while flow receded to near-zero in September and October, surface flows were sustained all year. The effect of augmentation on streamflow was most pronounced at the outlet (rkm 2.7) but was also detected downstream at rkm 1.1; however, reach scale variation had a greater effect on streamflow and connectivity then distance downstream from the augmentation point. Streamflow near the mouth of Porter Creek (rkm 0.2) was not responsive to summer flow augmentation treatments due to the thick alluvial fill in that reach (Fig. S2).

Wetted habitat

Stream drying consistently occurred in low-gradient reaches, characterized by alluvial gravel deposits and wide bar-riffle morphology, especially around rkm 2, and below of rkm 0.6 down to the Russian River confluence (Fig. 1, Fig. 3, Fig. S2). Higher gradient reaches, and more confined reaches with coarser bolder and bedrock hydraulic controls tended to maintain connectivity even at low flows. During 2017 and 2018, rewetting of almost all dry and intermittent reaches occurred in early July following an pulse flow augmentation of 24.6 L/s with the exception of the lowest 100 meters, where an aggraded alluvial gravel bar separates Porter Creek from the Russian River (Fig. 4, Fig. S2). In late summer of 2017 and 2018, after augmentation levels were reduced to 6.9 L/s, the length of dry or intermittent channel increased

to pre-augmentation levels or greater (Fig. 4). Unlike 2017 and 2018, Porter Creek maintained surface connectivity throughout the summer of 2019 except in the lowest reach closest to the confluence with the Russian River (Fig. 4). An augmentation of 13.9 L/s had no measurable effect on the length of wetted channel (Fig. 4).

2018 BACI Experiment Results

Streamflow Augmentation

Streamflow was augmented for the BACI experiment starting on June 30th and maintained through July 7th, 2018. A target flow of 24.6 L/s was programmed; however, actual augmentation varied from a minimum daily value of 23.5 L/s and maximum daily value of 25 L/s. Augmentation elevated ambient streamflow in the impact reach by nearly an order of magnitude (2.8 to 25.4 L/s, +/- 10%) during this experiment (Fig. 4 and Fig. 5).

Water Quality

Augmentation significantly increased dissolved oxygen in the impact sites (Fig. 5, Fig. 6), with an effect size of 2.8 mg/L (Table 1). This represents an average doubling of "before" DO levels, comparing all (15-minute) measurements for the week prior with the week after augmentation. Prior to augmentation on June 30th, DO in the BACI study impact sites (median of 4.5 mg/L, SE 0.51 mg/L) had lowered to levels known to impair swimming performance and food conversion efficiency for juvenile Coho salmon and steelhead (Bjornn and Reiser 1991, USEPA 1986). Augmentation increased dissolved oxygen to median of 7.2 mg/L (SE 0.36 mg/L), at which juvenile salmonids experience minimal impairment (USEPA 1986). However augmentation had a negligible effect on both daily average water temperature and diurnal water temperature fluctuation at our study sites (Fig. 5, Fig. 6, Table 1). Water temperature decreased from July 6th to 7th in both the control and impact sites (Fig. 5), suggesting these day-to-day changes were driven by external conditions rather than streamflow.

Hydraulic Habitat

Augmentation produced significant increases in riffle velocity, riffle depth, riffle width, and riffle crest depth (Table 1, Fig. 6). Pool depth and width had a non-significant response to augmentation with a small degree of observed change and large standard error (Table 1). Riffle width increased by an average of 1.7 meters (SE 0.08m), nearly double pre-augmentation widths in the impact reach (Fig. S3). Riffle velocity increased by an average of 14 cm/s which was a mean 49% increase in the impact reach (SE 4.5cm) (Table 1, Fig. S3). Riffle crest depth also increased by an average of 4.6 cm (SE 1.2 cm, Table 1), nearly tripling the mean pre-augmentation riffle crest depths in the impact reach (Fig. S3).

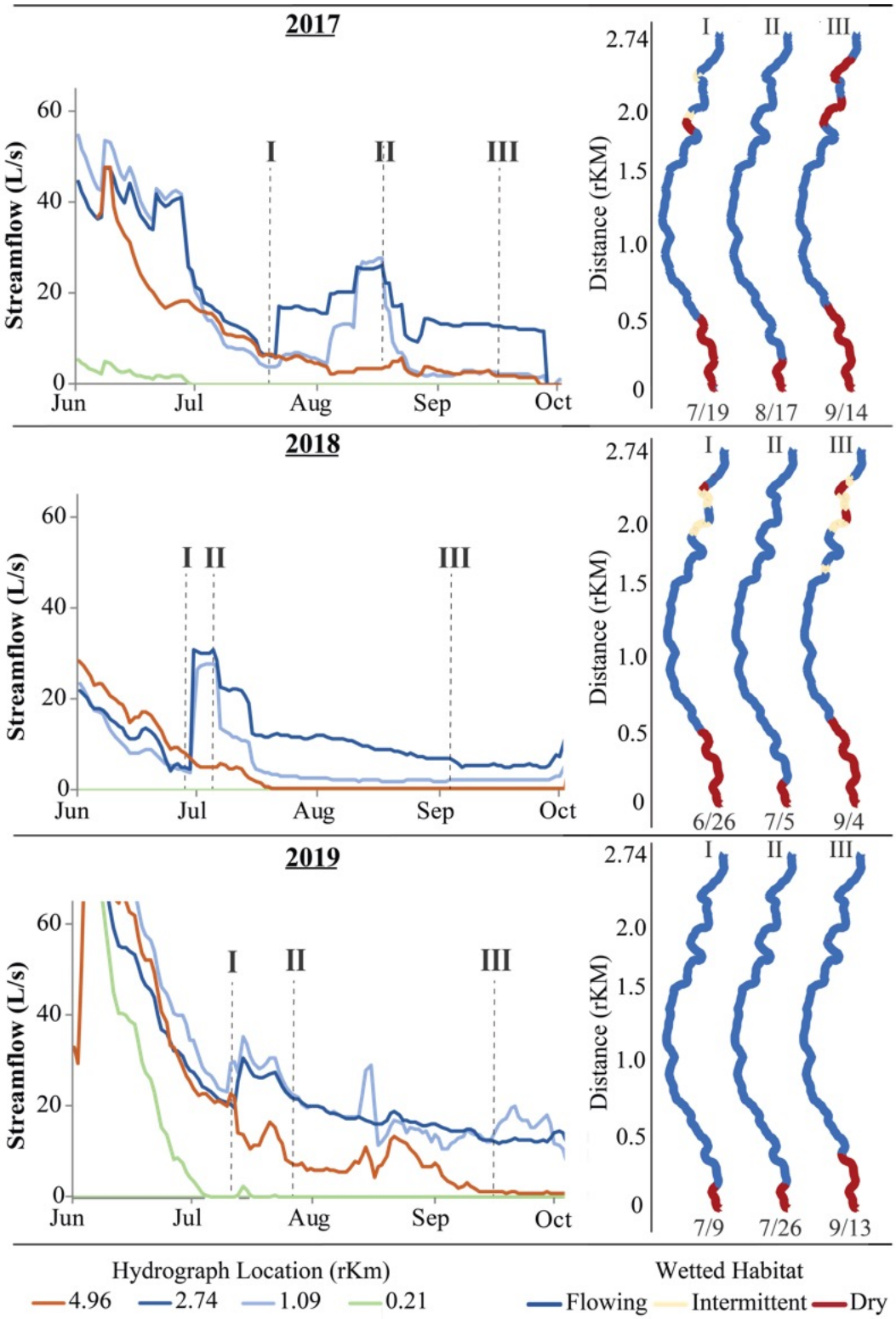


Figure 4. Hydrographs from 2017, 2018 and 2019 (left) showing reaches above (4.96 rKm) and below the point of augmentation (<2.74rKm) and corresponding wetted habitat surveys (right).

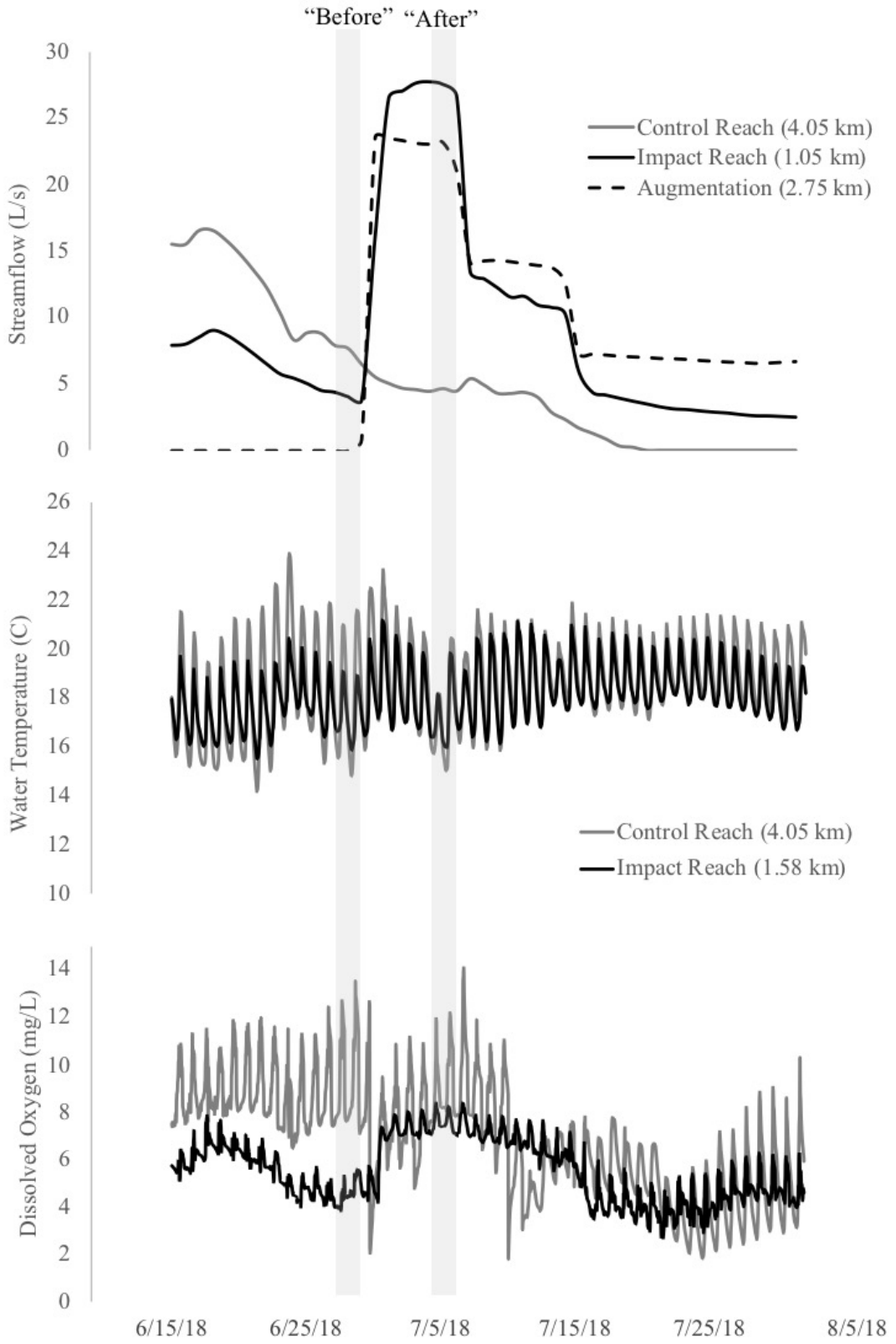


Figure 5. Streamflow, temperature, and dissolved oxygen during the 2018 BACI experiment in the control (gray) and impact (black) sites.

Table 1. Unscaled statistical model results for continuous (normally distributed) data from the 2018 BACI experiment. Results are only for the interaction terms (Location * Time) indicating an effect or lack of effect due to the augmentation treatment. The "estimate" effect size is measured in the units of the variable.

Variable	Units	Estimate	Std_Error	P_value
Riffle Velocity (average)	m/s	0.140	-0.045	0.020*
Riffle Depth (average)	m	0.088	-0.021	0.007**
Riffle Crest Depth	cm	4.627	-1.246	0.001**
Riffle Width	m	1.757	-0.076	0.000***
Pool Depth (average)	m	-0.094	-0.142	0.508
Pool Width	m	-0.115	-0.131	0.384
Dissolved Oxygen	mg_l	2.801	-0.077	0.000***
Water Temperature	C	0.085	-0.067	0.209
Invertebrate Flux	mg/hr	2.498	-1.302	0.091*
Invertebrate Standing Crop (riffles)	mg/cm2	0.006	-0.002	0.010*
Invertebrate Standing Crop (pools)	mg/cm2	0.003	-0.002	0.041*
O. mykiss Lengths	mm	-2.310	-2.010	0.241
O. mykiss Movement per Time	cm/s	6.69	2.982	0.026*
O. mykiss Occupied Volumes	cm3	-970.565	-3166.333	0.760

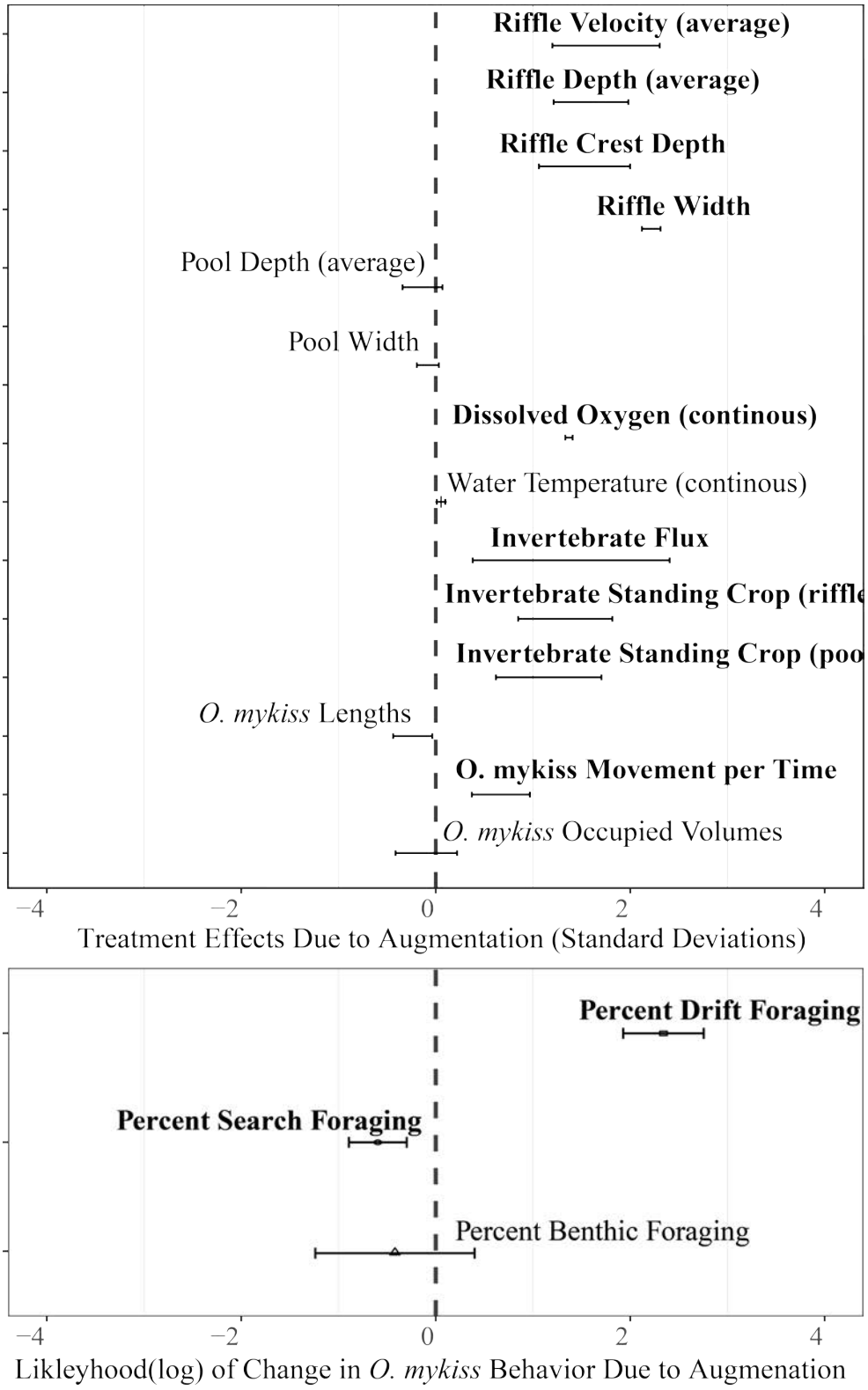


Figure 6. Summary of effects from flow augmentation on physical habitat, water quality, invertebrate flux, and foraging behavior. Effects on normally distributed data (top graph) are shown as change in standard deviations. Effects on proportion data (binomial) are shown as the log (likelihood) of change. Variables in bold were considered significant ($P < 0.1$).

Stream Invertebrates

The biomass (mg/hr) and number (#/hr) of drifting invertebrates increased significantly as a result of augmentation (Table 1, Fig. 6, Fig. 7, Fig. S4). The augmentation treatment effect increased drifting invertebrate flux by 2.49 mg/hr relative to the control site (Table 1). After augmentation, the biomass of drifting invertebrates (mg/hr) was 66% to 85% higher than "before" conditions in the impact reach (Fig. S4). One impact site had a negligible change in the *number* of drifting invertebrates per hour (34 to 32), while the other two impact sites saw large increases (3 to 41 and 8 to 47), Fig. S4. The increases in drifting invertebrates were largely due to increases in *chironomidae* (midges) which are highly vulnerable to predation by juvenile salmonids (Fig. 7). Smaller increases in other vulnerable taxa, including *diptera* and *limnephilidae*, were also observed after augmentation (Fig. 7). However, while the total number of vulnerable drifting invertebrates increased significantly, the proportion of vulnerable invertebrates remained virtually unchanged (i.e., <2% difference between "before" and "after" augmentation in both control and impact sites). We also measured statistically significant increases in riffle and pool benthic invertebrate standing crop (biomass/area of stream bed) (Fig. 6, Fig. S4) although riffle standing crop (increase of 60 mg/m^2) increased twice the magnitude of pool standing crop (increase of 30 mg/m^2).

Fish Behavior

Using the Vidsync software, we tracked 262 fish in 12 videos (6 pools x 2 dates) for a total of 2,086 unique location and behavior "observations." Each observation represents a 3-second interval on the video. *O. mykiss* accounted for 64% of all observations (1,327), while *O. kisutch* accounted for 32% (673 observations) and *H. symmetricus* accounted for the remaining 4% (86 observations). *H. symmetricus* only occurred in the impact reach and *O. kisutch* was absent from the control reach during the "after" period (Fig. 8). Due to low observations of *O. kisutch* in the control reach (and no observations of *H. symmetricus),* the BACI statistical models were only run for *O. mykiss*; however, "before" and "after" data in the impact reach are reported for all species (Fig. 8).

Counts of fish at the head of each surveyed pool (Fig. 3) increased for three species after augmentation in the impact reach (Fig. 6 and Fig. 8). Most notably the counts and proportion of drift foraging fish increased across all species while the counts and proportion of search foragers decreased in response to augmentation (Fig. 8, Table 1). Total observations of *O. kisutch* in the impact reach increased from 63 (before augmentation) to 383 (after augmentation), and the proportion of observed *O. kisutch* that were drift foraging increased from 12% to over 80% after augmentation (Fig. 8). *O. mykiss* observations increased from 236 to 275 and the proportion of drift foragers increased from 40% to 75% (Fig. 8) with a significant effect from treatment (Table 1). While *H. symmetricus* was less frequently observed, the number of observations tripled (18 to 59) after augmentation and the proportion of drift foragers increased from 0% to 86% (Fig. 8).

The within-pool movement of *O. mykiss* decreased in the control sites from a median of 10 cm/s to 4 cm/s. In the impact sites *O. mykiss* movement marginally increased and *O. kistuch* had almost no change in their movement as a result of augmentation, while *H. symmetricus* doubled its movement from 5 cm/s to 10 cm/s. The treatment effect on *O. mykiss* movement between the control and impact sites was statistically significant (Table 1, Fig. 6). In addition, occupied

volumes of foraging salmonids did not change before and after augmentation (Table 1, Fig. 6). Too few roach were observed to determine average occupied volumes.

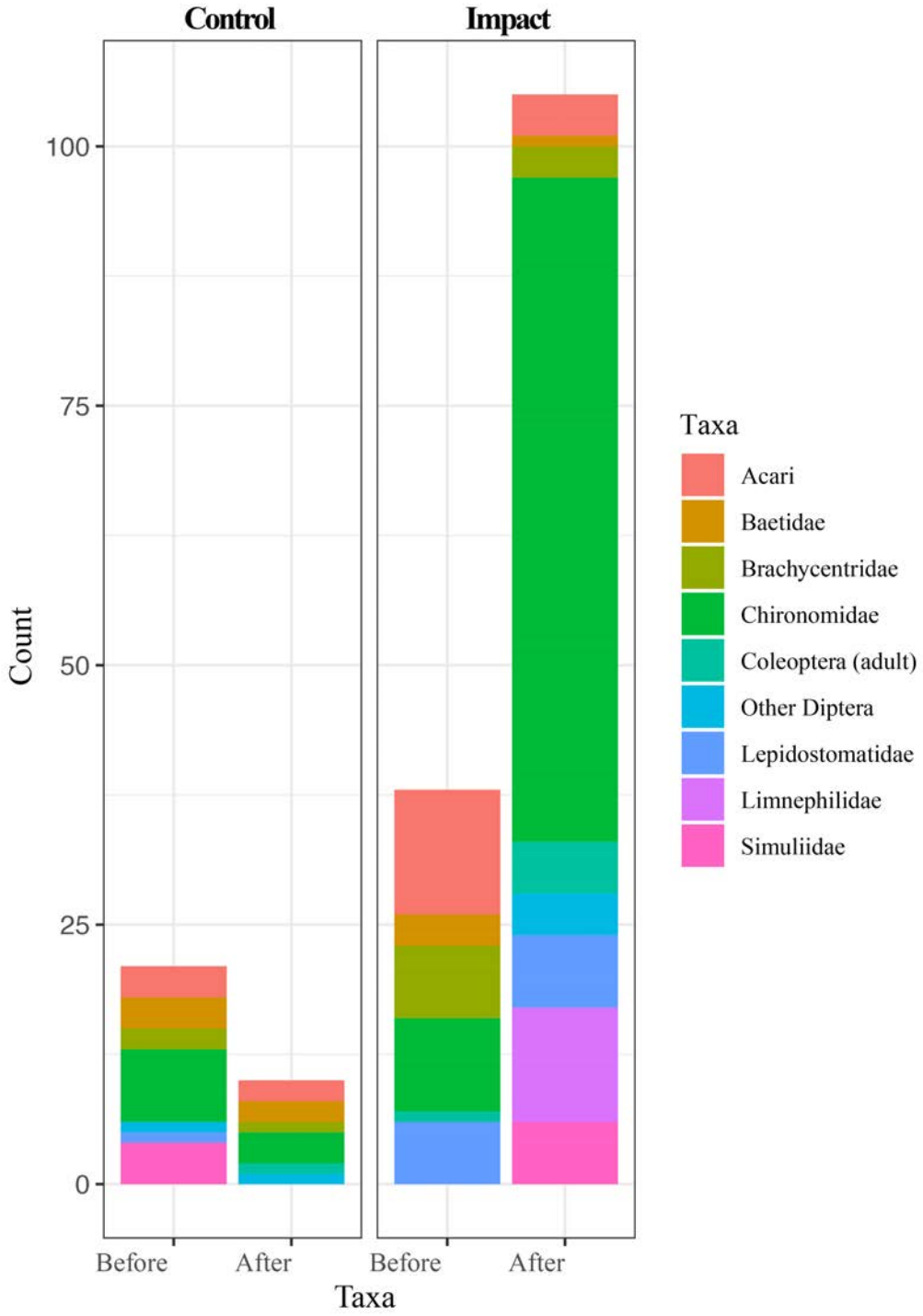


Figure 7. The abundance and composition of the nine most common invertebrates found in drift samples – grouped by reach (control/impact) and event (before/after). Counts are summed over all replicates within each reach and event. Twenty-three taxa were observed in the drift; however, these nine taxa made up 86% of the individuals observed.

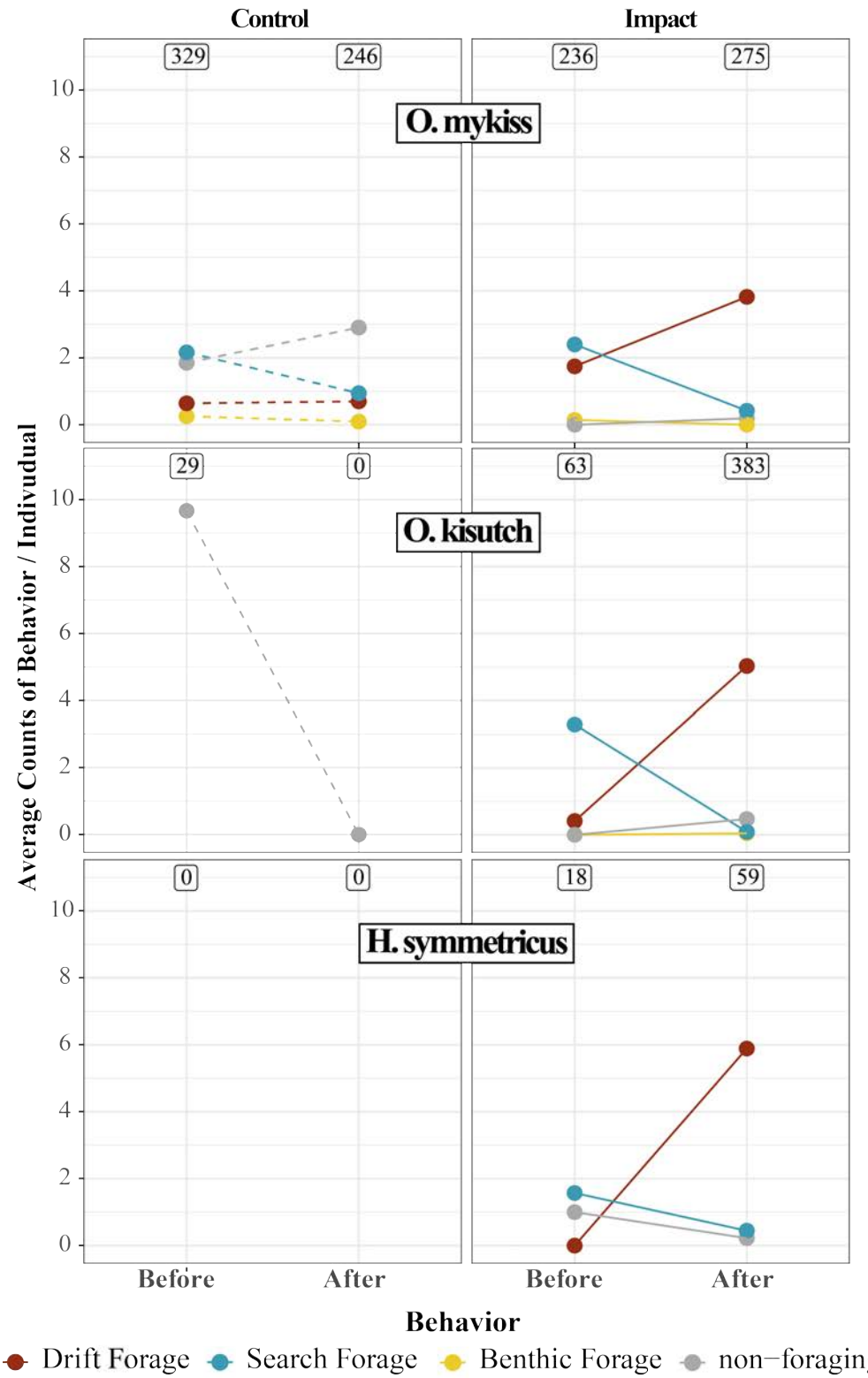


Figure 8. Average counts of juvenile steelhead and Coho, and adult California Roach, foraging behaviors – scaled per individual. Counts are grouped by reach (control/impact) and event (before/after). Total counts for each species (grouped by reach and event) are shown in the numeric labels.

DISCUSSION

Between 2017 and 2019 we conducted flow augmentation experiments to evaluate how dry season flow *enhancement* affected habitat connectivity and the foraging environment of rearing salmonids in a small intermittent stream. Our inter-annual wetted habitat mapping suggests that the effects of augmentation varied in response to ambient streamflow and channel characteristics (especially hyporheic conductivity). Flow augmentation had the greatest effect at times near, or just after riffle-pool disconnectivity. However, treatments of 6.9 L/s, and 13.9 L/s, were insufficient to re-wet disconnected reaches after several weeks of drying in 2017 and 2018, while in a wet summer (2019) flow augmentation had little effect on the extent of wetted habitat.

In our 2018 BACI experiment, we found that elevating mid-summer baseflow for one week, from 2.8 L/s to 25.4 L/s (+/- 10%), caused significant increases in dissolved oxygen, riffle width, depth and velocity, invertebrate drift and benthic invertebrate standing crop at sites more than 1 km downstream from the point of flow augmentation. We also documented consistent behavioral changes indicating that pool-dwelling salmonids were able to exploit the increased prey abundance and the improved metabolic environment in the treatment reach after flow augmentation. Counts of foraging salmonids near riffle-pool transition zones doubled, foraging movement remained steady (relative to decreasing movement in the control reach), and the proportion of drift foraging salmonids increased from an average of 26% to an average of 77% after augmentation. Collectively these results suggest that dry season flow enhancement can significantly improve habitat profitability for foraging salmonids, but that the timing and location of flow enhancement efforts relative to downstream points of interest are critical to the success of flow enhancement objectives.

Spatial and Temporal Effects of Augmentation on Habitat Connectivity

We found general support for the hypotheses that augmentation increases hydraulic connectivity (H1) and that augmentation effects diminish in a downstream direction (H2). However, while connectivity increased after augmentation in 2017 and 2018, the downstream effects of summer augmentation was more sensitive to ambient streamflow and reach-scale characteristics than to distance downstream. For example, in 2019, ambient flow remained high all summer and we observed negligible effects on downstream streamflow or connectivity from augmentation treatments (Fig. 5). Drying in 2017 and 2018 occurred primarily in reaches with deep, porous gravel deposits (around rkm 2 and downstream of rkm 0.6), which is consistent with findings from other research in coastal California (Lovill et al. 2018). Lovill et al (2018) found that sites with conductive, in-channel sediment fill were most likely to experience surface flow disconnection during low flows in nearby Elder Creek. The observation that flow-habitat relationships are reach and flow-specific is not novel (Rosenfeld 2017). However, this study shows that even relatively large magnitudes of flow augmentation can have a marginal or negligible effect on hydraulic connectivity if ambient streamflow is high or, conversely, under conditions of sustained drying and in locations where infiltration to the subsurface exceeds the rate of augmentation. Still –the effects of flow enhancement on the magnitude of *surface connectivity* (Fig. 4) may not reflect benefits to increasing hyporheic connectivity and water quality in pools, or the duration of disconnectivity, which are vital to salmonids rearing in intermittent streams (Obedzinksi et al. 2018; Hwan and Carlson 2016; Sloat and Osterback 2012; Woelfle-Erskine et al. 2017) and which we did not explore explicitly in this study.

Augmentation Effects on Water Quality and Hydraulic Habitat

We hypothesized that flow enhancement from augmentation would (H3) increase dissolved oxygen – by reducing biochemical cycling rates due to increased velocity and decreased residence time, and (H4) decrease water temperature – since we assumed the augmentation would be cooler then ambient flow and increased thermal mass of flow would resist atmospheric warming. Yet water temperature remained virtually unchanged in the impact reach while dissolved oxygen increased significantly (Fig. 5 and Fig. 6). During the augmentation treatment, water temperature in the augmentation pipe was actually slightly warmer then stream water temperature in the control reach (Fig. S5). We suspect that atmospheric and within-channel transport processes quickly dominated stream water temperature downstream from the point of augmentation and thus and the effect of augmentation temperature on in-stream water temperature was negligible by the time flow had reached our study sites. However, future augmentation efforts should not assume, based on these results, that stream temperature is insensitive to augmentation. The effect of augmentation on water temperature depends on the difference in initial temperatures, flow rates, and many other site and context specific factors effecting water temperature in streams (Ficklin et al. 2012)

Dissolved oxygen and water temperature typically have a negative correlation in streams (Wetzel, 2001), and the decoupled response of dissolved oxygen (significantly increasing) and water temperature (unchanged) to augmentation in Porter Creek requires further investigation. We did not monitor nutrient loading from the augmentation source or water quality metrics which may play a key role in how augmentation effects stream food webs and nutrient cycling. However, synoptic tests of dissolved oxygen from the pipe effluent were always near 100% saturation (DO > 9 mg/L at 18C), likely a result of aeration as water passed through the pipe (Fig. S6). Thus, one explanation is that the mass of augmented streamflow had, and retained, high oxygen content between the augmentation point and our downstream study sites. A possible mechanism for this explanation is that elevated water velocity can decreased residence time of flow in the hyporheic zone (within alluvial bars) and in pools (Tonina and Buffington 2007). Residence time of flow is directly related to interaction time with decomposers on the benthos and in the hyporheic zone, which are key drivers of carbon cycling in intermittent streams (Burrows et al. 2017). Therefore, decreased interaction time between decomposers and the volume of flowing water could lead to decreased to organismal oxygen consumption and decreased dissolved oxygen independently of water temperature.

Augmentation nearly doubled riffle width and increased average riffle velocity in the impact sites from 0.03m/s to 0.19m/s but had negligible and insignificant effects on pool width and depth (Fig. 6 and Fig. S4). We suspect that increased riffle velocity and riffle depth after augmentation reflects an increase in the total proportion of surface flow relative to hyporheic flow in riffles, *and* a decrease in the residence time of water in the biologically active hyporheic zone (Burrows 2017), however we did not directly measure hyporheic flow. Consistent with our conjecture, is a positive non-linear correlation we observed in 2017 between depth of flow over the upstream riffle crest and dissolved oxygen in the downstream pool in Porter Creek (Fig. 9, Rossi et al. 2020 in review). The strong collinearity between augmentation, RCT depth, riffle velocity, and dissolved oxygen (Table 1, Fig. 6), together with the RCT-DO relationship we observed in 2017 (Fig. 9) suggest a mechanistic relationship between these variables; however,

directly measuring hyporheic exchange and relating exchange and residence time to RCT depth is needed to further investigate the causal mechanism of this relationship.

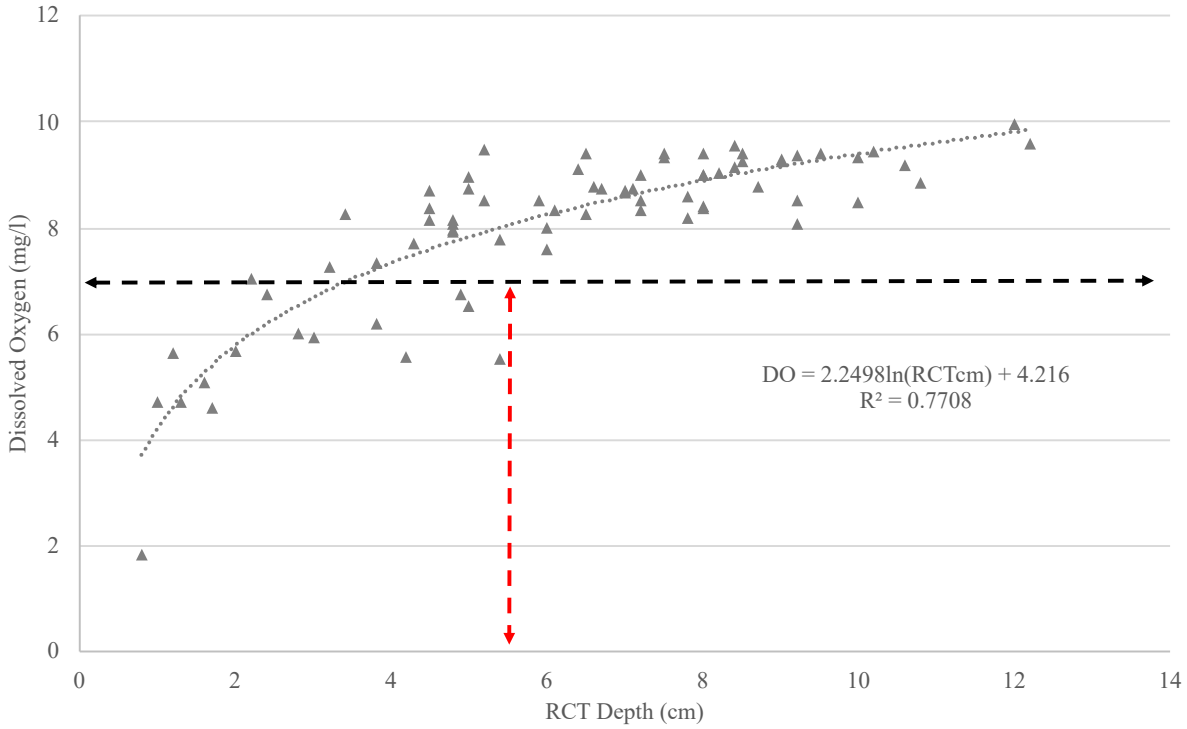


Figure 9. Correlation between riffle crest depth (in the upstream riffle) and dissolved oxygen in the receiving pool (downstream) from Porter Creek in 2017. The black horizontal line (7 mg/L) is often cited as a threshold below which juvenile salmonids begin to experience negative effects from low oxygen. RCT depths below 5.5 cm (horizontal red line) are associated with increased observations of DO below 7mg/L in Porter Creek.

Augmentation Effects on Stream Invertebrates and Fish

We observed an increase in invertebrate drift after augmentation. This expected response (H5) has been documented in previous studies, which have shown that increased riffle velocity and width can increase the production, hydraulic transport and behavioral drift of invertebrate species (Annear et al. 2004, Svendsen et al. 2004; Naman et al. 2016). Counter to our hypothesis (H6), we also observed a significant increase in benthic standing crop in both riffle and pool habitats. It is unclear whether increased benthic standing crop of invertebrates was due to increased secondary production or invertebrate behavior (e.g. invertebrates moving up from deeper in the benthic zone to take advantage of increased detrital transport due to elevated flow). Invertebrate behavior also responds to fish predation (Miyasaka and Nakano 1999) and although our statistical results show an insignificant change in benthic foraging due to augmentation (Fig. 6, Table 1), the large increase in drift foraging behavior could have reduced benthic predation enough to alter invertebrate behavior and increase invertebrate standing crop. Collectively, our findings indicate that the availability of invertebrate prey for fishes increased as a result of flow augmentation, reflected in both the higher flux of drifting invertebrates and greater density of benthic invertebrates.

Video monitoring revealed that juvenile Coho salmon, steelhead and adult Roach all responded to increased invertebrate drift and pool hydraulics at the riffle – pool transition area. We measured large increases in the number and proportion of drift foraging events (H7), and a decrease in the number and proportion of search foraging events (H8) in all three species at the head of the pool. Coho salmon had the strongest drift foraging response to augmentation in the impact reach (Fig. 8) – which was surprising as Coho are more commonly associated with search foraging in slower water environments then other salmonids (Naman et al. 2020). Steelhead and Roach also showed a strong behavioral shift toward drift foraging (Fig. 8). Despite the increase in benthic invertebrate densities, we did not observe a change in benthic foraging by fish – however this may due to the energetic profitability and preference of salmonids towards drift foraging (Fausch 1984).

While we did not monitor fish growth using mark-recapture methods during this study (due to its short, 1-week duration), multiple converging lines of evidence strongly suggests that augmentation in Porter Creek created a much more profitable foraging environment for juvenile salmonids. This evidence includes: (a) the increased drifting biomass and standing crop of invertebrates, (b) the increased counts of vulnerable prey taxa (especially *chironomidae*) in the drift, (c) the decreased metabolic and prey assimilation costs from increased dissolved oxygen, and (d) the behavioral response of fish towards energetically profitable drift foraging. After augmentation, foraging movement (distance per time) increased, as did the average number of foraging fish at the head of the pool, however, occupied volumes of foraging fish remained statistically unchanged. While theory suggests that increased drifting prey and drift foraging behavior would *decrease* occupied volume and aggression (Chapman 1966, Fausch and White 1981), the poor abiotic conditions prior to augmentation likely rendered large portions of the pool inhospitable (due to low DO, low prey resources – and high predation risk in still, intermittent pools). Thus, we interpret the increased counts of actively foraging fish, occupying a similar range of volumes (but moving faster within those volumes), together with increased vulnerable prey concentration and decreased metabolic costs – to indicate that a large proportion of the total pool volume *became* profitable foraging habitat due to augmentation, and that fish were heartily exploiting this habitat.

Another important effect of flow enhancement is its influence on fish movement *between* pools. After augmentation in 2018 riffle crest depth increased from a mean of 2.3 cm to a mean of 7 cm (Supplemental Fig. 4). Riffle depths of 2.3 cm are well below published riffle depths that support juvenile salmonid passage over riffles (USFWS 2019, CDFW 2017) and 7 cm are greater than twice the average body depth (USFWS 2019) of young-of-year *O. mykiss* (Tonkin et al. 2013), indicating that the conditions suitable for inter-pool movement and access to riffle foraging likely increased after augmentation. The increased flux of drifting prey together with increased freedom of salmonids to move between foraging habitats suggests that, after augmentation, drift foraging fish in Porter Creek would have been more able to achieve an *ideal free* foraging distribution – which has been shown to increase population level fitness of fish (Fretwell & Lucas 1970, Power 1984). However, we did not test whether fish density tracked invertebrate flux in this study."

Previous research also suggests that flow augmentation could have a positive effect on fish foraging profitability and growth. In their 48-day manipulative experiment, Harvey et al. (2006)

diverted a rate and proportion of flow comparable to what we augmented during this BACI experiment. The authors observed that fish in the control units grew 8.5 times more than fish in the impact (diverted) sites and tended to occupy microhabitats at the pool–riffle transition more frequently than did fish in diverted units. Harvey et al. (2006) hypothesized that these difference in growth and behavior were caused by changes in invertebrates drift and microhabitat hydraulics due to decreased flow. Our study supports those hypotheses, with reciprocal empirical, data on flow augmentation.

CONCLUSION

To our knowledge, this study represents the first controlled flow manipulation experiment to quantify the effects of flow enhancement on juvenile salmonids in a small, undammed stream. Flow augmentation from off channel ponds has been implemented opportunistically, as a restoration strategy for salmonids in Northern California (Deitch and Dolman 2017, Ruiz et al. 2019), and our study suggest that this method of flow enhancement can benefit rearing salmonids. However, we did not monitor effects of augmentation on non-target species (e.g. amphibians), explore the duration of augmentation needed to affect adult salmon survival or fitness, or investigate the ecological effects of altering the duration connectivity in an intermittent stream over many years. Our findings suggest that the timing and location of flow enhancement efforts may be as critical to their effect on habitat and ecology as the magnitude of flow restored, but that appropriately timed flow enhancement can significantly improve the profitability and use of pool habitat for juvenile salmonids and other drift foraging fish.

Acknowledgements
This study was co-authored by Mariska Obedzinksi, Weston Slaughter, Keane Flynn, Shelley Pneh, and Theodore Grantham. Critical field and analytical support came from California Sea Grant staff especially Sarah Nossaman Pierce, William Boucher, Andrew Bartshire, and Elizebeth Ruiz. Field and laboratory support from UC Berkeley also included Gunnar Reith, Sam Larkin, and Shannon Mckillop-Herr. Stream gauging was conducted by Trout Unlimited staff led by Mia Van Docto. We thank Gallo Vineyards, especially John Nagle and Tyler Hammond for both access and continued support for our scientific research. Support from CDFW staff -- David Hines and Corinne Grey was much appreciated. Project design and construction was funded through private, state, and federal funds, including a 2015 Wildlife Conservation Board (WCB) grant (Project WC-1553M). Gabriel Rossi was additionally supported by a National Science Foundation CZP EAR-1331940 for the Eel River Critical Zone Observatory.

Literature Cited

Annear, T. C., P. Aarrestad, A. Locke, H. A. Beecher, I. Chisholm, K. B. Mayes, J. Marshall, C. E. Coomer, J. Hunt, R. Jacobson, G. Jobsis, J. Kauffman, G. Smith, R. Wentworth, C. B. Stalnaker, C. C. Estes, and Instream Flow Council (U.S.). 2004. Instream flows for riverine resource stewardship. Instream Flow Council, Cheyenne, Wyo.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-Mass Relationships for Freshwater Macroinvertebrates in North America with Particular Reference to the Southeastern United States. Journal of the North American Benthological Society 18:308–343.

Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83–138 Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats. Edited by William R. Meehan. American Fisheries Society Special Publication.

Bogan, M. T., J. L. Hwan, and S. M. Carlson. 2015. High Aquatic Biodiversity in an Intermittent Coastal Headwater Stream at Golden Gate National Recreation Area, California. Northwest Science 89:188–197.

Boughton, D. A., H. Fish, J. Pope, and G. Holt. 2009. Spatial patterning of habitat for *Oncorhynchus mykiss* in a system of intermittent and perennial streams. Ecology of Freshwater Fish 18:92–105.

Brodeur, R. D. 1991. Ontogenetic variations in the type and size of prey consumed by juvenile coho,Oncorhynchus kisutch, and chinook,O. tshawytscha, salmon. Environmental Biology of Fishes 30:303–315.

Burrows, R. M., H. Rutlidge, N. R. Bond, S. M. Eberhard, A. Auhl, M. S. Andersen, D. G. Valdez, and M. J. Kennard. 2017. High rates of organic carbon processing in the hyporheic zone of intermittent streams. Scientific Reports 7:13198.

CDEC (California Data Exchange Center). 2020. Annual precipitation data for the Sonoma County Airport Weather Station. Retrieved from California Data Exchange Center [May 7th, 2020]. https://cdec.water.ca.gov/dynamicapp/selectQuery

CDFW (California Department of Fish and Wildlife). 2017. Critical Riffle Analysis for Fish Passage in California. California Department of Fish and Wildlife Instream Flow Program Standard Operating Procedure CDFW-IFP-001, 25 p. Available at: https://www.wildlife.ca.gov/Conservation/Watersheds/Instream-Flow/SOP.

CDFW (California Department of Fish and Wildlife). 2013. Standard Operating Procedure for Discharge Measurements in Wadeable Streams in California. California Department of Fish and Wildlife Instream Flow Program Standard Operating Procedure CDFW-IFP-002, 24 p. Available at: http://www.dfg.ca.gov/water/instream_flow.html.

Carlisle, D.M., Wolock, D.M., Konrad, C.P., McCabe, G.J., Eng, K., Grantham, T.E., and Mahler, B., 2019, Flow modification in the Nation's streams and rivers: U.S. Geological Survey Circular 1461, 75 p. https://doi.org/10.3133/cir1461.

Chapman, D. W. 1966. Food and Space as Regulators of Salmonid Populations in Streams. The American Naturalist 100:345–357.

Connell, J. H. 1974. Field Experiments in Marine Ecology. Pages 21–54 Experimental Marine Biology. Edited by R. Mariscal. Academic Press, New York, NY.

Deitch, M., and B. Dolman. 2017. Restoring Summer Base Flow under a Decentralized Water Management Regime: Constraints, Opportunities, and Outcomes in Mediterranean-Climate California. Water 9:29.

Deitch, M. J., G. M. Kondolf, and A. M. Merenlender. 2009. Surface water balance to evaluate the hydrological impacts of small instream diversions and application to the Russian River basin, California, USA. Aquatic Conservation: Marine and Freshwater Ecosystems 19:274–284.

Ebersole, J. L., P. J. Wigington, J. P. Baker, M. A. Cairns, M. R. Church, B. P. Hansen, B. A. Miller, H. R. LaVigne, J. E. Compton, and S. G. Leibowitz. 2006. Juvenile Coho Salmon Growth and Survival across Stream Network Seasonal Habitats. Transactions of the American Fisheries Society 135:1681–1697.

Fausch, K. D., and R. J. White. 1981. Competition Between Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*) for Positions in a Michigan Stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220–1227.
Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–451.
Fausch, K. D., S. Nakano, and S. Khano. 1997. Experimentally induced foraging mode shift by sympatric chairs in a Japanese mountain stream:7.
Ficklin, D. L., Y. Luo, I. T. Stewart, and E. P. Maurer. 2012. Development and application of a hydroclimatological stream temperature model within the Soil and Water Assessment Tool: STREAM TEMPERATURE MODEL. Water Resources Research 48.
Fretwell, S. D., and H. L. Lucas, JR. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–32.
Grantham, T. E., M. Mezzatesta, D. A. Newburn, and A. M. Merenlender. 2014. Evaluating Tradeoffs Between Environmental Flow Protections And Agricultural Water Security: Environmental Flows And Agricultural Water Security. River Research and Applications 30:315–328.
Grantham, T. E., D. A. Newburn, M. A. McCarthy, and A. M. Merenlender. 2012. The Role of Streamflow and Land Use in Limiting Oversummer Survival of Juvenile Steelhead in California Streams. Transactions of the American Fisheries Society 141:585–598.
Hahm, W. J., D. N. Dralle, D. M. Rempe, A. B. Bryk, S. E. Thompson, T. E. Dawson, and W. E. Dietrich. 2019. Low Subsurface Water Storage Capacity Relative to Annual Rainfall Decouples Mediterranean Plant Productivity and Water Use From Rainfall Variability. Geophysical Research Letters 46:6544–6553.
Hanak, E., J. Mount, C. Chappelle, J. Lund, J. Medellin-Azuara, P. Moyle, and N. Seavy. 2015. What If California's Drought Continues? San Francisco: PPIC Water Policy Center:20.
Harmel, R. D., Cooper, R. J., Slade, R. M., Haney, R. L., and Arnold, J. G. 2006. Cumulative uncertainty in measured streamflow and water quality data for small watersheds. Transactions of the ASABE 49:689–701.
Harrelson, C. C., C. L. Rawlins, and J. P. Potyondy. 1994. Stream channel reference sites: An illustrated guide to field technique. Page RM-GTR-245. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO.
Harvey, B. C., R. J. Nakamoto, and J. L. White. 2006. Reduced Streamflow Lowers Dry-Season Growth of Rainbow Trout in a Small Stream. Transactions of the American Fisheries Society 135:998–1005.
Harvey, B. C., J. L. White, R. J. Nakamoto, and S. F. Railsback. 2014. Effects of Streamflow Diversion on a Fish Population: Combining Empirical Data and Individual-Based Models in a Site-Specific Evaluation. NA Journal of Fisheries Management 34:247–257.
Hwan, J. L., and S. M. Carlson. 2016. Fragmentation of an Intermittent Stream During Seasonal Drought: Intra-annual and Interannual Patterns and Biological Consequences: Stream Contraction During Seasonal Drought. River Research and Applications 32:856–870.
Hwan, J. L., A. Fernández-Chacón, M. Buoro, and S. M. Carlson. 2018. Dry season survival of juvenile salmonids in an intermittent coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 75:746–758.
Jeffres, C., and P. Moyle. 2012. When Good Fish Make Bad Decisions: Coho Salmon in an Ecological Trap. North American Journal of Fisheries Management 32:87–92.

Kendy, E., Aylward, B., Ziemer, L.S., Richter, B.D., Colby, B.G., Grantham, T.E., Sanchez, L., Dicharry, W.B., Powell, E.M., Martin, S. and Culp, P.W. 2018. Water transactions for streamflow restoration, water supply reliability, and rural economic vitality in the western United States. JAWRA Journal of the American Water Resources Association, 54(2), pp.487-504.

Leopold, L. B., and M. G. Wolman. 1957. River Channel Patterns: Braided, Meandering, Straight. U.S. Geological Survey Professional Papers, U.S. Geological Survey.

Lovill, S. M., W. J. Hahm, and W. E. Dietrich. 2018. Drainage from the Critical Zone: Lithologic Controls on the Persistence and Spatial Extent of Wetted Channels during the Summer Dry Season. Water Resources Research 54:5702–5726.

Matthews, W. J., B. C. Harvey, and M. E. Power. 1994. Spatial and temporal patterns in the fish assemblages of individual pools in a midwestern stream (U.S.A.). Environmental Biology of Fishes 39:381–397.

McBain and Trush, Trout Unlimited. 2000. Allocating Streamflows to Protect and Recover Threatened Salmon and Steelhead Populations in the Russian River and other Northcoast Rivers of California. Unpublished Report. Accessed April 2019. URL: http://www.krisweb.com/biblio/ncc_troutunlimited_mcbainetal_2000.pdf

Miyasaka, H., S. Nakano, and T. Furukawa-Tanaka. 2003. Food habit divergence between white-spotted charr and masu salmon in Japanese mountain streams: circumstantial evidence for competition. Limnology 4:1–10.

Mierau, D. W., W. J. Trush, G. J. Rossi, J. K. Carah, M. O. Clifford, and J. K. Howard. 2018. Managing diversions in unregulated streams using a modified percent-of-flow approach. Freshwater Biology 63:752–768.

Naman, S. M., J. S. Rosenfeld, and J. S. Richardson. 2016. Causes and consequences of invertebrate drift in running waters: from individuals to populations and trophic fluxes. Canadian Journal of Fisheries and Aquatic Sciences 73:1292–1305.

Naman, S. M., J. S. Rosenfeld, P. M. Kiffney, and J. S. Richardson. 2018. The energetic consequences of habitat structure for forest stream salmonids. Journal of Animal Ecology 87:1383–1394.

Naman, S. M., J. S. Rosenfeld, E. Jordison, M. Kuzyk, and B. C. Eaton. 2020. Exploitation of Velocity Gradients by Sympatric Stream Salmonids: Basic Insights and Implications for Instream Flow Management. North American Journal of Fisheries Management 40:320–329.

National Marine Fisheries. 2012. Final Recovery Plan for Central California Coast coho salmon Evolutionarily Significant Unit. NMFS.

Neuswanger, J. R., M. S. Wipfli, A. E. Rosenberger, and N. F. Hughes. 2016. Measuring fish and their physical habitats: versatile 2D and 3D video techniques with user-friendly software. Canadian Journal of Fisheries and Aquatic Sciences 73:1861–1873.

Obedzinski, M., S. Nossaman Pierce, G. E. Horton, and M. J. Deitch. 2018. Effects of Flow-Related Variables on Oversummer Survival of Juvenile Coho Salmon in Intermittent Streams. Transactions of the American Fisheries Society 147:588–605.

Poff, N. L., and J. K. H. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows: Review of altered flow regimes. Freshwater Biology 55:194–205.

Popescu, V. D., P. D. Valpine, D. Tempel, and M. Z. Peery. 2012. Estimating population impacts via dynamic occupancy analysis of Before–After Control–Impact studies. Ecological Applications 22:1389–1404.
Power, M. E. 1984. Habitat Quality and the Distribution of Algae-Grazing Catfish in a Panamanian Stream. The Journal of Animal Ecology 53:357.
Power, M. E., K. Bouma-Gregson, P. Higgins, and S. M. Carlson. 2015. The Thirsty Eel: Summer and Winter Flow Thresholds that Tilt the Eel River of Northwestern California from Salmon-Supporting to Cyanobacterially Degraded States. Copeia 103:200–211.
Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, and B. Statzner. 1988. Biotic and Abiotic Controls in River and Stream Communities. Journal of the North American Benthological Society 7:456–479.
Rantz, S. E. 1982. Measurement and computation of streamflow: Volume 2, Computation of Discharge. Pages 285–631. Water Supply Paper.
Rosenfeld, J. S. 2017. Developing flow-ecology relationships: Implications of nonlinear biological responses for water management. Freshwater Biology 62:1305–1324.
Rossi, G.J, D. W. Mierau, W. J. Trush, J. K. Carah. 2020. Hydraulic Properties of the Riffle Crest and Applications for Stream Ecosystem Management. Manuscript Submitted to Journal of the American Water Resources Association (April 2020).
Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length–mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society 21:336–343.
Sloat, M. R., and A.-M. K. Osterback. 2013. Maximum stream temperature and the occurrence, abundance, and behavior of steelhead trout (*Oncorhynchus mykiss*) in a southern California stream. Canadian Journal of Fisheries and Aquatic Sciences 70:64–73.
Smokorowski, K. E., and R. G. Randall. 2017. Cautions on using the Before-After-Control-Impact design in environmental effects monitoring programs. FACETS 2:212–232.
Svendsen, C. R., T. Quinn, and D. Kolbe. 2004. Review of Macroinvertebrate Drift. Wildlife Research Program, Environmental and Safety Division, Seattle City Light:92.
Taube, Clarence. M. 2000. Instructions for winter lake mapping. Chapter 12 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.Taube, Clarence M. 2000.:6.
Tonina, D., and J. M. Buffington. 2007. Hyporheic exchange in gravel bed rivers with pool-riffle morphology: Laboratory experiments and three-dimensional modeling: Hyporheic exchange in gravel bed rivers. Water Resources Research 43.
Tonkin, J. D., B. O. David, and Nathania Brooke. 2013. Some morphometric measurements of juvenile rainbow trout (Oncorhynchus mykiss) and inanga (Galaxias maculatus) relevant to fish passage remediation. Figshare.
Underwood, A. J. 2009. Components of Design in Ecological Field Experiments. Annales Zoologici Fennici 46:93–111.
US EPA. 1986. Ambient Water Quality Criteria for Dissolved Oxygen. United States Environmental Protection Agency, Washington, DC.
USFWS. 2017. Fish Passage Engineering Design Criteria. U.S. Fish and Wildlife Service, Northeast Region R5, Hadley, Massachusetts.

Vander Vorste, R., M. Obedzinski, S. Nossaman Pierce, S. M. Carlson, and T. E. Grantham. 2020. Refuges and ecological traps: extreme drought threatens persistence of an endangered fish in intermittent streams. Global Change Biology:gcb.15116.
Walters, A. W. 2016. The importance of context dependence for understanding the effects of low-flow events on fish. Freshwater Science 35:216–228.
Wetzel, R. G. 2001. Limnology: lake and river ecosystems. 3rd ed. Academic Press, San Diego.
Wigington, P., J. Ebersole, M. Colvin, S. Leibowitz, B. Miller, B. Hansen, H. Lavigne, D. White, J. Baker, M. Church, J. Brooks, M. Cairns, and J. Compton. 2006. Coho salmon dependence on intermittent streams. Frontiers in Ecology and Environment 4:513–518.
Woelfle-Erskine, C., L. G. Larsen, and S. M. Carlson. 2017. Abiotic habitat thresholds for salmonid over-summer survival in intermittent streams. Ecosphere 8:e01645.
Wohl, E. 2017. The significance of small streams. Frontiers of Earth Science 11:447–456.

SUPPLEMENTAL MATERIALS

Supplemental Table 1. Operational definitions of environmental flow terminology

Terminology	Operational Definition
Flow alteration	The anthropogenic modification of a stream's natural flow regime. This can be through flow impoundment, withdrawal, augmentation or channel influences (like aggradation).
Flow augmentation	The anthropogenic addition of water to a river or stream.
Flow restoration	Efforts to recover specific or general elements (timing, duration, frequency, magnitude) of the "unimpaired" or "natural" hydrograph, in systems that have been impaired. This can be accomplished by reducing flow alteration, by flow augmentation, or sometimes by habitat modification.
Flow enhancement	Efforts to recover specific or general elements of desired biotic and ecological response through flow restoration or flow augmentation.

Supplemental Table 2. Definition of Foraging Behaviors Used in VidSync Analysis

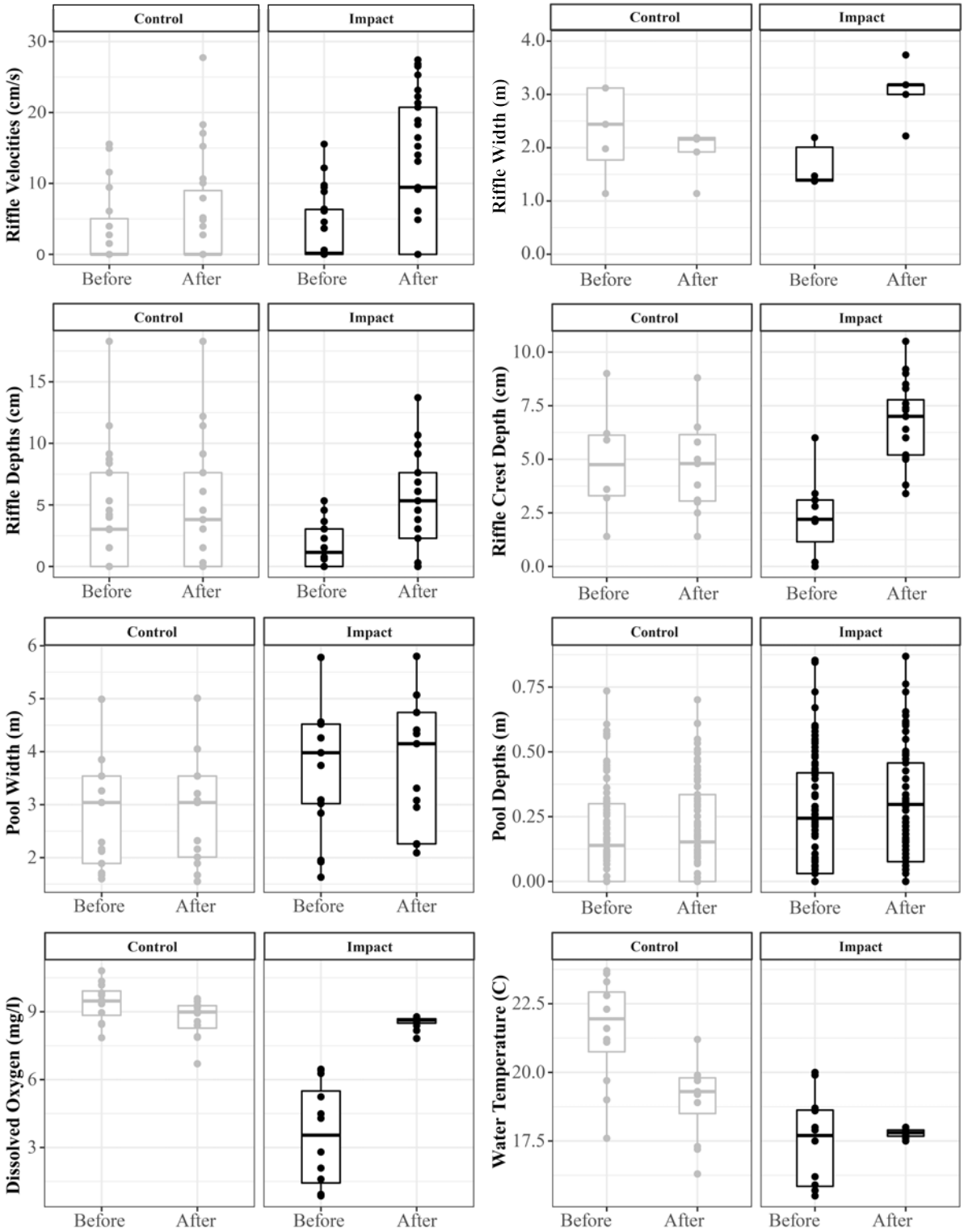
Foraging Mode	**Definition**
Drift Foraging	Fish holds focal points in the water column and makes short forays to intercept drift, with only occasional attacks on benthic prey near their focal points (Nakano et al. 1999a).
Benthic Foraging	Fish primarily cruise over larger areas of stream-bed and capture benthic prey by making forceful attacks at the substrate (Nakano et al. 1999a).
Search Foraging	Fish undertake continuous undirected swimming, foraging was not associated with a focal point, and fish consumed drift, falling, or benthic prey (adapted from Neilsen 1992).
Foraging Event	**Definition**
Surface Strike	A fish swims towards the surface and either attempts to or successfully bites an item floating on or just under the water surface (Suttle et al. 2004).
Attacks	A fish makes a rapid, aggressive darting approach toward another fish without making direct contact ("attacks" in Neilsen 1992).
Nips	A fish rapidly approached another fish and gives it a bite (Neilsen 1992).

Supplemental Table 3. Summary Statistics for Wetted Habitat Mapping in 2017, 2018, and 2019. Values are computed as percent of channel length from augmentation (rkm 2.74) to Russian River confluence (rkm 0).

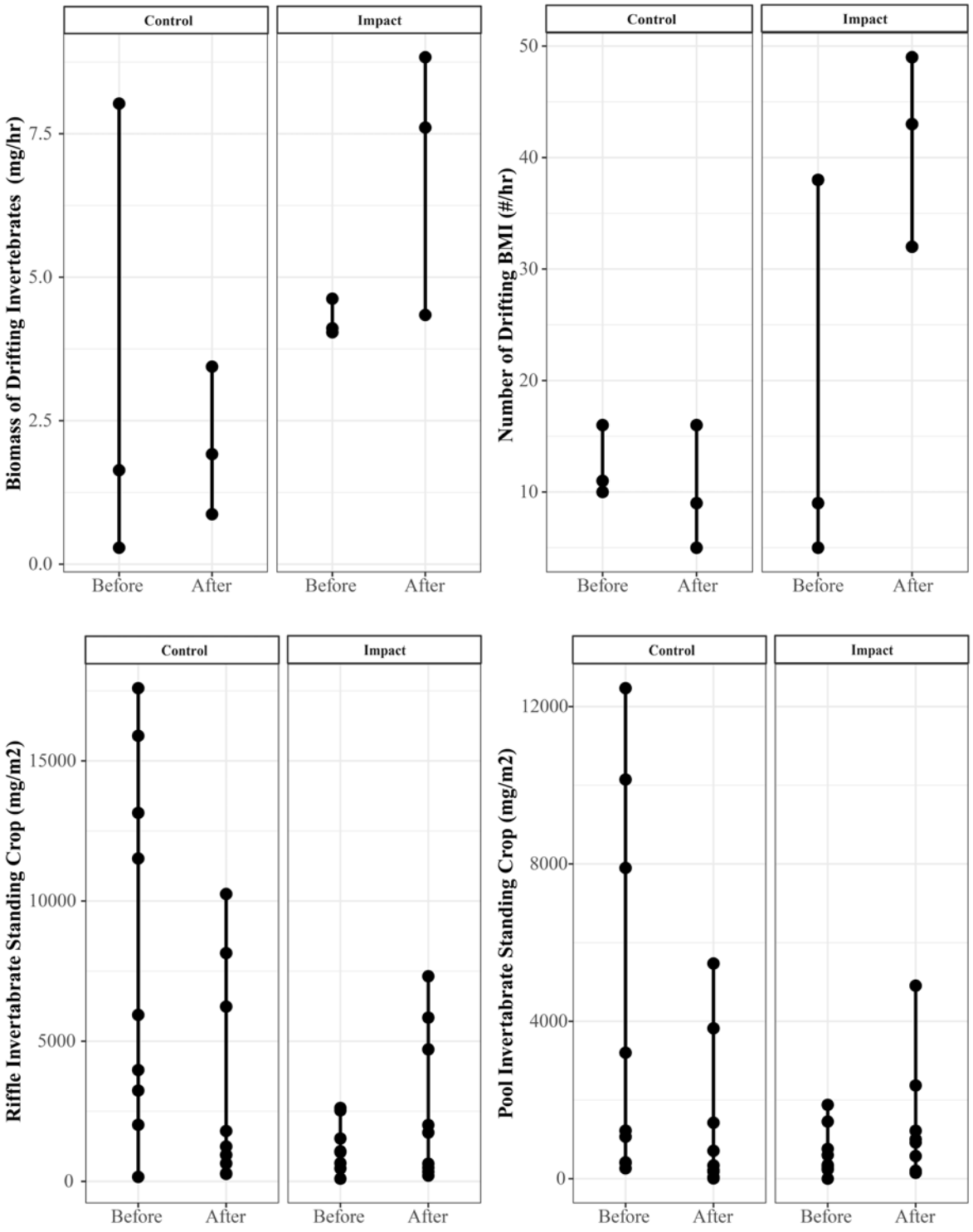
Date	Augmentation (L/s)	%Wet	%Intermittent	%Dry	% Intermittent or Dry
6/26/18	0	0.66	0.10	0.23	0.34
7/5/18	24.6	0.94	0.00	0.06	0.06
9/4/18	6.3	0.57	0.15	0.29	0.43
7/19/17	0	0.72	0.04	0.24	0.28
8/17/17	24.6	0.92	0.00	0.08	0.08
9/14/17	6.3	0.61	0.00	0.39	0.39
7/9/19	0	0.94	0.00	0.06	0.06
7/26/19	24.6	0.93	0.00	0.07	0.07
9/13/19	6.3	0.84	0.00	0.16	0.16

Supplemental Figure 1. The plumbing manifold for the Porter Creek augmentation structure.

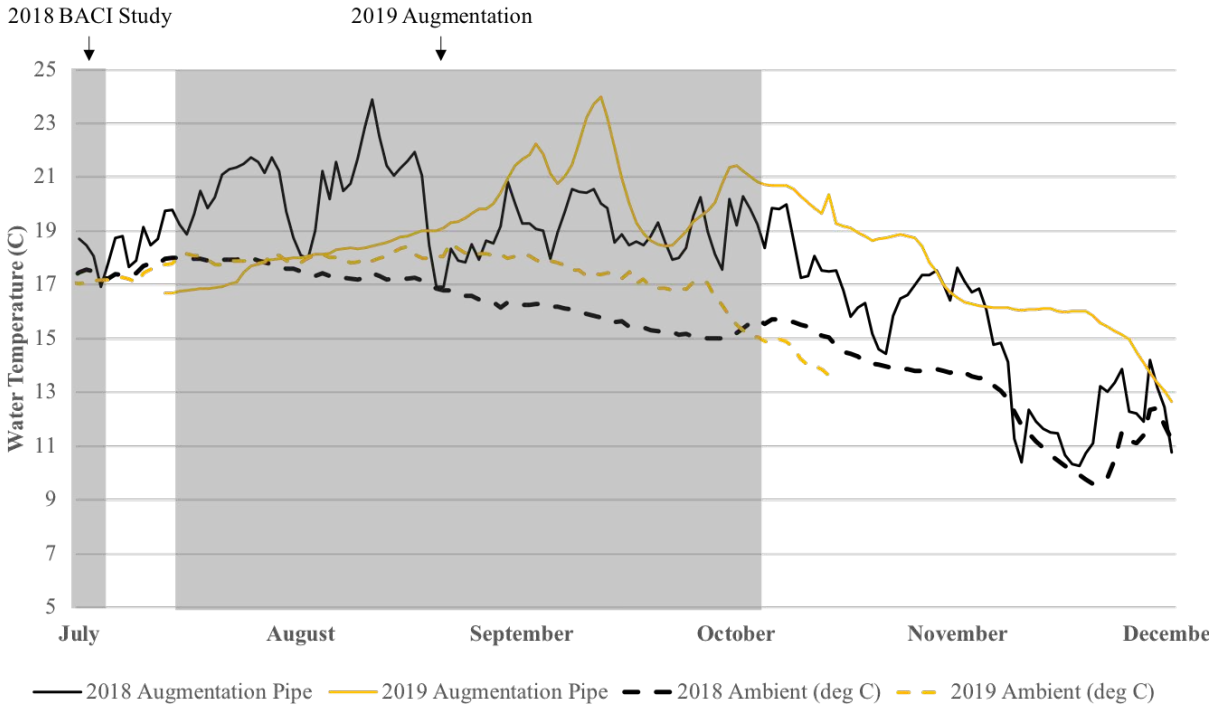
Supplemental Figure 2. The Porter Creek – Russian River confluence showing the highly porous, and often backwatered channel of lower Porter Creek. This reach goes dry every year and seems particularly sensitive to river stage.



Supplemental Figure 3. Hydraulic habitat and water quality (manual) variables collected in the control and impact sites, before and after streamflow augmentation in Porter Creek (June 29 to July 7th 2018)



Supplemental Figure 4. Invertebrate drift flux and standing crop, collected control and impact sites, before and after streamflow augmentation in Porter Creek (June 29 to July 7th 2018).



Supplemental Figure 5. Measured water temperature in the augmentation pipe in 2018 and 2019. Water temperature in the augmentation pipe was not measured in 2017 and was only measured after July in 2018 and 2019.

Supplemental Figure 6. The lower augmentation point (see Fig. 1) in Porter Creek, augmentation rate is 13.9 L/s

Chapter 2 – 3 Transition

In Chapter 1, I observed that streamflow and invertebrate drift in Elder Creek were only weakly correlated across the spring-summer recession – leading me to wonder about how these variables interacted seasonally to affect salmon growth in different streams. In addition, the poor correlations between drift and foraging mode led me to speculate that the increase of benthic and search foraging in late summer may not only reflect declining drift profitability but also the potentially increasing availability of benthic standing crop and infall of aquatic and terrestrial prey; however, I did not measure these prey fluxes in Chapter 1. After spending time on Porter Creek (Chapter 2) and Elder Creek (Chapter 1) I was struck by their extreme differences in physical habitat and apparent food web structure – yet both streams had sustained runs of *O. mykiss* and Porter Creek was also home to a recovering population of *O. kisutch*. How could these vastly different streams support the same species? In conversations with Mary Power and Bill Trush I began to develop a conceptual model for how stream hydraulics and secondary production would interact to support rearing salmon during the Mediterranean recession (See Figure 1 in Chapter 3).

Collectively these observation, and our new conceptual model led me to design a comparative study between Elder and Porter Creek in which I would collect seasonal data from each level of the salmon bearing food web, and measure multiple prey fluxes over the spring-summer Mediterranean recession (Figure T2-3)–to try and understand how *O. mykiss* were able to adapt and grow in these different streams.

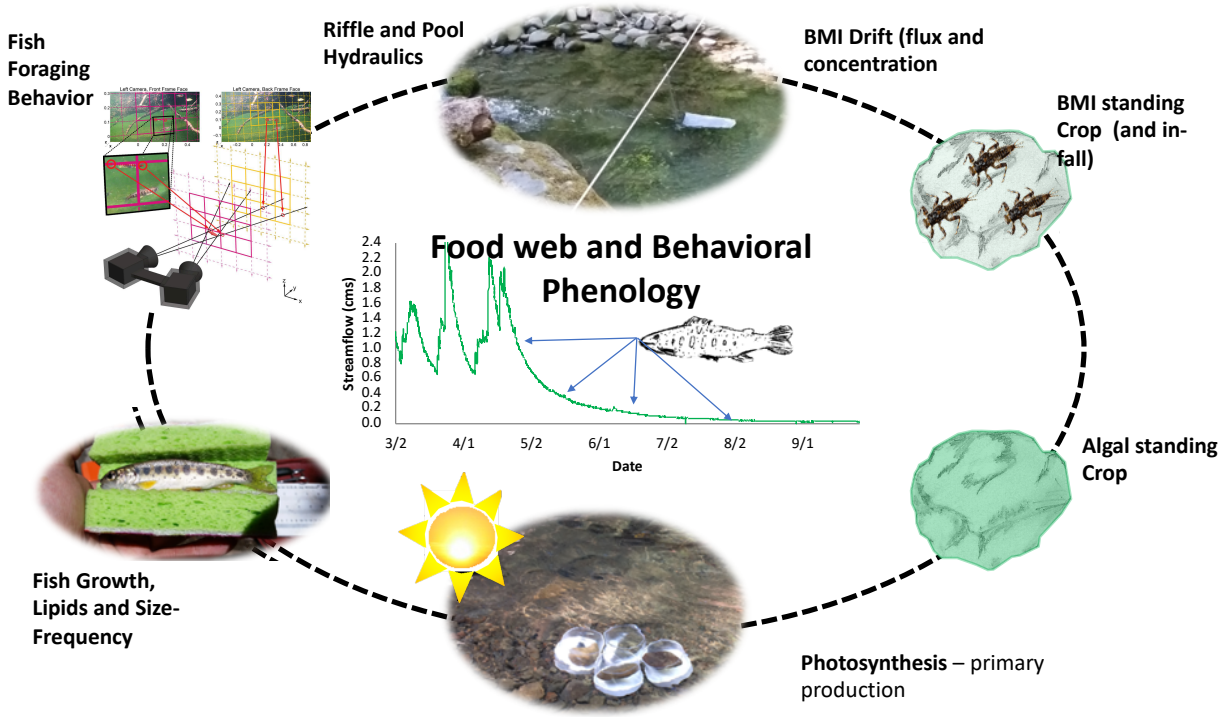


Figure T2-3. The original study design for a comparative food web study between Elder and Porter Creek (Chapter 3) for which I planned to measure: streamflow, dissolved oxygen, and water temperature; epibenthic primary production and algal standing crop; seasonal invertebrate drift, standing crop, and infall and, salmonid foraging behavior and movement (using 3-D videogrammetry), and salmonid growth and lipid allocation.

CHAPTER 3

Seasonal growth potential of *Oncorhynchus mykiss* in streams with contrasting prey phenology and streamflow recessions

ABSTRACT

The growth of stream predators depends on hydraulic habitat, prey concentration, and their interaction. However, the seasonality of this interaction has received little attention in salmon ecology. Here we propose a conceptual model for how the seasonal recession of hydraulic habitat *relative to* the phenology of prey biomass affects the growth and foraging behavior of juvenile steelhead *(Oncorhynchus mykiss)* in Mediterranean coastal streams. We evaluated our conceptual model by comparing two California streams – one perennial, cool, and shaded; the other intermittent, seasonally warm, and sunny. Both streams offered profitable foraging opportunities for pool-dwelling *O. mykiss,* but modeled growth potential for drift foraging fish peaked at least two months earlier, and measured mid-July lipid storage was nearly twice as high, in the intermittent stream. In contrast, modeled and measured early-summer growth was higher in the perennial stream. By late summer, foraging profitability declined in both streams. However abiotic conditions approached lethal tolerance levels in the intermittent stream whereas the perennial stream maintained suitable abiotic conditions all summer. Seasonal changes in growth *potential* were explained by the timing of streamflow recession relative to the phenology of prey fluxes. But ecological interactions (especially intraspecific competition) and flexible foraging behavior both appear to have mediated *realized* foraging opportunity. These observations lead us to speculate that juvenile *O. mykiss* life histories should differ between streams, due to the timing of their spring-summer growth potential and to differing late summer survival rates. Collectively, these stream types could contribute to a stabilizing portfolio of juvenile salmonid life histories.

INTRODUCTION

Foragers in seasonally dynamic environments must track fluctuating food resources while avoiding risks and managing metabolic costs that shift through space and time (Elton 1927, Dill 1983, Fausch 1984). Few if any habitats are more dynamic than rivers, where fluctuations in streamflow over diel, seasonal, and inter-annual time scales drive changing environmental conditions. Streamflows expand, contract, link and disconnect habitats; and periodically, reset food webs via bed scouring floods, or dewatering during drought (Power et al. 1988, Trush et al 2000, Poff et al. 1997). This hydrologic variability exerts a strong effect on the spatial and temporal patterns of hydraulic habitat (depth, velocity, shear-stress), as well as energy flow, biomass and biotic interactions in river food webs (Power and Dietrich 2002, Power et al. 2013). For foraging predators in streams, the *interaction* of hydraulic habitat with prey biomass is a driver of growth potential (Fausch et al. 1984, Hughes and Dill 1990). However, hydraulic habitat is not necessarily strictly coupled to the phenology of aquatic and terrestrial carbon fluxes that drive prey biomass (See Chapter 1). Therefore, to understand seasonal growth potential for

predators in river ecosystems, it is necessary to understand how hydraulic habitat changes *relative to* the phenology of prey biomass.

Mediterranean streams along the Pacific Coast of California epitomize the importance of interacting hydrologic seasonality and prey phenology for aquatic consumers. In these systems, the timing and rate of the annual spring-summer streamflow recession relative to seasonal fluctuations in food availability is a key driver of growth potential for many aquatic consumers such as foot hill yellow legged frog (*Rana boylii*) (Railsback et al. 2016, Kupferberg et al. 2011), pacific salmon (*Oncorhynchus)* (Hayes et al. 2008, Smith and Li 1983), and benthic macroinvertebrates (Beche et al. 2006, Gasith and Resh 1999). Streamflow begins to recede after the last spring rains following approximate power law functions (Dralle et al. 2017), and causing non-linear declines in flow velocity and instream hydraulic complexity. Simultaneously, as days lengthen from spring into summer and channels warm and clear, primary (algal and plant) and secondary (invertebrate) productivity initially increase, enhancing terrestrial and benthic food supplies for secondary consumers (Gasith and Resh 1999, Power et al. 2013, Nakano and Murakami 2001). Later in the summer; however, primary and secondary productivity can decline with habitat contraction, thermal stress and stagnation during late-summer drought (Hayes et al. 2008, Power 2013, Smith and Li 1983, Gasith and Resh 1999).

Juvenile salmon foraging in Pacific coastal streams make an ideal case study to investigate the effect of the seasonal interaction of hydraulic habitat and prey phenology on consumers for two reasons. First there has been extensive, mechanistic and bioenergetic modeling of how levels of hydraulic habitat and prey biomass affect salmonid growth potential (Hughes and Dill 1990, Harvey and Railsback 2009, Piccolo et al. 2014). And second the continuous change in physical and biotic variables that occur over the seasonal hydrograph recession is an ideal backdrop for natural experiments (Yarnell et al. 2010). The foraging environment and energetic costs experienced by juvenile salmonids rearing in streams, as well as their ability to capture drifting prey, are controlled by stream hydraulics and water quality conditions (Smith and Li 1983, Fausch et al. 1984, Nielson 1992, Harvey and Railsback 2009, Piccolo et al. 2014). However, the concentration and quality of prey available for foraging salmonids is determined, in large part, by the phenology of primary and secondary production in streams or donor habitats (Power and Rainey 2000, Wiplfi and Baxter 2010, Naman et al. 2016). While the interaction of stream hydraulics, water quality, and prey concentration is central to predicting salmonid performance in bioenergetics (e.g. Fausch 1984, and Dill 1990, Naman et al. 2019a) and food web models (Power et al. 1995, Bellmore et al. 2017, Saunders et al. 2018), the seasonal and phenological aspect of this interaction has received little treatment in the literature (but see Wiplfi and Baxter 2010 and Ebersole 2006).

In this study, we investigated the growth potential and foraging behavior of juvenile steelhead trout (*O. mykiss*) across changing levels of prey phenology and hydraulic habitat in two Mediterranean streams. Both are salmon bearing, rainfall dominated California coastal streams; however, Elder Creek is perennial, cool, and shaded; while Porter Creek is intermittent, seasonally warm, and sunny. We hypothesized that (H1) countervailing gradients of (waning) hydraulic advection and (waxing) secondary productivity in both systems should produce a distinct seasonal spring or early summer peak in growth potential for drift foraging juvenile salmonids (see Fig. 1 for a schematic). We modeled growth potential, as net rate of energetic

intake (NREI) using drift foraging bioenergetics model (Hughes and Dill 1990, Rosenfeld and Taylor 2009, Caldwell et al. 2018). Pool-dwelling juvenile salmon feed primarily on drift or infall of invertebrates (Chapman 1966, Naman et al. 2018), which are largely fueled by the growth of epilithic periphyton in spring and early summer in Mediterranean streams (Power and Dietrich 2002). Therefore we also hypothesized that the seasonal interactions between stream hydraulics, primary production, and epilithic periphyton would create an earlier peak in the flux (mass/time) of invertebrates drifting into pools (H1a), driven by high velocity; and a later peak in invertebrate concentration (mass/volume) in pools (H1b) – driven by increasing (primary and then) secondary production and declining velocity (Fig. 1).

We also hypothesize that (H2) salmonid foraging behavior should change seasonally as fish adjust to changing prey availability and increasing metabolic costs (Dill 1983, Nielson 1992, Rossi at al. 2020 in review, Fig. 1). As the profitability of drift foraging declines, fish are expected to switch from drift to search foraging (H2a), and aggression may increase (H2b) (Nielson 1992, see Chapter 1). Finally, we hypothesized (H3a) that the timing of peak spring and summer seasonal growth opportunity and (H3b) the severity of late summer metabolic stress, driven by declining prey and water quality conditions (Bjornn and Reisser 1991) would vary between streams due to their different seasonal hydraulic regimes and prey phenologies, which, in turn are driven by differences in watershed geology, local climate, land cover, and antecedent food web states (Power et al. 2008, Hahm et al. 2019)

METHODS

Study Sites

Both study streams flow through the Northern California Coast Range north of the San Francisco Bay Area (Fig. 2). Elder Creek is a 16.7 km^2 tributary of the upper South Fork Eel River in Mendocino County, California (39.7181° N, 123.6527° W), Fig. 2. The watershed is located within the University of California Angelo Coast Range Reserve. The channel of Elder Creek is dominated by cobbles and boulders, with streambed gradients ranging from 2% - 5% (McBain and Trush 2000). The watershed is forested, primarily by old Douglas fir (*Pseudotsuga menziesii*), and broadleaf trees e.g. live oak (*Quercus* spp.) (Rempe and Dietrich 2018). The stream is shaded by a dense riparian canopy, primarily comprised of white alder (*Alnus rhombifolia*), with some bigleaf maple (*Acer macrophyllum*) and Oregon ash (*Fraxinus latifolia*). Elder Creek experiences a characteristic Mediterranean-climate flow recession between April and October (Dralle et al. 2017); however, typical dry season low flows rarely drop below 0.015 to 0.03 m^3/s. The basin is underlain by deep water-holding argillite shales of the Northern California Coastal belt, which sustains perennial flow, even during prolonged drought (Lovill et al. 2018, Rempe and Dietrich 2018).

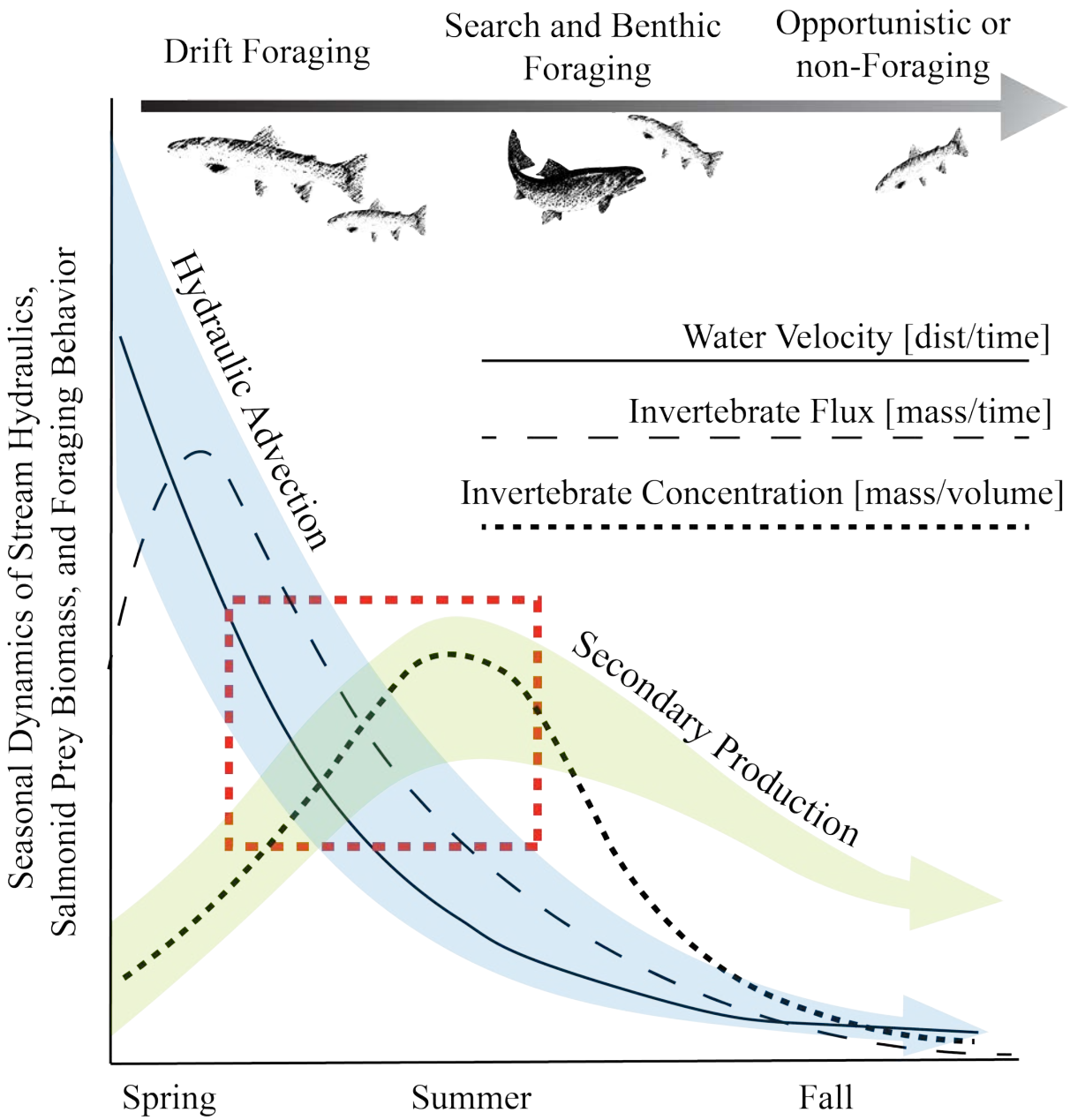


Figure 1. A schematic of seasonal gradients in hydraulic advection and secondary production during the annual flow recession in Mediterranean streams. These combine to produce earlier peaks in drift flux (dashed line) and later peaks in drift concentration (dotted line) from riffles into pools. Growth opportunity for juvenile salmonids is expected to peak (red box) when stream hydraulics support prey capture and prey transport *and* ascending secondary production supports prey biomass. The timing and duration (left to right) and magnitude (top to bottom) of peak growth potential will vary between streams (or reaches) and years as gradients of hydraulic advection and secondary production change. Foraging salmonids adapt their behavior (top) to changing contexts of habitat and prey concentrations.

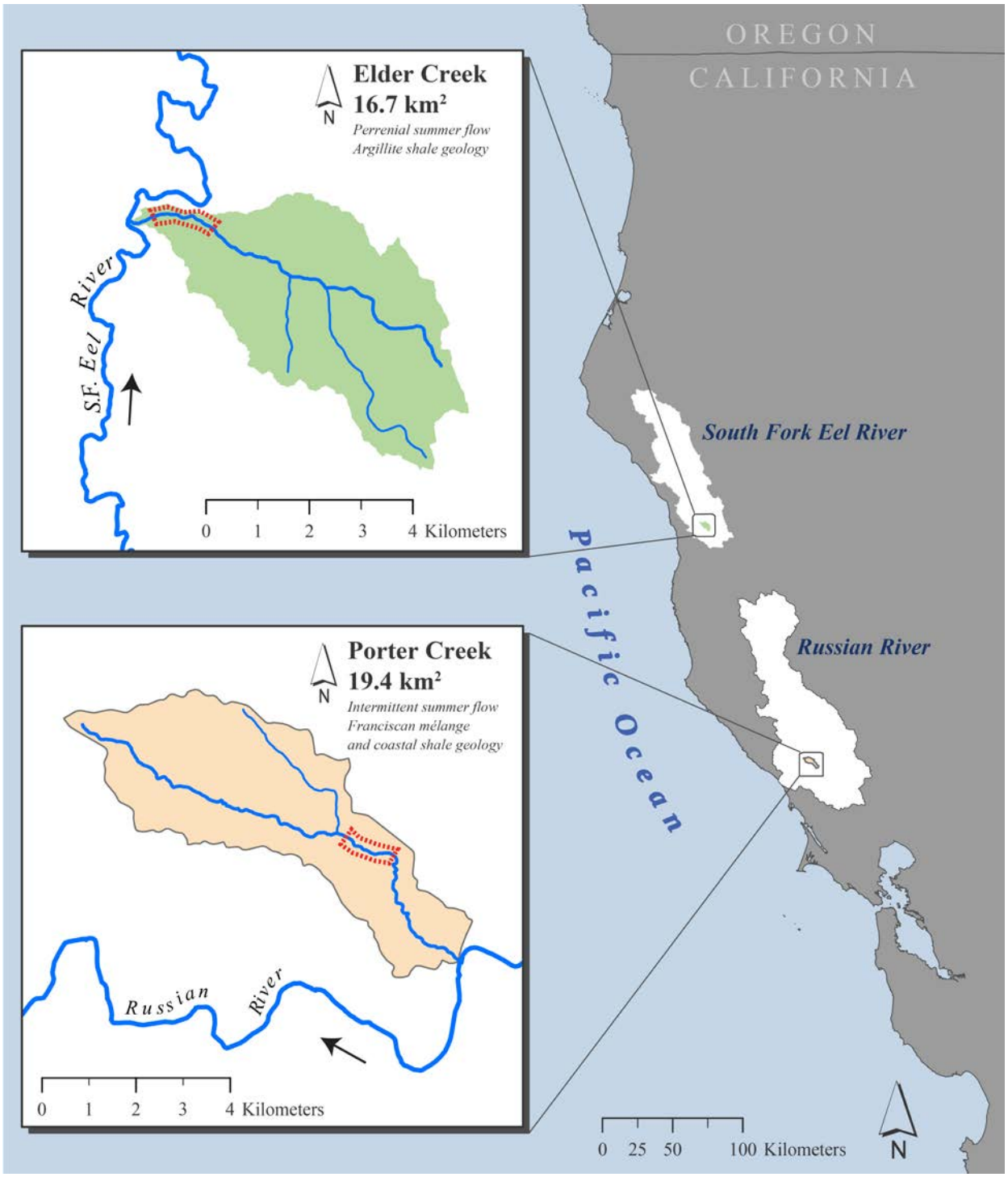


Figure 2. Map of study streams and receiving watersheds—Elder Creek, tributary to the South Fork Eel River in Mendocino County (to the north) and Porter Creek tributary to the Russian River in Sonoma County (to the south). Study reaches are shown in red boxes.

Porter Creek is a tributary to the Russian River in Sonoma County, California (Fig. 2). The 19.4 km^2 watershed is located in California's Coast Range and flows west to east into the Russian River, near the town of Healdsburg. The watershed is entirely privately owned, and managed for timber, livestock and especially wine grape production, although the upper watershed is relatively unimpaired except for some light rural development. Porter Creek is generally low gradient (0.5% to 3%), with a pebble and grave-dominated bed, punctuated by bedrock features in some reaches. The watershed includes mixed coniferous forest of Douglas fir (*Pseudotsuga menziesii*), deciduous oak (*Quercus* spp) and exotic annual grass savanna. The riparian community is a mix of alders (*Alnus* spp.*)*, buckeye (*Aesculus californica*), willow (*Salix* spp*)*, Oregon ash, redwood (*Sequoia sempervirens*) as well as invasive shrubs such as Himalayan blackberry (*Rubus armeniacus*). Except in the wettest years, Porter Creek becomes intermittent during dry season for much of its length, although the upstream-most reaches are typically perennial. The basin's geology is primarily Franciscan complex mélange, although the southern slopes and upper watershed are a mix of mélange and coastal belt shales (Jennings 1977). The Franciscan mélange geology of the Porter Creek basin has much lower hydraulic infiltration capacity and a shallower Critical Zone than Elder Creek, leading to low storage of winter precipitation, flashy hydrologic responses to winter storms, and flow intermittency in the dry season summer (Hahm et al. 2019).

Sampling Regime

Four riffle-pool habitat units were selected in each stream as study site replicates (Fig. 3). The riffle-pool unit is a ubiquitous geomorphic feature in alluvial streams and provides a discrete habitat unit for evaluating juvenile salmonid rearing and foraging during the low-flow period (Matthews et al. 1994, Naman et al. 2018). We selected riffle-pool units that supported multiple age classes of foraging salmonids and had suitable morphology for monitoring behavior (see below).

To test our hypotheses about seasonal interactions between the hydraulic recession, the phenology of prey biomass, and their effect on salmonid growth potential, we measured the following variables between late-April and August: (1) streamflow, dissolved oxygen, and water temperature; (2) seasonal riffle-pool hydraulics (depth, velocity, width, volume); (3) epibenthic primary production and algal standing crop; (4) seasonal invertebrate drift, standing crop, and infall and, (5) salmonid foraging behavior and movement (using 3-D videogrammetry). Habitat and food web sampling events occurred in 2018 on April 28-30; May 13-15; June 13-15; July 11-13; and, August 8-11. Using these data, we compared the seasonality of hydraulics and salmonid prey phenology in both streams, developed a drift foraging bioenergetics model to help predict the timing of *O. mykiss* growth potential, and quantified seasonal changes in the foraging behavior of juvenile *O. mykiss*. We also captured fish to estimate pool-scale size-distributions, growth, and *O. mykiss* lipid content. Fish sampling occurred in 2018 on May 21-23; June 4-8, July 16-19 and (in Elder Creek only), on September 26-27. Methods for each of these data collection are described below and in Appendix 1.

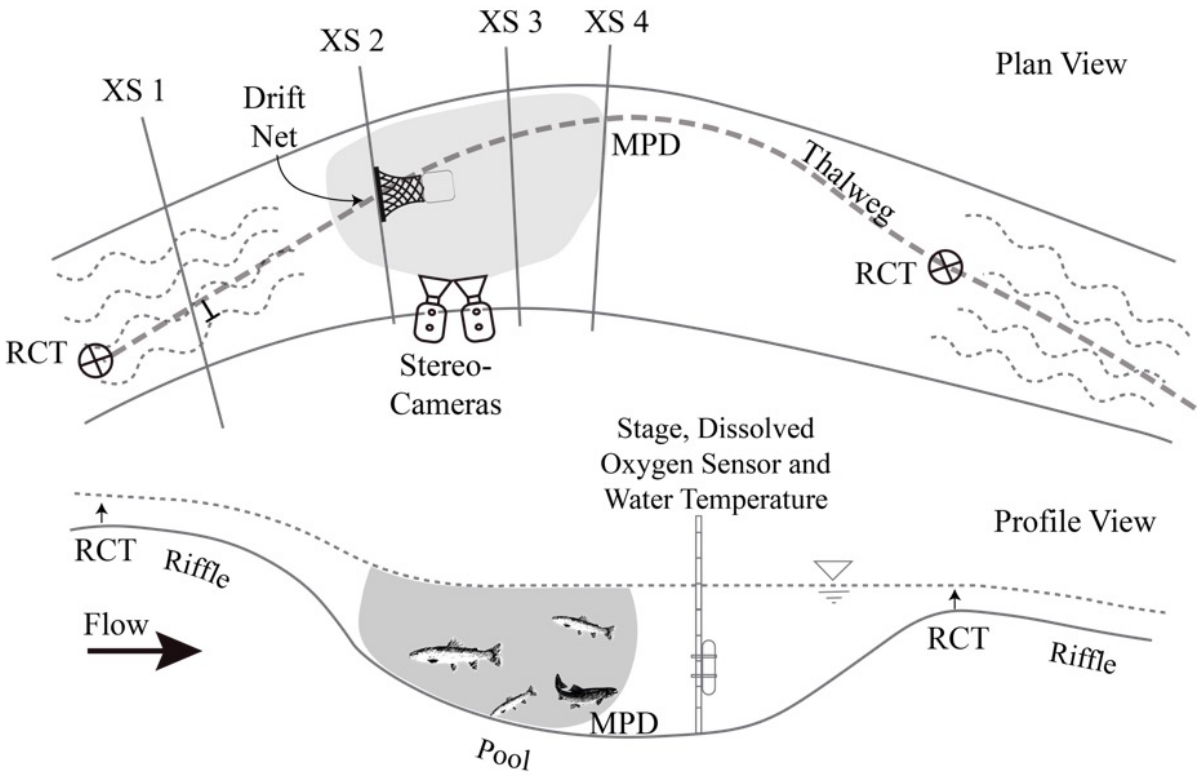


Figure 3. Riffle-Pool study site design (from Chapter 2). RCT = Riffle crest thalweg; MPD = maximum pool depth; shaded area = pool head patch which was filmed.

Seasonal Gradients in Water Quality and Stream Hydraulics

Streamflow, Dissolved Oxygen, and Water Temperature

Streamflow (Q, Table 1) for Elder Creek was retrieved from USGS gaging station 11475560 "Elder Creek near Branscomb CA," which is 0.6 km upstream from the Elder Creek's confluence with the SF Eel River. Each of our Elder Creek study sites were within 0.4 km of this gage. In Porter Creek, streamflow was retrieved from Trout Unlimited (TU) gaging data. TU gaging followed best practices in Rantz (1982) and CDFW Standard Operating Procedures for Discharge Measurements in Wadeable Streams (CDFW 2013).

Dissolved oxygen and water temperature are primary drivers of salmonid tolerance to abiotic conditions (Bjornn and Reiser. 1991), and water temperature was explicitly included in our bioenergetic model (see description of *Seasonal Net Rate of Energy Intake* below). We measured dissolved oxygen and stream temperature using continuous HOBO U26 data loggers in one Elder Creek and one Porter Creek pool. The dissolved oxygen loggers were calibrated prior to deployment, and the output data were corrected using HOBOware Pro's Dissolved Oxygen Assistant software. Calibration measurements were taken using a handheld YSI Pro20 in each pool. In addition, we collected monthly, manual water temperature and dissolved oxygen measurements in each pool when we measured primary production.

Table 1. Operational definitions for habitat, invertebrate, and fish variables.

Terms and Variables	Operational Definition	Units
Pool head patch	The head of the pool – from where the upstream riffle enters the pool to the maximum pool depth (Fig. 3).	m^3
Q	Streamflow	m^3/s or l^3/s
Temperature	Water temperature measured at the maximum pool depth	^oC
DO	Dissolved oxygen at the pool maximum depth	mg/L
Max Depth	Maximum depth at XS 3 (e.g. max pool depth)	m
$Velocity_{max}$ XS_i	The maximum velocity measured on cross-section_i	m/s
$Velocity_{mean}$ XS_i	The maximum velocity measured on cross-section_i	m/s
RCT	Riffle crest depth measured in the thalweg of the shallowest cross section across the hydraulic control	cm
Riffle Width	Wetted width of flow at XS 1 in the upstream riffle	m
Epibenthic Photosynthesis	Primary production rate of epibenthic diatoms.	$mg_{O2} \cdot hr^{-1} \cdot cm^{-2}$
Riffle Epibenthic Algal Standing Crop	Biomass of invertebrates per stream bed area.	mg/cm^2
Pool Epibenthic Algal Standing Crop	Biomass of invertebrates per stream bed area.	mg/cm^2
Drift Flux	Mass of invertebrates caught, per hour, in thalweg drift net	mg/hr
Drift Concentration	Mass of invertebrates per volume measured at head of pool.	mg/cm^3
Invertebrate Standing Crop	Mass of invertebrates per area of the pool bed.	mg/cm^2
Invertebrate Infall	Mass of invertebrates entering from above per area of pool surface per time	$mg \cdot cm^{-2} \cdot hr^{-1}$
Foraging Mode	Counts of observed foraging modes and behaviors: drift foraging, search foraging, benthic foraging, surface strikes, aggression, (see SI Table X1for definitions).	#
Movement per Time	Distance that juvenile salmonids moved per second during x-y minute sample time intervals, computed from VidSync.	cm/s
NREI	Net Rate of Energy Intake, modeled for a 100-mm drift foraging *O. mykiss* in the pool head patch	j/s
Specific Growth	Mass gained in a short interval/starting mass of fish	% body weight gained per day
Lipids	The percent of lipid content in muscle tissue of juvenile salmonids (estimated using non-lethal Fatmeter™).	%

Riffle-Pool Hydraulics

To collect data on seasonal gradients of pool hydraulics (Hypotheses 1 and 3) we installed a cross-stream transect midway through the upstream riffle (XS1), and three cross-stream transects in the downstream pool of each study site. Pool transects were placed where the riffle enters the pool (XS2), a second bisecting the focal area for video (behavior) analysis (XS2), and a third over the maximum depth of the pool (XS3), Fig. 2. Depth and velocity (Table 1) were measured at 0.25-m increments along each cross section. Velocity was measured with a Marsh-McBirney Flo-Mate 2000 Electro-magnetic Flow Meter. The wetted width of each transect was measured during each sampling event. Volume was also calculated between each cross section, and estimated for the whole pool, on each survey date, using the "average end" method (Taube 2000).

The Phenology of *O. mykiss* Prey

Primary Production

The phenology of secondary production (including invertebrate salmon prey) is linked to the seasonality of primary production in streams (Power et al. 2002). To track the seasonality of primary production (H1b) we estimated epibenthic primary productivity in riffles and pools, by measuring periphyton net primary production (NPP) and respiration (R) on individual cobbles using the light/dark incubation method of Hall and Moll (1975). Analysis was conducted using transparent, airtight chambers under light (net primary production) and dark (respiration) conditions. Gross primary production (NPP + R) was computed per area of the stream bed (mg 0_2 / time / bed area) dividing GPP by the area of each sampled. Detailed methods are described in Appendix 1. Cobbles were selected from both riffles (n=4 riffles per stream) and pools (n=4 pools per stream) on each event. Two cobbles were pulled from each riffle and pool for a total of 16 cobbles per site over five sampling events, or a total of 160 cobbles analyzed over the summer.

Algal Standing Crop

Epibenthic periphyton is the primary source of carbon for many benthic invertebrates that feed salmon in California streams (Power and Dietrich 2002). Seasonal changes in the standing crop of epibenthic periphyton affect energy flow to salmon and the phenology of salmon prey abundance. Epibenthic periphyton standing crop was estimated using two methods, ash free dry mass (AFDM) and Chlorophyll-a (Chl-a) analysis. After net primary production and respiration measurements were made, cobbles were scrubbed with a stiff brush and the algal material was rinsed with filtered water onto trays and then funneled into 50ml Falcon tubes. Rinsate was stored in the field in a cooler with ice, transported to the laboratory, and processed within 2 days of being collected. Half the rinsate was used for AFDM analysis and half for Chlorophyll-a analysis.

The AFDM samples were filtered onto 47 mm glass fiber filters (Whatman 934-AH), dried for 24 hours at 60C, and weighed (to 0.0001 g) to estimate dry mass (O'Brien and Werh 2010).The weighed samples were then ashed in a muffle furnace at 500C for 4–5 h, allowed to cool and re-weighed to the nearest 0.0001g. Ash free dry mass was computed as difference between dry mass and the mass of ash after combustion (O'Brien and Werh 2010).

A second volume of rinsate from each rock was filtered for Chlorophyll-a analysis (Heaney 1978). Ethanol (10ml at 90% concentration) was used to extract the Chlorophyll from each filter into solution. Chlorophyll-a florescence was measured from these extractions using a Turner Designs TD-700 fluorometer. Florescence was converted Chlorophyll-a concentration (µg/mL) and multiplied by the volume of the solvent to estimate the total mass Chlorophyll-a in each sample (µg) (Heaney 1978). Finally the mass of Chlorophyll-a was divided by the top area of each cobble ($\mu g/cm^2$) to estimate algal biomass density (Heaney 1978).

Invertebrate Drift, Standing Crop, and Infall

To directly quantify the phenology of invertebrate prey abundance and concentration for juvenile salmonids, we measured invertebrate drift from riffles entering pools, the standing crop of benthic invertebrates on riffle and pool cobbles, and the infall of terrestrial and adult aquatic invertebrates onto the surface of pools. Invertebrate analysis was conducted at six total sites (3 Elder Creek pools and 3 Porter Creek pools) over 5 sampling events (for 30 total drift samples). We measured invertebrate drift in the "pool head patch" (Table 1), once per site during each monthly sampling event. Drift was sampled for 2 hours (+/- 10 minutes) between 16:00 and 19:00, using a 50 cm x 20 cm mouth aperture, 500-µm mesh drift net. The drift net was installed just below the water surface along XS-2 (Fig. 2) and adjusted on each occasion to capture the region of highest velocity at each sampled streamflow. Drift flux (mg/hr) was computed by summing the mass of drifting invertebrates captured in the drift net and dividing the total mass by the duration of the drift sample. Drift concentration (mg/m^3) was computed by dividing drift flux by the discharge through the drift net (m^3/sec).

Benthic invertebrate standing crop was measured from 3 riffle cobbles and 3 pool cobbles for each site, during each sampling event. A total of 171 cobbles were sampled (90 from Elder Creek and only 81 from Porter Creek since Porter Creek riffles were dry in August). Stones to be used for benthic sampling were collected from the stream bed in each habitat type using the step-toe procedure (Harrelson et al. 1994). To avoid losing epibenthic prey, aquarium nets were held directly downstream of each stone as it was dislodged. All invertebrates on the stone surface and in the aquarium net were removed by hand, and by washing and elutriating the rinsate through 500-µm mesh. The stone's dimensions (a- and b-axes) and shapes were recorded and the exposed surface area of each stone was computed. Standing crop (mg/m^2) was computed by dividing the sum of biomass on each cobble by its exposed surface area.

Infall of invertebrates was collected in 484 cm^2 (22cm x 22cm) square transparent plastic pan traps. Pan traps were filled with ~ 3 cm of water and a small amount of dish-soap to break the water surface tension. One trap was set on each riffle near the channel margin and two traps were set in each pool. Traps were tied with paracord to the stream margin, and left floating on the water surface for 22 to 28 hours (morning to morning). After the pans were removed from the stream, the invertebrates were collected by elutriating the pan water through 500-µm mesh. Infall ($mg \cdot cm^{-2} \cdot hr^{-1}$) was computed by dividing the mass of invertebrates by the area of the pan trap over the duration for which it was set on the pool surface. A total of 90 pan traps were analyzed (3 pans per site x 3 sites per stream x 2 streams x 5 dates = 90 pan traps).

All invertebrate samples (drift, standing crop, and infall) were preserved in the field in labeled 50ml centrifuge tubes filled with the field ethanol. In the laboratory, drift and benthic samples

were sorted and invertebrates identified to family or genus (Merritt et al. 2008) under 10X magnification. Each invertebrate was measured to the nearest 0.5mm under a dissecting scope and biomass (mg dry mass) was estimated from length-weight regressions (Benke et al. 1999, Sabo et al. 2002).

Behavior, Bioenergetics, Growth, and Lipid Allocation

Videogrammetry for Seasonal Observations of Foraging Behavior

Salmonid foraging behavior and foraging movements were monitored by video, and analyzed using the open source software VidSync (Neuswanger et al. 2016, See Chapter 1). Detailed videogrammetry methods are described in Appendix 2. Videos were collected with stereo-pairs of mounted GoPro cameras (model: HERO 4 Black, recorded at 30 frames per second with 1080p resolution) installed at monumented stations at the head of each pool (Fig. 2). We chose the head of the pool because the first point of entry for invertebrate drift from the riffle is a preferred foraging location for pool dwelling salmonids (Harvey et al. 2006, Smith and Li 1983). Thirty video clips (6 sites x 5 dates) were analyzed using Vidsync. We attempted to take a minimum of two length measurements of each salmonid for which we had more than one 3-second observation. For analysis of salmonid behavior, we assigned fish into four age-length bins based and literature values and our own observations (Table 2). Each VidSync observation also included relative 3-D positions of fish, times stamps, foraging mode or aggression attributes. These data were exported into the statistical software R (version 3.5.1) and scripts were developed to compute fish lengths, distance traveled per time, foraging volume occupied, and as well as counts and proportion of observed behavior (see data availability).

Table 2. Length-age assignments of juvenile steelhead used for behavioral analysis in VidSync.

Name	Length (mm)	Reference
Small young of year (*YOY*)	30 - 60	Author's observations
Large young of year (*YOY*)	61 - 80	Kelson and Carlson (2019) found 80-90 mm was a cutoff *YOY* and 1+ in Elder Creek during late summer.
Small parr (1+)	81 - 120	Moyle (2002)
Large parr (1+ to resident)	> 120	Moyle (2002)

Seasonal Net Rate of Energy Intake and Foraging Movement

The seasonal change in growth potential of drift foraging was estimated using a drift foraging bioenergetic model (Caldwell et al. 2018, Rosenfeld and Taylor 2009). Growth potential was inferred from the modeled net rate of energetic intake (NREI, joules time^{-1}), which is the energy acquired by juvenile fish for growth (gross energy intake – swimming and other metabolic costs). However, it is important to recognize that modeled growth potential does not always correlate well with realized growth (Hughes et al. 2003, Piccolo et al. 2014, see Discussion). The model was developed in R version 3.5.1. and is based on equations from Rosenfeld and Taylor (2009) and Hayes et al. (2000). Gross energetic intake is a function of drift concentration (mg/m^3), discharge rate through the foraging volume, fish size, prey size and capture probability (Caldwell et al. 2018, Rosenfeld and Taylor 2009). Swimming costs are a function of fish size and focal point velocity and water temperature (Caldwell et al. 2018, Rosenfeld and Taylor

2009). Water temperature was incorporated into the swimming costs (Rosenfeld and Taylor 2009); however, we assumed a constant energy assimilation efficiency of 0.6 (Tucker and Rasmussen 1999). The fish focal point velocity (measured at 6/10ths depth) and drift concentration were measured at the thalweg location on cross section 2 at the head of each pool (Fig. 3).

We modeled NREI for a 100mm drift foraging steelhead at a single foraging location in the channel thalweg. We considered the head of the pool a conservative estimate of drift foraging profitability to compare the seasonality of drift foraging growth potential across streams (Harvey et al. 2006, Smith and Li 1983 Van Leeuwen et al. 2011). Caldwell et al. (2018) also noted that NREI for different size classes of drift foraging *O. mykiss* and foraging locations downstream from the head of the pool locations followed a similar seasonal pattern over the hydrograph recession, although the magnitudes changed. The model was run for n = 3 pools in each stream, and n = 5 dates for a total of 30 model runs (3 pools x 2 streams × 5 dates).

Synoptic Growth and Lipid Content

We caught pool dwelling steelhead to evaluate seasonal changes in the size distributions and to collect growth and lipid content data. Fish were collected from 3 study pools in each stream using three-pass backpack electrofishing (Smith-Root backpack electrofisher model LR24). We blocked the upstream and downstream extent of each pool prior to sampling. At each sampling event, species, fork length, and fish mass data were collected. During the May and June sampling events, juvenile *O. mykiss* over 60mm fork length and 2g mass were implanted with a passive integrated transponder (PIT tags). All recaptured fish were remeasured for length and mass, allowing us to estimate June to July growth (recapture rates fish from May and September were too low to estimate growth). Specific growth rate (% body weight gained per day) for all recaptured *O. mykiss* was computed as:

$$SGR = \frac{\log(W_t) - \log(W_i)}{t} * 100$$ Cook et al. 2000

Where: W_t = fish weight after time "t" since first tagging and W_i = fish weight at first tagging.

In addition to calculating growth, we estimated July lipid content in the muscle tissue of juvenile *O. mykiss*. Lipid content was estimated using a non-invasive hand held device, the Distell Model 992 Fish Fatmeter (Distellc Inc., West Lothian, Scotland—https://www.distell.com). The Fish Fatmeter is cordless, handheld unit that emits a low-powered microwave (frequency, 2 GHz 2,000 MHz; power, 2 mW), which responds to water content in the muscle tissue of the fish (Klefoth et al. 2013). Using stored calibration data for rainbow trout, the Fish Fatmeter converted the response of the sensor to a displayed percentage fat content. An average of 8 readings was taken for each sampled fish. During July we sampled 81 *O. mykiss* from three pools in Elder Creek and 67 *O. mykiss* from three Porter Creek pools.

RESULTS

Seasonal Gradients in Water Quality and Stream Hydraulics

Streamflow, Dissolved Oxygen, and Water Temperature

Continuous, non-linear streamflow recessions occurred in both streams between April and July; however, streamflow was nearly an order of magnitude greater in Elder Creek than in Porter Creek from April 28th until July 10th (Fig. 4A). Between July 10th and July 17th, streamflow rapidly declined to zero in Porter Creek and riffles began to dry (Fig. 4A). Not every riffle in Porter Creek dried out on the same day, but all riffles in our study reach receded to zero depth between July 10th and July 17th. By September 9th, one of the Porter Creek study pools had dried completely, and the other three where low and stagnant with no living fish. In Elder Creek, streamflow continued to decline slowly in July and August, reaching a minimum of 0.014 m^{-3}/s in early September (Fig. 4A).

Median daily dissolved oxygen was near 10mg/L (and near 100% saturation) in both streams between April and July, and never dropped below 7 mg/L in Elder Creek all summer (Fig. 4B). Just before riffles dried on Porter Creek, daily average DO, dropped rapidly from 9mg/L on July 10th to 5.5 mg/L on July 13th and 4 mg/L on July 22nd (Fig. 4B), which is below levels shown to impair swimming performance and food conversion efficiency for juvenile *O. mykiss* steelhead (Bjornn and Reiser 1991). Daily average water temperature increased in both streams from April to peak in mid-July (Fig. 4C). Elder Creek was consistently 3.2° C cooler than Porter Creek through July, with average daily temperatures peaking at 17.8 ° C on July 27th in Elder Creek compared to 21.1 ° C in Porter Creek on August 11th (Fig. 4C). After riffle drying disconnected pools in Porter Creek, both daily average and diurnal temperature flux initially decreased for approximately 4 weeks (until mid-August) and then rapidly increased as the pools also began to dry, with diel flux > 15° C from mid-August through early September (Fig. 4C).

Riffle-Pool Hydraulics

Residual pool depths, or depth at zero flow (Lisle 1987), in the Elder Creek study sites ranged from 0.6 to 0.9 meters, nearly twice as deep as in Porter Creeks residual depths (0.35m to 0.6m). However, total pool depth declined at a similar rate in both streams, decreasing ~ 20% between April and August, excluding one Porter Creek pool that went completely dry (Fig. 5A). Mean and maximum riffle and pool head patch flow velocity also declined in both streams, approximately following power law trends over the study period (Fig. 5B). Velocities were consistently ~ 3× higher in Elder Creek, with pool head patch velocities declining from a mean of 0.24 m/s in late-April to 0.07 m/s in August, compared with 0.08 m/s to 0 m/s for the same period in Porter Creek (Fig. 5B). Wetted riffle widths declined between April and June in Elder Creek, but the rate of decline was very low from June to August, whereas in Porter Creek riffle widths declined through July and riffles dried completely between July 10th and July 17th (Fig. 5C). Riffle depth (Fig. 5D) also declined in both streams following power law trends. In Elder Creek, average riffle depth dropped from a median of 0.18m in April to 0.06m in August; whereas in Porter Creek, median average riffle depth declined from 0.09m in April to 0.05m on July 10th before rapidly declining from 0.05m to 0 on July 17th (Fig. 5D).

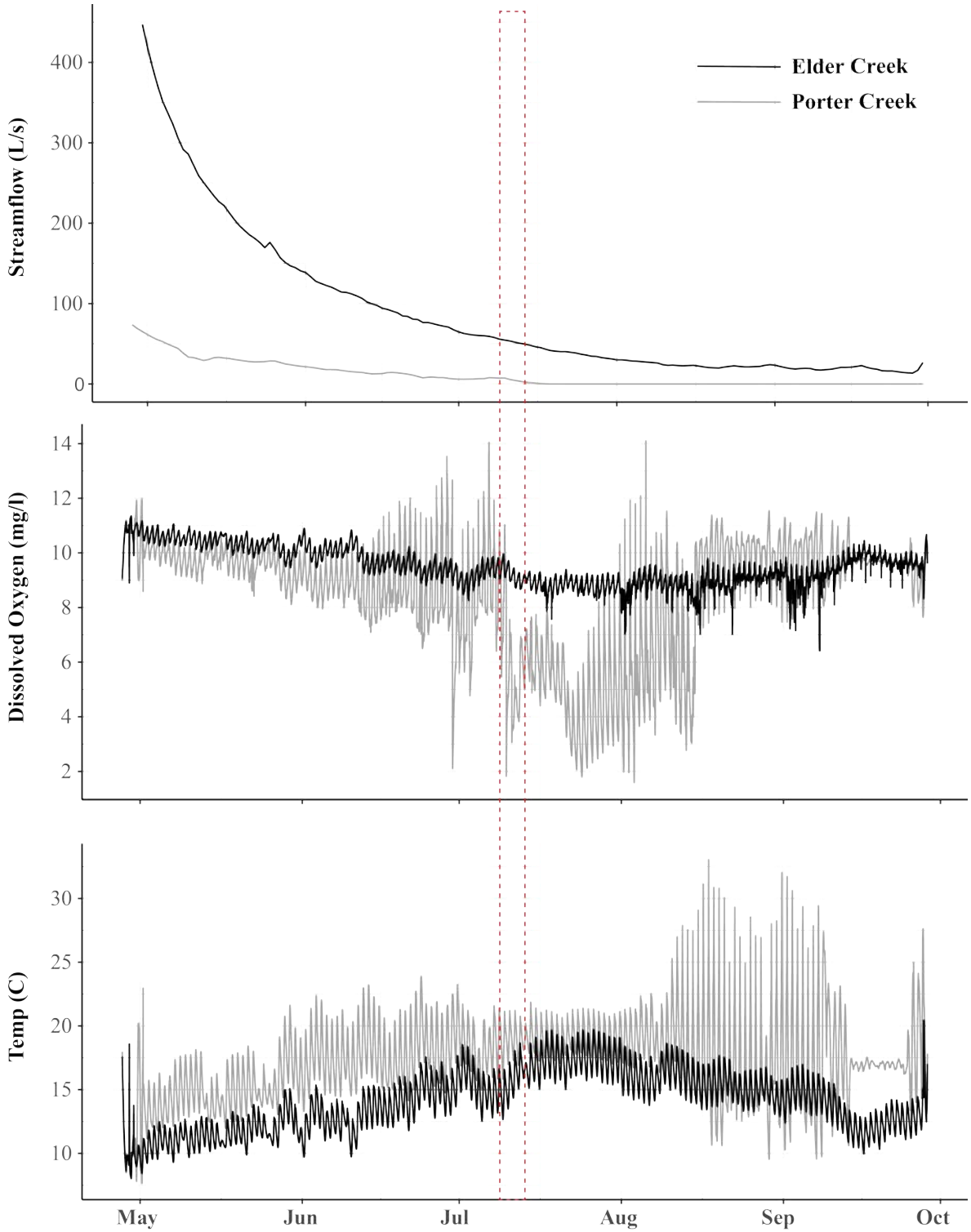


Figure 4. Continuous daily average streamflow (top) and hourly dissolved oxygen (middle), and hourly water temperature (bottom) in Elder and Porter creeks. The dashed red line shows the period during which riffles and pool first disconnected in Porter Creek (July 10-17th). This pool dried entirely in mid-September.

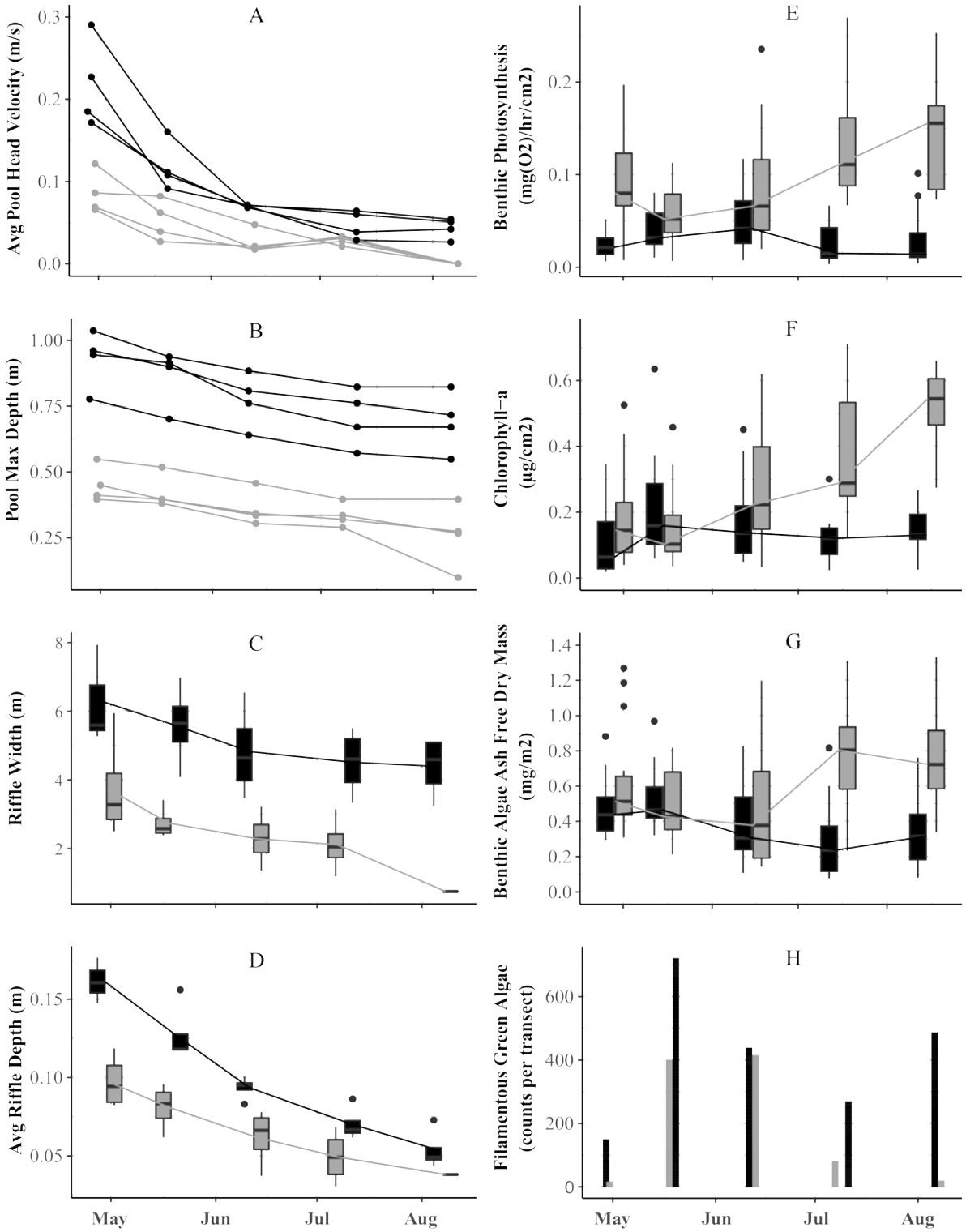


Figure 5. Spring to summer contrasts in riffle-pool hydraulics (left) with phenology of benthic primary production, epibenthic diatoms and counts of filamentous green algae (right) in four Elder Creek (black) and four Porter Creek (gray) pools.

The Phenology of *O. mykiss* Prey

Primary Production and Algal Standing Crop

Epibenthic photosynthesis was consistently 3 to 5 times higher in Porter Creek then Elder Creek and the seasonal patterns of primary production were also distinct between the two streams (Fig. 5E). In Elder Creek epibenthic photosynthesis rates increased from April to June and decreased from June to August (Fig. 5E). Conversely, in Porter Creek epibenthic photosynthesis decreased from April to May and increased slightly in June before jumping up by a factor of 3 in July and August – after riffle-pool disconnectivity (Fig. 5E). Epibenthic algal standing crop – both ash free dry mass (AFDM) and Chl-a, followed similar patterns to photosynthesis – however Chl-a in Porter Creek continued to increase through August (Fig. 5F and Fig. 5G). Filamentous green *Cladophora* peaked in May in Elder Creek and in June in Porter Creek, although *Cladophora* rebounded in July and August in Elder Creek – whereas it senesced and decayed in Porter Creek during July (Fig. 5H).

Invertebrate Drift, Standing Crop, and Infall.

The total biomass of drifting invertebrates between late-April and August was similar in Elder and Porter Creeks; however, the phenology of biomass flux and concentration were very different (Fig. 6A - 6C). In Elder Creek, drifting invertebrate flux (mg/hr) and concentration (mg/m^3) were low in late-April, but increased rapidly to May (peak of flux) and June (peak of concentration), after which both declined sharply to July, and remained steady but low in August (Fig. 6A). In Porter Creek, both flux and concentration of drift were highest at during our first measurement in late-April, indicating a peak that occurred earlier than our study period. Drift flux and concentration both declined rapidly in Porter Creek, with the largest decline between May and June, before all drift ceased with loss of riffle-pool connectivity in mid-July (Fig. 6A).

Benthic invertebrate standing crop on cobbles had near-diametrically opposite patterns in Porter and Elder Creek between April and August (Fig. 6B). Like drift concentration, Elder Creek invertebrate standing crop increased sharply from April to June, before decreasing in July and increasing slightly in August (Fig. 6B). Porter Creek invertebrate standing crop was highest in April, decreasing sharply to June before increasing in July and August (Fig. 6B).

Unlike drift and standing crop, infall of terrestrial and adult aquatic invertebrates followed a similar seasonal pattern and magnitude in both streams – although late-April infall in Porter Creek was appreciably higher then Elder Creek. Both streams saw an increase in infall between May and July (Fig. 6C). Infall decreased sharply from July to August in Porter Creek – while only declining moderately in Elder.

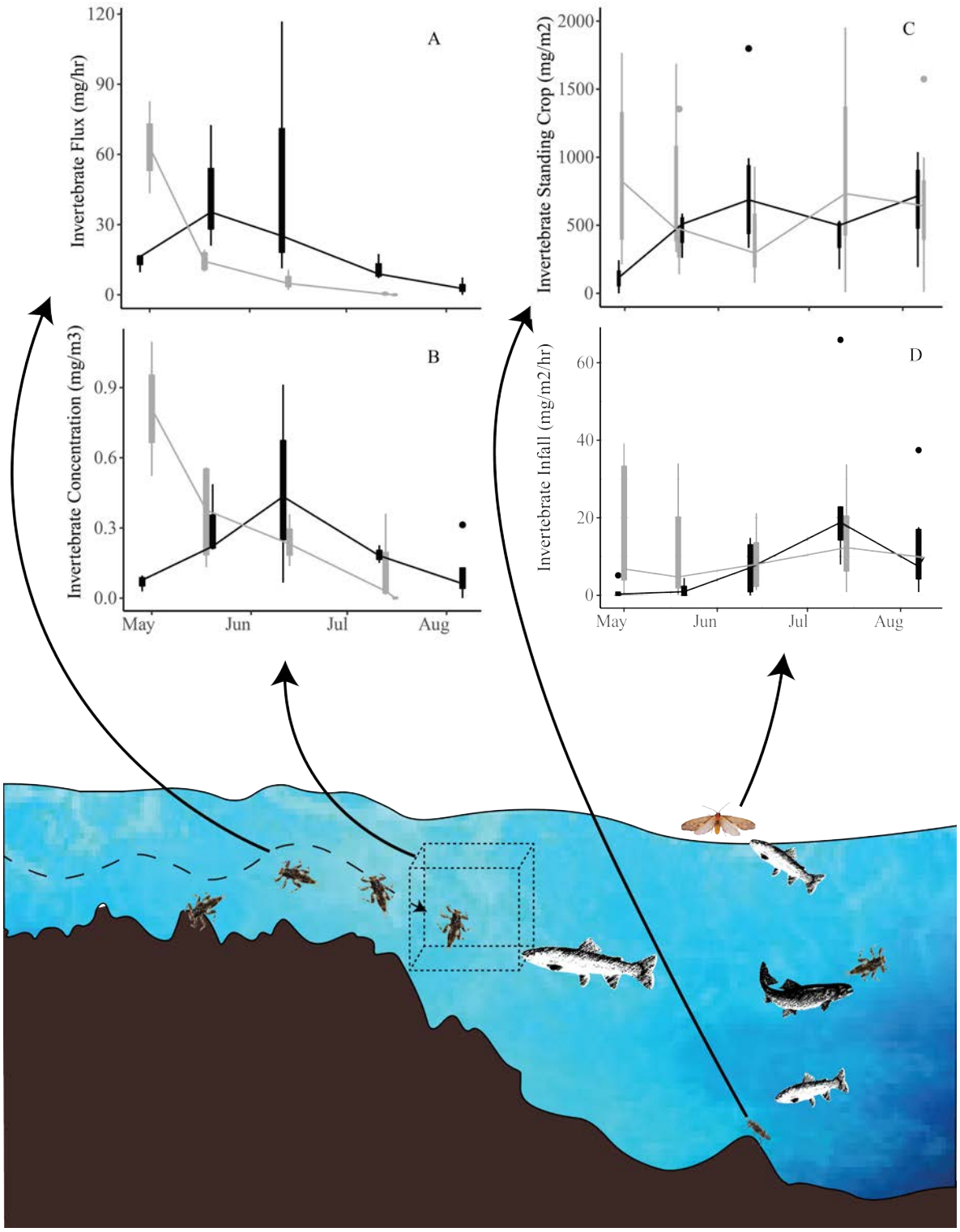


Figure 6. Seasonal gradients of drifting flux (A) and concentration (B), benthic standing crop (C), and infall (D) of invertebrates in Elder Creek and Porter Creek pools. The dashed box represents a 1-cubic meter volume of drift concentration in the pool-head patch, which was applied to the drift foraging volume in the NREI model (see Methods).

O. mykiss Foraging Behavior, Bioenergetics, Growth, and Lipid Allocation

Foraging Behavior

Using VidSync we compiled 4457 observations of juvenile *O. mykiss* foraging behavior in Elder Creek (2737 observations) and Porter Creek (1730 observations). Although we observed juvenile *O. kisutch* in both streams, most observations (>89%) were for juvenile *O. mykiss*, and we observed few instances of interspecific interaction between juvenile Coho salmon and steelhead trout. We thus restricted our behavioral, movement, and NREI modeling analysis (described below) to juvenile *O. mykiss*. Below we describe the seasonality of foraging behavior for Elder Creek (first) and Porter Creek (second).

Seasonal Foraging Behavior in Elder Creek

In Elder Creek we observed very few *O. mykiss* during our first (late-April) video samples, mostly *large parr* (Fig. 7A-7D). Counts of *large parr* peaked in early summer but counts of *small parr* and young-of-year (YOY) peaked in late summer. Of our total *large parr* counts (April to August), nearly 70% occurred in May and June (Fig. 7D); whereas, over 80% of *small parr* counts occurred from June to August (Fig. 7C, Table S2). Of our total *large YOY* counts (April to August), only 10% occurred in between April and June, and 90% occurred in July and August (Fig. 7B and Table S2). The sharp increase in *large YOY* counts (and the more gradual increase in *small parr*) between June and July corresponded to a sharp decrease of *large parr* over the same period (compare Fig. 7B and 7D). In July and August *large parr* were rarely observed in pool head patches in August, whereas *YOY*, especially *small YOY* were actively foraging in these patches in August.

Elder Creek *YOY* were far more likely to engage in search, benthic, and surface foraging then were parr. Thirty-six percent of *small YOY* behavioral observations and 46% of *large YOY* behavioral observations were search foraging (Table S2). The proportion of drift foraging *O. mykiss* declined from 97% (in April) to 58% (in August), and the proportion of search foraging fish increased over that same period from 0% (in April) to 35% (July). These trends are similar to observations in 2016 (Chapter 1), showing a consistent increase in search foraging and decline in drift foraging between spring and summer (see Chapter 1 Figure 5). Benthic foraging made up only 4% of all foraging observations, but 16% of observations for *small YOY*, with most occurring in August (Fig. 7A, Table S2). Counts of surface strikes were very low in April, May, and June, but increased by an order of magnitude between June and July (Fig. S1), which is consistent with the peak invertebrate infall in Elder Creek (Fig. 6D) and emergence phenology in the South Fork Eel (Uno and Power 2015). Aggressive interactions were generally rare in Elder Creek, but were highest in June, when prey concentration peaked. Another increase in aggression occurred in August (Fig. S1) although more posturing then actual physical contact.

Seasonal Foraging Behavior in Porter Creek

In Porter Creek, 91% of all *large parr* counts (April to August) occurred during our first sampling event in late-April (Fig. 7H). *Large YOY* were present in April but increased markedly from 9% of total summer counts in April to 49% of total summer counts occurring in June (Fig. 7f). Both large and small parr counts declined over that same April to June period: 91% to 5% of total *large parr* observations and 48% to 17% of total *small parr* observations (Fig. 7G and 7H). Total counts of all juvenile *O. mykiss* in Porter Creek peaked in June (a month earlier then Elder Creek), and were dominated by *large YOY* (Fig. 7f). Total counts declined in July, and sharply

declined in August to near zero when only 6% percent of all salmonids observed occurred. In our September electro-fishing, no fish were observed in any of the Porter Creek study pools, which by then were stagnant and turbid from decomposing organic matter (Fig. S3).

As in Elder Creek, *YOY* in Porter Creek were more likely to be search foragers across all months (Table S2), and the proportion of drift foraging fish (across all ages) declined from 85% in April to 0% in August, while the proportion of search foraging fish increased from 12% in April to 47% in July. Unlike Elder Creek, non-foraging or sheltering *O. mykiss* were commonly observed in July and accounted for most observed fish in August (82%). As in Elder Creek, benthic foraging was rare (3.8% of total foraging observations), weighted toward *large YOY* (8.5% of large *YOY* foraging attempts) and most common in July. Observed surface strikes in Porter Creek peaked in April (Fig. S1) and as in Elder Creek, this peak was simultaneous with the peak invertebrate infall (Fig. 6D). Aggressive interactions were also most frequent in April when prey concentration peaked, and (as in Elder Creek) increased again in August (Fig. S1).

Modeled Growth Potential, Measured Foraging Movement, Growth, and Lipid Allocation
Modeled net rate of energy intake (NREI) for drift foraging *O. mykiss* tracked seasonal drift concentration in both streams (more closely then drift flux), and swimming costs stayed relatively low (although higher in July in Porter Creek due to higher temperatures). Modeled drift foraging NREI was low in Elder Creek in April and increased in May and June before declining to near zero in July (Fig. 8a). The Elder Creek model predicting slightly negative energy intake in August. In Porter Creek, NREI was highest in April and declined sharply to near zero by June. The model predicted negative energy intake in Porter Creek in both July and August. Porter Creeks peak NREI (in April) was higher than Elder Creeks peak NREI (in June); however, the duration of positive NREI between April 28th and August 10th was nearly twice as long in Elder Creek as in Porter Creek (Fig. 8a).

We also tracked the movement patterns (distance per time) of 345 foraging *O. mykiss* Elder Creek and 235 foraging *O. mykiss* in Porter Creek using the VidSync software (Fig. 8b). In both streams, *large parr* moved least, and were the most likely to be drift foragers (Fig. 8b, Table S2). Small parr movement patterns approximately tracked drift foraging NREI in both streams – peaking in June in Elder Creek and April in Porter Creek -- before declining in both streams in July and August. *YOY* movement patterns, particularly large *YOY*, were nearly the opposite of drift foraging NREI, with movement increasing in June, July, and August, when a large portion of *YOY* were search foraging.

Most recaptured *O. mykiss* in Elder and Porter Creek gained mass between June 1st and July 17th although 4 out of 21 Porter recaptures (~20%) lost mass (Fig. 9a). Between June and July, median specific growth rate (SGR) was 3× higher for Elder Creek (0.6%/day) than Porter Creek (0.2%/day). Our very limited growth data from July to September indicate zero or negative growth rates over this period in Elder Creek, and all Porter Creek salmonids had either emigrated from our study pools or perished by September (Fig. S2). However, lipid content, measured only in mid-July, was 2× higher in Porter Creek (mean 4.6%) than Elder Creek (mean 2.3%) (Fig. 9b).

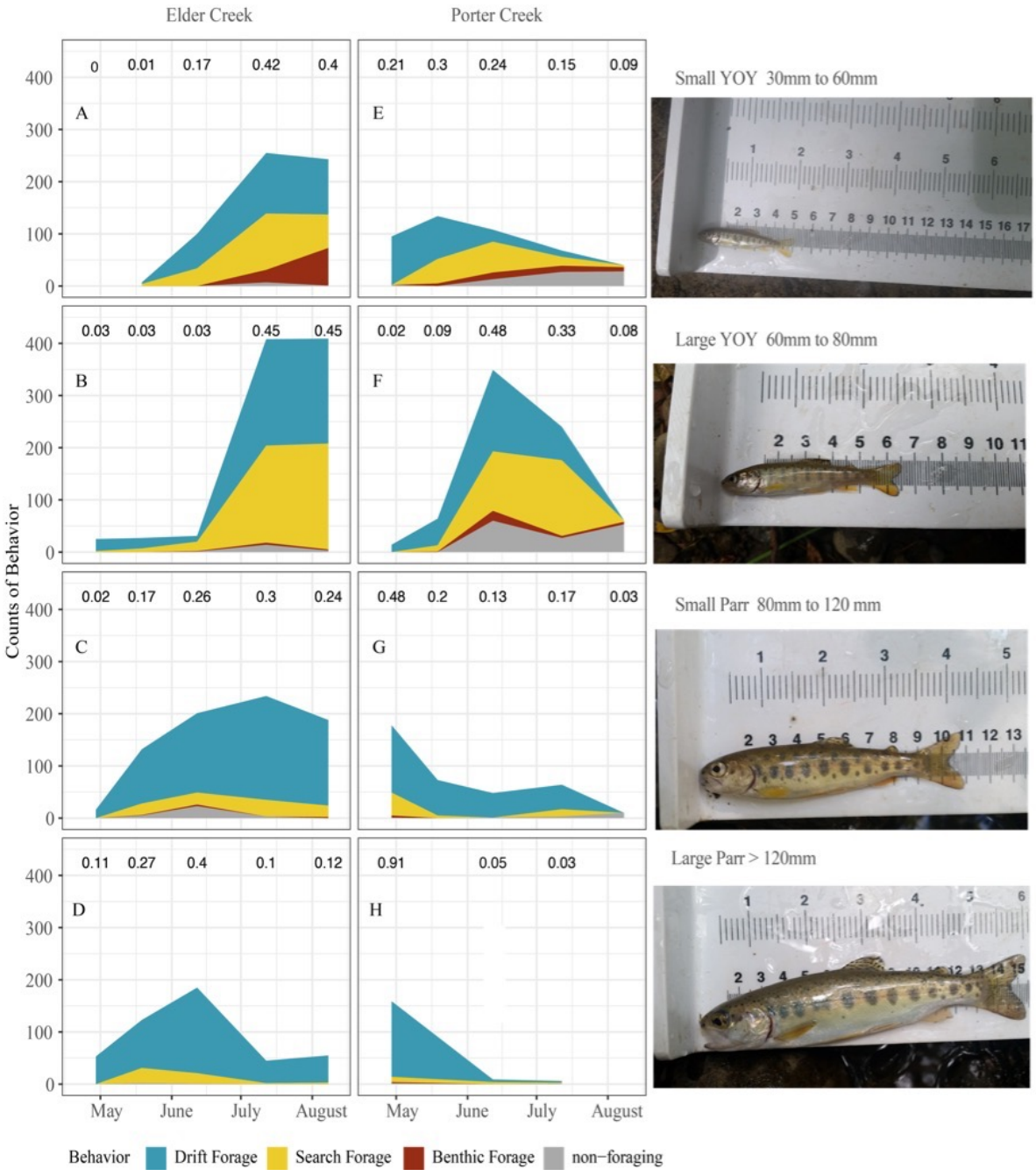


Figure 7. Seasonal changes in observations of foraging behavior of different size classes of juvenile *O. mykiss* from Elder (left) and Porter (right) creeks. Data is based on 4457 combined behavioral observations from Elder Creek (2737 observations) and Porter Creek (1730 observations). Decimal number across the top of each plot shows the proportion of total observations by date for each size-age class.

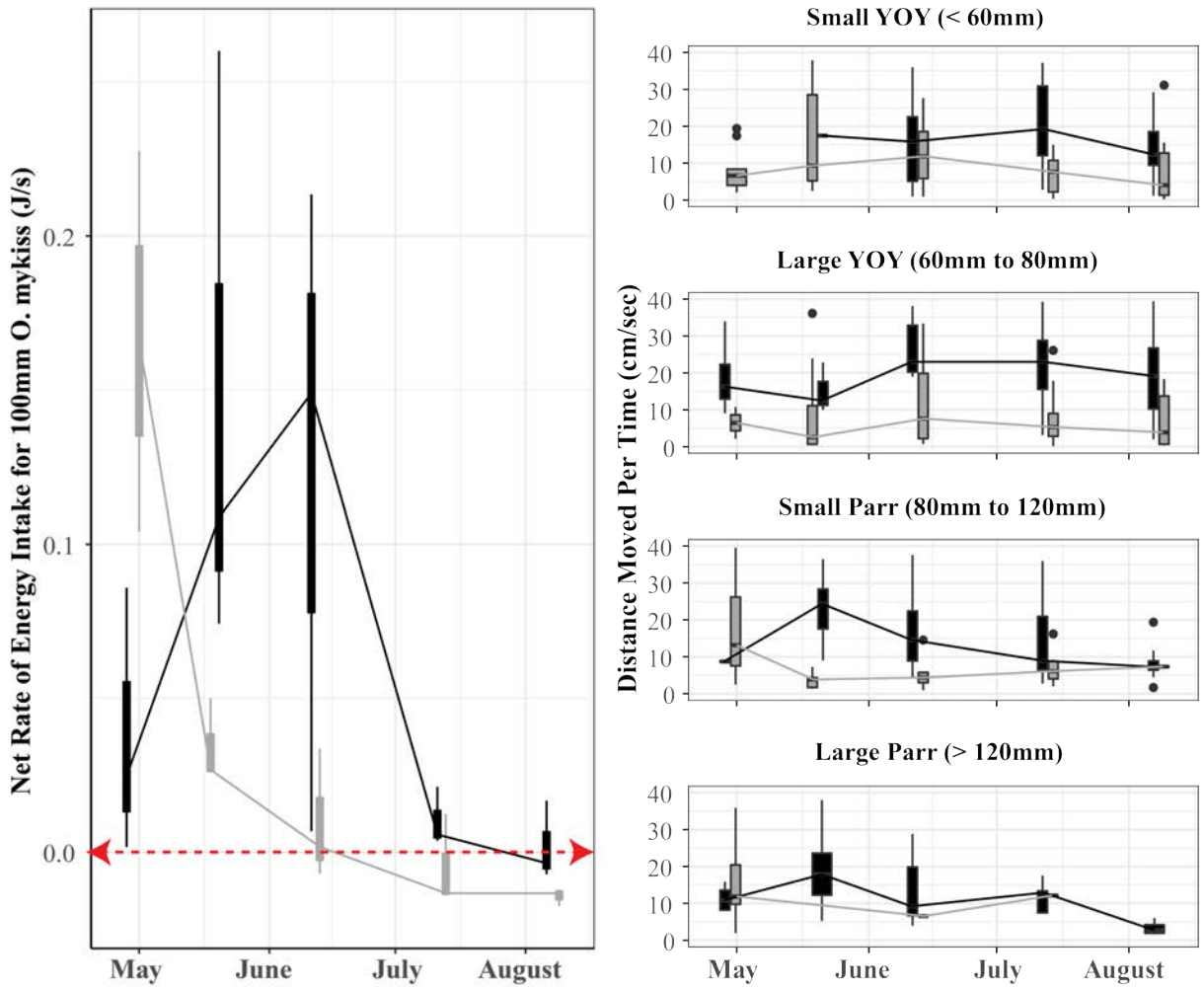


Figure 8. Modeled Net Rate of Energy Intake (NREI) for a 100mm drift foraging *O. mykiss*, at the head of 3 pools in Porter Creek and 3 pools in Elder Creek (left), showing zero NREI (red line). Average distance moved per time (right) of 580 individually tracked foraging *O. mykiss* (computed from VidSync) binned by size-age class. Elder Creek observations are represented by the black boxplots and Porter Creek are shown in gray.

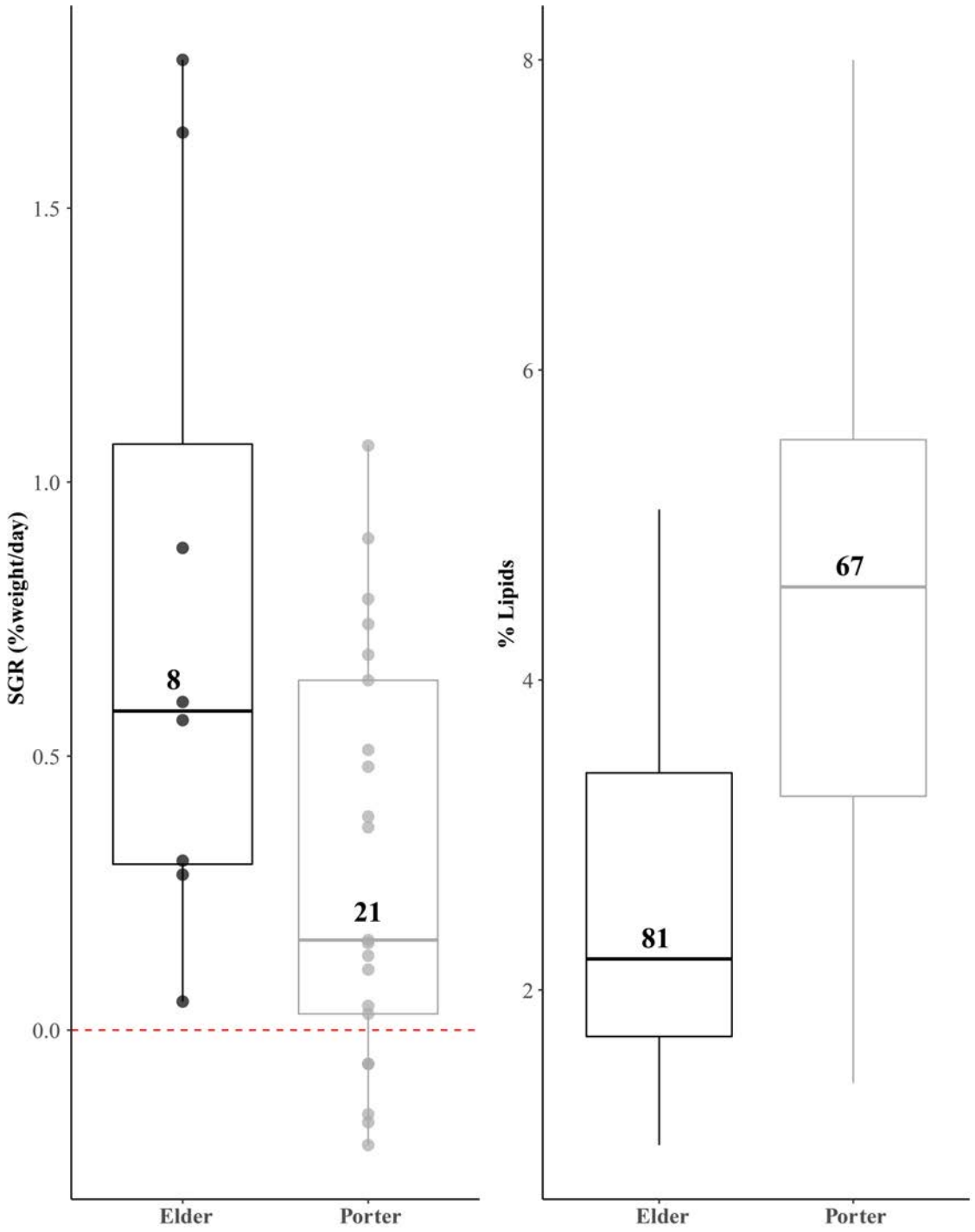


Figure 9. Specific growth rate (SGR) of juvenile *O. mykiss* between June 1st and July 17th in Elder Creek and Porter Creek (A) and measured lipid content in muscle tissue of juvenile *O. mykiss* in mid-July (B). Numbers inside the boxplots represent the number of recaptures (A) or fish for which lipids where measured (B) in each stream.

DISCUSSION

Elder Creek (perennial, shaded, cold) and Porter Creek (intermittent, sunny, and seasonally warm) occupy near-antipodal positions on a hydrologic spectrum of Mediterranean-climate streams. Our study shows that their seasonal pool hydraulics, salmonid prey phenologies, and patterns *O. mykiss* growth potential are equally distinct across the Mediterranean flow recession (Figs. 5, 6 and 8). Both Elder and Porter Creek offered profitable foraging opportunities for pool-dwelling *O. mykiss* during the spring and summer of 2018, yet the timing of peak prey concentration and drift foraging profitability was at least two months earlier in Porter Creek (Fig. 6 and 8), and the severity of Porter Creek's late summer abiotic conditions (drying pools, low dissolved oxygen and high temperature), was also much greater (Fig. 4 and 5). We suggest that the profitability of salmonid foraging in both streams—while driven by these stream-specific seasonal changes in food and habitat, was also strongly mediated by ecological interactions (intraspecific competition) and behavioral flexibility. We argue that a better evaluation of salmon foraging profitability in Mediterranean streams can be made by adapting bioenergetics models to account for non-drift related foraging behaviors (e.g. Harvey and Railsback 2014) and the context specific effects of ecological interactions on foraging opportunity (Naman et al. 2019b). We also speculate that juvenile *O. mykiss* life histories in the two systems are attuned to the distinct timing of spring growth potential and opportunity for over-summer survival and that collectively these streams types could contribute to a stabilizing portfolio of juvenile salmonid life histories.

The seasonality of stream hydraulics, prey phenology, and *O. mykiss* growth opportunity in Elder and Porter Creeks

We hypothesized that countervailing seasonal gradients in hydraulics and prey phenology (Fig. 1) would create a spring or early-summer peak in growth opportunity for drift foraging juvenile salmonids (H1) but that the timing of peak growth opportunity would vary between streams (H3). Our observations in Elder and Porter creeks support both of these hypotheses. In Elder Creek pools, declining velocity and increasing drift concentration during early-summer produced maximal *O. mykiss* drift foraging NREI in June; whereas, Porter Creek's drift foraging NREI peaked on or (more likely) prior to our first sample on April 28th, then declined precipitously from April to July. We also hypothesized that drift flux (H1a) would peak before drift concentration (H1b) – which was observed in Elder Creek and unconfirmed in Porter Creek (Fig. 5).

The biomass of benthic prey also had distinct phenologies between Elder and Porter Creek. Benthic invertebrate standing crop in pools generally tracked the seasonality of drift from late-April to June. However, in both streams benthic prey increased in late summer (July in Porter Creek and August in Elder Creek). In contrast, infall of terrestrial and adult aquatic invertebrates *increased* between May and July in both streams (more so in Elder) as drifting prey declined. In August, both infall and drift decreased. The increased flux of invertebrate infall in mid-summer, after drift and standing crop declined, amplify the importance of asynchronous timing in prey subsidies for salmonids (Nakano and Murakomi 2001). We observed a large increase in surface strikes by *O. mykiss* between June and July on Elder Creek (Fig. S1), suggesting that fish are tracking the subsidy of infall and perhaps the relative value of infall is increasing as drifting prey

declines. A similar increase in surface strikes was *not* observed in Porter Creek, perhaps because of adverse water quality conditions in July (Fig. 4). However, we did not account for benthic prey infall in our bioenergetics model (see *Bioenergetic considerations for future work* below).

The behavioral and ecological drivers of "realized" *O. mykiss* foraging profitability

Specific growth rates were positive for all recaptured *O. mykiss* in Elder Creek and for most recaptured *O. mykiss* in Porter Creek between June and July. However, growth was much lower in Porter Creek and four recaptured fish in Porter Creek lost weight during this period (Fig. 9a). While we recaptured relatively few fish (8 in Elder Creek and 21in Porter Creek), the observations of mostly positive growth in Porter between June and July, when the drift foraging net rate of energy intake (NREI) model predicted zero or negative energetic intake (Fig. 8a), and low dissolved oxygen was expected to further impair growth, suggests two possible causes. First, our model assumptions may not reflect realistic prey capture success rates or prey energy density (Hughes et al. 2003, Rosenfeld et al. 2014, Piccolo et al. 2014). And second, fish may be profiting from non-drift foraging behaviors e.g. search, benthic, or surface foraging. Both explanations are plausible; however the second is more likely. NREI was modeled at the most profitable *drift* foraging position (near the head of the pool) and NREI models tend to *over*-predict, rather then under-predict growth (Hughes et al. 2003, Piccolo et al. 2014). Thus, drift foraging NREI in June and July is probably an over-estimate, especially at downstream positions, occupied by YOY, where drifting prey concentration would be lower due consumption by upstream fish and drift settling. Yet most recaptured *YOY* grew between June and July in both streams. Young-of-year salmonids tended to occupy positions downstream from the head of the pool, and engaged in significant (>50%) non-drift foraging behavior over this period (Fig. 6). *Small YOY*, which where the most common benthic foragers, also experienced positive growth between June and July. Based on these lines of evidence, it appears likely that *YOY* (and likely small parr) were energetically benefiting from non-drift related foraging in June and July.

We hypothesized that (H2) salmonid foraging behavior would shift as drift foraging profitability declined and that aggression would increase (Fig. 1). As expected, we observed increasing search and benthic foraging after peak drift foraging NREI (e.g. see May in Porter and July in Elder on Fig. 6). Contrary to our expectations though, aggression was highest during periods of highest prey concentration and highest modeled NREI (Fig. S1). Most observed aggression occurred between search foraging *YOY* whose greater movement and occupied volumes increased their direct interaction. The relationship between aggression and peak prey concentration may also reflect adaptation to the highly seasonal nature of food availability in both streams e.g. late summer food supply and growth potential is negligible (Fig. S2 and see Kelson and Carlson 2019), so there is increased pressure to exploit late-spring and early summer growth opportunities.

We also did not anticipate the extent to which fish size, via intraspecific interference, would mediate seasonal changes in foraging behavior and access to profitable drift foraging habitat. For example, counts of drift foraging *small parr* and *large YOY* in Elder Creek increased dramatically between June and July (Fig. 6b and 6c)—at the same time as the decrease in drift foraging *large parr* at the head of the pool (Fig. 6d). We saw the same thing in Porter Creek between May and June (compare Fig. 6f and 6h). This was not due to increasing habitat suitability since depths and velocities at the head of pool were already suitable in May and June

for large YOY (e.g. compare velocities in Fig. 5, to suitability for *O. mykiss* in Holmes et al. 2014). Rather, the withdrawal of *large parr* from active drift foraging at the head of the pool appears to have allowed a large number of *YOY* and *small parr* to take advantage of these more profitable drift foraging locations. The timing of *large parr* withdrawal from the head of the pool appears to correspond to the zero NREI for drift foraging (May in Porter and July in Elder) – although the temporal resolution of our NREI model and behavioral observations is too coarse draw a statistically significant conclusion about this.

The effect of fear and competition on foraging behavior and space use has been well documented in ecological literature (Brown et al. 1988, Chapman 1966), and specifically for size-mediated microhabitat dominance hierarchies in salmonids (e.g. Nakano et al. 1995, Harvey and White 2017, Naman 2019b). Nielson (1992) speculated that the seasonal change in social interactions may over-ride habitat variables in determining microhabitat rearing profitability and our observations support this hypothesis, and our work supports this speculation. The response of dominant *O. mykiss* parr to the seasonal decline of drift foraging profitability indirectly improved energetic opportunities for subdominant *O. mykiss* YOY, who could move into pool head stations as the larger fish vacated them.

Bioenergetic considerations for future work

Our NREI model was far from an exhaustive treatment of the pool-scale profitability of salmonid foraging in Elder and Porter creeks. Rather, drift foraging NREI, modeled at the head of the pool, was intended here as a metric of the seasonal change in profitability for this foraging mode. In addition, our NREI model didn't account for the effects of low dissolved oxygen in Porter Creek pools in July and August, which likely further decreased realized Porter Creek NREI in late-summer.

The bioenergetics of non-drift related foraging behaviors for stream rearing salmonids has received little treatment and we did not model it here (but see Harvey and Railsback 2014 and Caldwell et al. 2018). Non-drift foraging behavior accounted for sizable proportions of our total *O. mykiss* video observations (37% in Elder Creek and 47% in Porter Creek across all size/age groups). While rare compared to search foraging, surface and benthic foraging were probably under-estimated in our video analysis, since we focused on the pool-head patch. Downstream from this patch, fish in the pool tended to have more diverse foraging behavior. Efforts to model and predict the energetic profitability of search, surface, and benthic foraging, and link these foraging modes to non-drift related prey fluxes (Nielson 1992) would greatly improve the capacity of resource managers and ecologists to predict salmonid fitness and management outcomes, especially in streams with strongly seasonal drift patterns (Fausch 1997, Nislow 1998). This would require refinements in measuring non-drifting prey flux and concentration. For example, measuring the renewal rate (mass/area/time) of benthic prey in pools is necessary to model the energetic profitability of this prey resource to consumers like salmonids. Our measurements of benthic standing crop (mass/area, Fig. 5c) shows seasonality snapshots of this prey resource but may not accurately reflect renewal rate.

We also note that small parr movement rates (distance per time) tracked drift foraging NREI in both streams, while *large YOY* movement increased as drift foraging NREI for *large parr* decreased (compare Fig. 7A and 7B). Movement data computed from programs like VidSync

could be used to refine swimming costs equation in energetic models particularly for search foraging fish, actively swimming through the water column. Most NREI models currently assume swimming costs are proportional to focal point velocity (Rosenfeld and Taylor 2009) which is incorrect for actively swimming animals. Harvey and Railsback (2014) incorporate "velocity shelters" into swimming costs for search foragers but do not use measured swimming speeds. In addition VidSync data can provide critical information on occupied foraging volumes which is a key area of uncertainty in search foraging models (Harvey and Railsback 2014). Finally, as noted above, our study strongly suggests that the consequences of intra-specific competition on the *realized* NREI of foragers should also be integrated into future bioenergetics modeling.

Life history diversity in streams with contrasting prey phenology and streamflow recessions?

Researchers have long observed that *O. mykiss* and *O. kisutch* spawn in intermittent tributaries (Wigington et al. 2006), some of which go completely dry in late summer (Erman and Hawthorne 1976); and that intermittent streams can be productive winter rearing environments for juvenile salmon (Ebersole et al. 2006). Our study suggests that, at least in some years, intermittent streams can also provide profitable growth conditions in later spring (April and May), although conditions for growth deteriorate rapidly as streamflow and drift concentration decline, and mortality increases with the duration of riffle-pool disconnection (Obedzinksi et al. 2018, Hwan and Carlson 2016). The combination of highly profitable early spring growth potential (Fig. 8), inhospitable late summer abiotic conditions (Fig. 4 and 5), and anecdotally low over-summering survival (Obedzinksi, *personal communication* 2020) leads us to speculate that 0+ emigration from Porter Creek to non-natal rearing habitat (e.g. mainstem or estuarine habitat) may be a life history adaptation to stream drying (Hayes et al. 2008). In addition, we observed that Porter Creek *O. mykiss* had nearly twice the July muscle-lipid content as Elder Creek *O. mykiss*, even after riffle-pool disconnection (Fig. 9). Lipid levels have been shown to predict early migration in Atlantic salmon (Morgan et al. 2002), and summer lipids have been correlated to survival of *O. mykiss* under harsh winter conditions (Biro et al. 2004). It is unclear whether the observed difference in lipid content between Elder Creek and Porter Creek fish is a product of higher feeding rates in early spring in Porter Creek, local adaption to surviving inhospitable late-summer/fall conditions, or some other cause. But this observation bolsters our speculation of early 0+ outmigration as a possible life history tactic for *O. mykiss* Porter Creek, where instream summer survival is often expected to be low. Whether early outmigrants from Porter Creek survive to contribute to the adult population in the Russian River system is also an open question, but such a pattern has been documented elsewhere. In particular, Erman and Hawthorne (1976) documented the importance of breeding in an intermittent tributary by resident *O. mykiss*, emphasizing that while the tributary dried during summer, juveniles produced there contributed an estimated 39% - 47% of the adult population.

In contrast to the patterns observed in intermittent Porter Creek, Kelson and Carlson (2019) showed that outmigration timing and late summer densities of *O. mykiss* in the perennial and well oxygenated (Fig. 4) Elder Creek remained relatively constant across both drought and wet water years. High growth potential in early summer (Fig. 8, see also Kelson and Carlson 2019), and lower apparent summer mortality suggest that over-summering anadromous and older resident life histories would be favored in Elder Creek compared to Porter Creek. When

considered together, these contrasting patterns suggest that systems with different seasonal interactions between hydrology and secondary production (Fig. 1) likely contribute to life history diversity in *O. mykiss*. Life-cycle monitoring would be necessary to quantitatively test these conjectures about life history diversity in Elder and Porter Creek *O. mykiss*. However, the modeled differences in the timing of growth potential, the different likelihood of summer survival, and the measured difference in summer lipid allocation, suggests benefit for a portfolio of *O. mykiss* life history strategies— namely in the size, age, physiology and timing of *O. mykiss* at outmigration. The possibility of a stabilizing portfolio of juvenile salmon life histories (Mobrand et al. 1997, Hilborn et al 2003, Schindler et al. 2010) over the North Coast region, produced by selective forces in contrasting perennial and intermittent tributaries, is a compelling avenue of future research.

Acknowledgments
The conceptual model (Fig. 1) from this chapter was influenced by discussions with Bill Trush and Mary Power. The manuscript received excellent reviews and feedback from Mary Power, Stephanie Carlson, and Theodore Grantham. This project would not have happened without field, analytical, and intellectual support from Shelley Pneh, Weston Slaughter, Keane Flynn, and Kobie Boslough. Jason Neuswanger provided helpful council on VidSync and the ecology of drift foraging salmonids. Additional invertebrate and VidSync support came from Sam Larkin, Shannon Mckillop-Herr, Vicky Fong, and Elena Hauser. Porter Creek electro-fishing, access and field work was supported by California Sea Grant staff including Maridka Obedzinksi, Sarah Nossaman Pierce and William Boucher. Porter Creek stream gauging was conducted by Trout Unlimited staff led by Mia Van Docto. Gabriel Rossi was supported by a National Science Foundation CZP EAR-1331940 for the Eel River Critical Zone Observatory, and generous contributions from California Trout.

Data Availability
https://orcid.org/0000-0003-3010-9480

Literature Cited
Beche, L. A., E. P. Mcelravy, and V. H. Resh. 2006. Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams in California, U.S.A. Freshwater Biology 51:56–75.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-Mass Relationships for Freshwater Macroinvertebrates in North America with Particular Reference to the Southeastern United States. Journal of the North American Benthological Society 18:308–343.

Biro, P. A., A. E. Morton, J. R. Post, and E. A. Parkinson. 2004. Over-winter lipid depletion and mortality of age-0 rainbow trout (Oncorhynchus mykiss). Canadian Journal of Fisheries and Aquatic Sciences 61:1513–1519.

Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83–138 Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats. Edited by William R. Meehan. American Fisheries Society Special Publication.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22:37–47.

CDFW (California Department of Fish and Wildlife). 2013. Standard Operating Procedure for Discharge Measurements in Wadeable Streams in California. California Department of Fish and Wildlife Instream Flow Program Standard Operating Procedure CDFW-IFP-002, 24 p. Available at: http://www.dfg.ca.gov/water/instream_flow.html.

Cook, J. T., M. A. McNiven, G. F. Richardson, and A. M. Sutterlin. 2000. Growth rate, body composition and feed digestibility conversion of growth-enhanced transgenic Atlantic salmon Salmo salar. Aquaculture, 188:15–32.

Dill, L. M. 1983. Adaptive Flexibility in the Foraging Behavior of Fishes. Canadian Journal of Fisheries and Aquatic Sciences 40:398–408.

Dralle, D. N., N. J. Karst, K. Charalampous, A. Veenstra, and S. E. Thompson. 2017. Event-scale power law recession analysis: quantifying methodological uncertainty. Hydrology and Earth System Sciences 21:65–81.

Elton, C. S. 1927. Animal ecology. Reprinted 2001. University of Chicago Press, Chicago.

Erman, D. C., and V. M. Hawthorne. 1976. The Quantitative Importance of an Intermittent Stream in the Spawning of Rainbow Trout. Transactions of the American Fisheries Society 105:675–681.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–451.

Fausch, K. D., S. Nakano, and S. Khano. 1997. Experimentally induced foraging mode shift by sympatric chairs in a Japanese mountain stream:7.

Gasith, A., and V. H. Resh. 1999. Streams in Mediterranean Climate Regions: Abiotic Influences and Biotic Responses to Predictable Seasonal Events. Annual Review of Ecology and Systematics 30:51–81.

Hall, C. A. S., and R. Moll. 1975. Methods of Assessing Aquatic Primary Productivity. Pages 19–53 in H. Lieth and R. H. Whittaker, editors. Primary Productivity of the Biosphere. Springer Berlin Heidelberg, Berlin, Heidelberg.

Harrelson, C. C., C. L. Rawlins, and J. P. Potyondy. 1994. Stream channel reference sites: An illustrated guide to field technique. Page RM-GTR-245. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO.

Harvey, B. C., R. J. Nakamoto, and J. L. White. 2006. Reduced Streamflow Lowers Dry-Season Growth of Rainbow Trout in a Small Stream. Transactions of the American Fisheries Society 135:998–1005.

Harvey, B. C., and S. F. Railsback. 2009. Exploring the Persistence of Stream-Dwelling Trout Populations under Alternative Real-World Turbidity Regimes with an Individual-Based Model. Transactions of the American Fisheries Society 138:348–360.

Harvey, B. C., and S. F. Railsback. 2014. Feeding modes in stream salmonid population models: is drift feeding the whole story? Environmental Biology of Fishes 97:615–625.

Hayes, S. A., M. H. Bond, C. V. Hanson, E. V. Freund, J. J. Smith, E. C. Anderson, A. J. Ammann, and R. B. MacFarlane. 2008. Steelhead Growth in a Small Central California Watershed: Upstream and Estuarine Rearing Patterns. Transactions of the American Fisheries Society 137:114–128.

Heaney, S. I. 1978. Some observations on the use of the in vivo fluorescence technique to determine chlorophyll-a in natural populations and cultures of freshwater phytoplankton. Freshwater Biology 8:115–126.

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

Holmes, R. W., M. A. Allen, and S. Bros-Seeman. 2014. Habitat suitability criteria, juvenile steelhead in the Big Sur River. Technical Report 14-1. Water Branch Instream Flow Program, California Department of Fish and Wildlife, Sacramento, USA.

Hughes, N. F., J. W. Hayes, K. A. Shearer, and R. G. Young. 2003. Testing a model of drift-feeding using three-dimensional videography of wild brown trout, Salmo trutta , in a New Zealand river. Canadian Journal of Fisheries and Aquatic Sciences 60:1462–1476.

Jennings, C.W., Strand, R.G., and Rogers, T.H., 1977, Geologic map of California. Published by California Division of Mines and Geology, scale 1:750,000. URL: https://ngmdb.usgs.gov/Prodesc/proddesc_16320.htm

Kelson, S. J., and S. M. Carlson. 2019. Do precipitation extremes drive growth and migration timing of a Pacific salmonid fish in Mediterranean-climate streams? Ecosphere 10:e02618.

Klefoth, T., C. Skov, K. Aarestrup, and R. Arlinghaus. 2013. Reliability of non-lethal assessment methods of body composition and energetic status exemplified by applications to eel (Anguilla anguilla) and carp (Cyprinus carpio). Fisheries Research 146:18–26.

Kupferberg, S. J., A. J. Lind, V. Thill, and S. M. Yarnell. 2011. Water Velocity Tolerance in Tadpoles of the Foothill Yellow-legged Frog (Rana boylii): Swimming Performance, Growth, and Survival. Copeia 2011:141–152.

Matthews, W. J., B. C. Harvey, and M. E. Power. 1994. Spatial and temporal patterns in the fish assemblages of individual pools in a midwestern stream (U.S.A.). Environmental Biology of Fishes 39:381–397.

McBain and Trush, Trout Unlimited. 2000. Allocating Streamflows to Protect and Recover Threatened Salmon and Steelhead Populations in the Russian River and other Northcoast Rivers of California. Unpublished Report. Accessed April 2019. URL: http://www.krisweb.com/biblio/ncc_troutunlimited_mcbainetal_2000.pdf

Miyasaka, H., S. Nakano, and T. Furukawa-Tanaka. 2003. Food habit divergence between white-spotted charr and masu salmon in Japanese mountain streams: circumstantial evidence for competition. Limnology 4:1–10.

Merritt, R. W., and K. W. Cummins. 2008. An introduction to the aquatic insects of North America: [includes color plates and CD with interactive key. Kendall Hunt, Dubuque, Iowa.

Mobrand, L. E., J. A. Lichatowich, L. C. Lestelle, and T. S. Vogel. 1997. An approach to describing ecosystem performance “through the eyes of salmon” 54:10.

Morgan, I. J., I. D. McCarthy, and N. B. Metcalfe. 2002. The influence of life-history strategy on lipid metabolism in overwintering juvenile Atlantic salmon. Journal of Fish Biology 60:674–686.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences 98:166–170.

Nakano, S. 1995 Competitive interactions for foraging microhabitats in a size-structured interspecific dominance hierarchy of two sympatric stream salmonids in a natural habitat. Canadian Journal of Zoology. 73:1845–1854.

Naman, S. M., J. S. Rosenfeld, and J. S. Richardson. 2016. Causes and consequences of invertebrate drift in running waters: from individuals to populations and trophic fluxes. Canadian Journal of Fisheries and Aquatic Sciences 73:1292–1305.

Naman, S. M., J. S. Rosenfeld, P. M. Kiffney, and J. S. Richardson. 2018. The energetic consequences of habitat structure for forest stream salmonids. Journal of Animal Ecology 87:1383–1394.
Naman, S. M., J. S. Rosenfeld, J. R. Neuswanger, E. C. Enders, and B. C. Eaton. 2019a. Comparing correlative and bioenergetics-based habitat suitability models for drift-feeding fishes. Freshwater Biology 64:1613–1626.
Naman, S. M., R. Ueda, and T. Sato. 2019b. Predation risk and resource abundance mediate foraging behaviour and intraspecific resource partitioning among consumers in dominance hierarchies. Oikos 128:1005–1014.
Neuswanger, J. R., M. S. Wipfli, A. E. Rosenberger, and N. F. Hughes. 2016. Measuring fish and their physical habitats: versatile 2D and 3D video techniques with user-friendly software. Canadian Journal of Fisheries and Aquatic Sciences 73:1861–1873.
Nielsen, J. L. 1992. Microhabitat-Specific Foraging Behavior, Diet, and Growth of Juvenile Coho Salmon. Transactions of the American Fisheries Society 121:617–634.
Nislow, K. H., C. Folt, and M. Seandel. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon 55:12.
O'Brien, P. J., and J. D. Wehr. 2010. Periphyton biomass and ecological stoichiometry in streams within an urban to rural land-use gradient. Hydrobiologia 657:89–105.
Piccolo, J. J., B. M. Frank, and J. W. Hayes. 2014. Food and space revisited: The role of drift-feeding theory in predicting the distribution, growth, and abundance of stream salmonids. Environmental Biology of Fishes 97:475–488.
Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The Natural Flow Regime. BioScience 47:769–784.
Power, M. E., and W. E. Dietrich. 2002. Food webs in river networks. Ecological Research 17:451–471.
Power, M. E., J. R. Holomuzki, and R. L. Lowe. 2013. Food webs in Mediterranean rivers. Hydrobiologia 719:119–136.
Power, M. E., and W. E. Rainey. (n.d.). Food webs and resource sheds: towards spatially delimiting trophic interactions. Page 24 Ecological Consequences.
Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, and B. Statzner. 1988. Biotic and Abiotic Controls in River and Stream Communities. Journal of the North American Benthological Society 7:456–479.
Railsback, S. F., B. C. Harvey, S. J. Kupferberg, M. M. Lang, S. McBain, and H. H. Welsh. 2016. Modeling potential river management conflicts between frogs and salmonids. Canadian Journal of Fisheries and Aquatic Sciences 73:773–784.
Rantz, S. E. 1982. Measurement and computation of streamflow: Volume 2, Computation of Discharge. Pages 285–631. Water Supply Paper.
Rosenfeld, J. S., and J. Taylor. 2009. Prey abundance, channel structure and the allometry of growth rate potential for juvenile trout. Fisheries Management and Ecology 16:202–218.
Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length–mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society 21:336–343.
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.

Smith, J. J., and H. W. Li. 1983. Energetic factors influecning foraging tactics of juvenile steelhead trout, Salmo gairdneri. P173–180 Predators and Prey in Fishes. Edited by D. L. G. Noakes, D. G. Lindquist, G. S. Helfman, and J. A. Ward. Smith, J. J., and H. W. Li.
Taube, Clarence. M. 2000. Instructions for winter lake mapping. Chapter 12 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.
Trush, W. J., S. M. McBain, and L. B. Leopold. 2000. Attributes of an alluvial river and their relation to water policy and management. Proceedings of the National Academy of Sciences 97:11858–11863.
Tucker, S., and J. B. Rasmussen. 1999. Using 137 Cs to measure and compare bioenergetic budgets of juvenile Atlantic salmon (Salmo salar) and brook trout (Salvelinus fontinalis) in the field. Canadian Journal of Fisheries and Aquatic Sciences 56:875–887.
Van Leeuwen, T. E., J. S. Rosenfeld, and J. G. Richards. 2011. Adaptive trade-offs in juvenile salmonid metabolism associated with habitat partitioning between coho salmon and steelhead trout in coastal streams: Adaptive trade-offs of juvenile salmonids. Journal of Animal Ecology 80:1012–1023.
Wipfli, M. S., and C. V. Baxter. 2010. Linking Ecosystems, Food Webs, and Fish Production: Subsidies in Salmonid Watersheds. Fisheries 35:373–387.
Yarnell, S. M., J. H. Viers, and J. F. Mount. 2010. Ecology and Management of the Spring Snowmelt Recession. BioScience 60:114–127.

Appendix 1

To estimate epibenthic primary productivity in riffles and pools we measured periphyton photosynthesis and respiration on cobbles using the light/dark incubation method of Hall and Moll (1975). We collected representative cobbles from each riffle and pool using the step-toe procedure (Harrelson et al. 1994); however, we only retained the coarse gravel to small cobble size class (46mm to 128mm b-axis). We removed any evident benthic invertebrates by hand, and placed the cobbles into air tight, transparent chambers containing a known volume of stream water. Cobbles were placed in clear 500 mL chambers with threaded tops (Nalgene, product #). An entry port for the dissolved oxygen probe was drilled in the lid, and a rubber cork was used to seal the hole after measurement. After placing the cobbles into the chambers we immediately measure dissolved oxygen and water temperature in the chamber using an optical dissolved oxygen probe (YSI PRO PLUS, SI Inc., Yellow Springs, OH),) We sealed the chamber lid, checking to ensure that no bubbles formed. For the light incubation, chambers were placed on the stream bed for 60-90 minutes.

At the end of the light incubation we removed the cork and immediately measured dissolved oxygen and water temperature in the chamber. After light incubation, we added new stream water to the chamber, covered the chamber with a fitted, opaque lid so no light could penetrate (dark incubation), measured dissolved oxygen and water temperature, and incubated at ambient temperature (in the stream) for 60-90 minutes. At the end of the dark incubation we measured dissolved oxygen and water temperature, and also measured the surface area of the cobble. Light incubation was used to compute net primary production (NPP), which is a combined measure of gross primary production (GPP) and respiration (R).

NPP was computed as:

$$Net\ Primary\ Production\ (\frac{mg0_2}{time}) = \frac{(DO_{Light\_end} - DO_{Light\_start}}{t_{Light}}) * Volume_{light}$$

Where:

DO = dissolved oxygen (mg/L)
t_{Light} = duration of light incubation (hr)
Volume = volume of water in chambers (L)

Dark incubation was used to compute respiration as:

$$Respiration\ (\frac{mg0_2}{time}) = \frac{(DO_{t2_{Dark}} - DO_{t1_{Dark}})}{t2_{Dark} - t1_{Dark}} * Volume_{dark}$$

Gross primary production (mg 0_2 / time) was computed as NPP + R. Finally, gross primary production per area of the stream bed (mg 0_2 / time / bed area) was computed by dividing GPP by the area of cobble. Cobbles were selected from both riffles (n=4 riffles per stream) and pools (n=4 pools per stream). Two cobbles were pulled from each riffle and pool for a total of 16 cobbles per site over five sampling events. Which resulted in 160 cobbles analyzed [16 (cobbles) × 2 (streams) × 5 (sampling events) = 160].

Appendix 2

Videogrammetry for Seasonal Salmonid Observations and Behavior

Salmonid foraging behavior and foraging movements were monitored by video, and analyzed using the open source software VidSync (Neuswanger et al. 2016). Videos were collected with stereo-pairs of mounted GoPro cameras (model: HERO 4 Black, recorded at 30 frames per second with 1080p resolution) installed at monumented stations at the head of each pool (Fig. 2). We chose the head of the pool because the first point of entry for invertebrate drift from the riffle is a preferred foraging location for pool dwelling salmonids (Harvey et al. 2006). Recordings lasted approximately 30 minutes and were collected between 16:00 and 18:00 once, in each pool, during each sampling event. However, video from one Elder Creek pool and one Porter Creek pool were unsuitable for analysis due to insufficient overlap between the left and right cameras and poor camera angles to capture fish, leaving n=3 sites from each stream for VidSync analysis.

Thirty video clips (6 sites × 5 dates) were analyzed using the videogrammetry program Vidsync (Neuswanger et al. 2016). Vidsync allows the user to triangulate a 3-D position, in relative space, using known lines of sight from two or more cameras. For each video, we followed the video correction and calibration procedure described in Neuswanger et al. (2016). To analyze the videos, we selected the 10 -minute clip with the highest counts of juvenile salmonids in the video frame. Within this 10-minute clip, we used a random number generator to select six 30-second subsamples. In each subsample, we used VidSync software to track the nose-point location of each observed fish on 3-second intervals, and assign a foraging mode at each interval. We attempted to take a minimum of two length measurements of each salmonid for which we had more than one 3-second observation. For analysis of salmonid behavior we assigned fish into

four age-length bins based and literature values and our own observations (Table 2). Foraging modes were designated based on common literature descriptions (Chapter 1 and Table S1). VidSync output from these analyses included relative X, Y, Z - positions of fish, times stamps, foraging mode or behavioral event, and body length. Data for each subsample were organized by object (e.g., fish ID) and event (type of measurement). These data were exported into the statistical software R (version 3.5.1) and scripts were developed to compute fish lengths, distance traveled per time, foraging volume occupied, and as well as counts and proportion of observed behaviors.

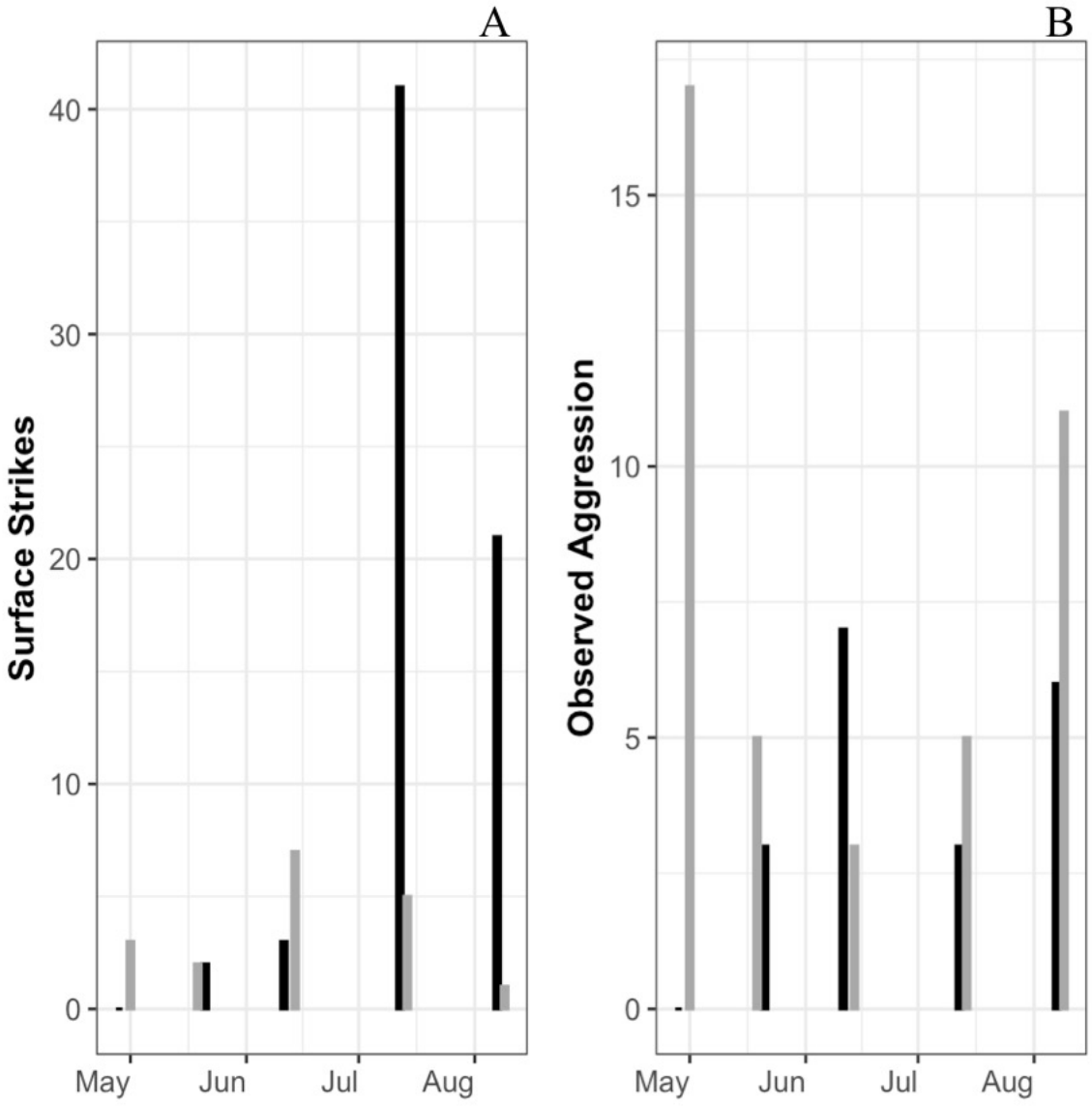
SUPPLEMENTAL MATERIALS

Supplemental Table 1. Definitions of foraging behaviors used in video scan samples (From Chapter 1).

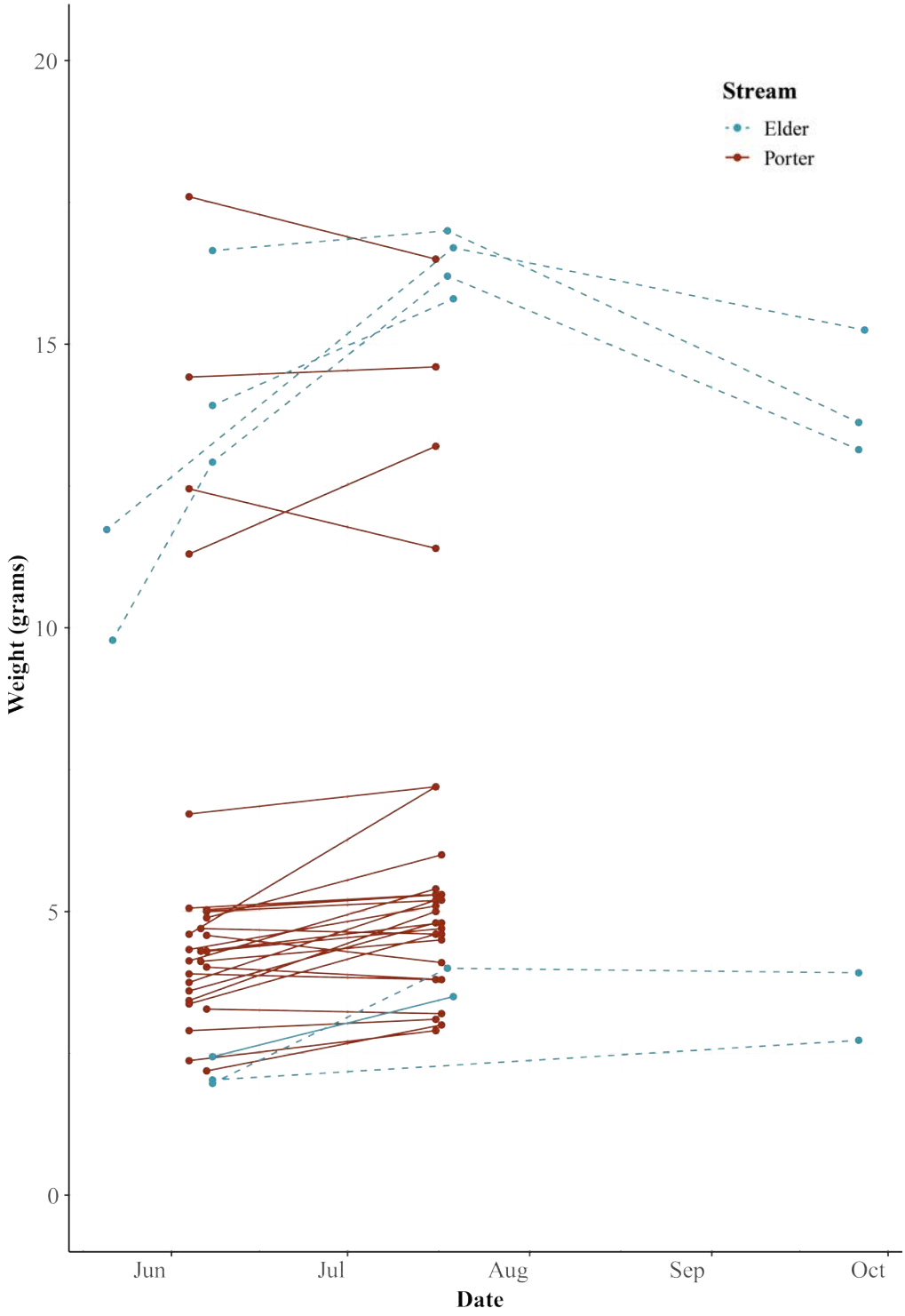
Foraging Mode	**Definition**
Drift Foraging	Fish holds focal points in the water column and makes short forays to intercept drift, with only occasional attacks on benthic prey near their focal points (Nakano et al. 1999a).
Benthic Foraging	Fish primarily cruise over larger areas of stream-bed and capture benthic prey by making forceful attacks at the substrate (Nakano et al. 1999a).
Search Foraging	Fish undertake continuous undirected swimming, foraging was not associated with a focal point, and fish consumed drift, falling, or benthic prey (adapted from Nielsen 1992).
Behavioral Event	**Definition**
Surface Strike	A fish swims towards the surface and either attempts to or successfully bites an item floating on or just under the water surface (Suttle et al. 2004).
Attacks	A fish makes a rapid, aggressive darting approach toward another fish without making direct contact ("attacks" in Nielsen 1992).
Nips	A fish rapidly approached another fish and gives it a bite (Nielsen 1992).

Supplemental Table 2. Counts and proportions of *O. mykiss* behavioral observations by stream and fish size/age.

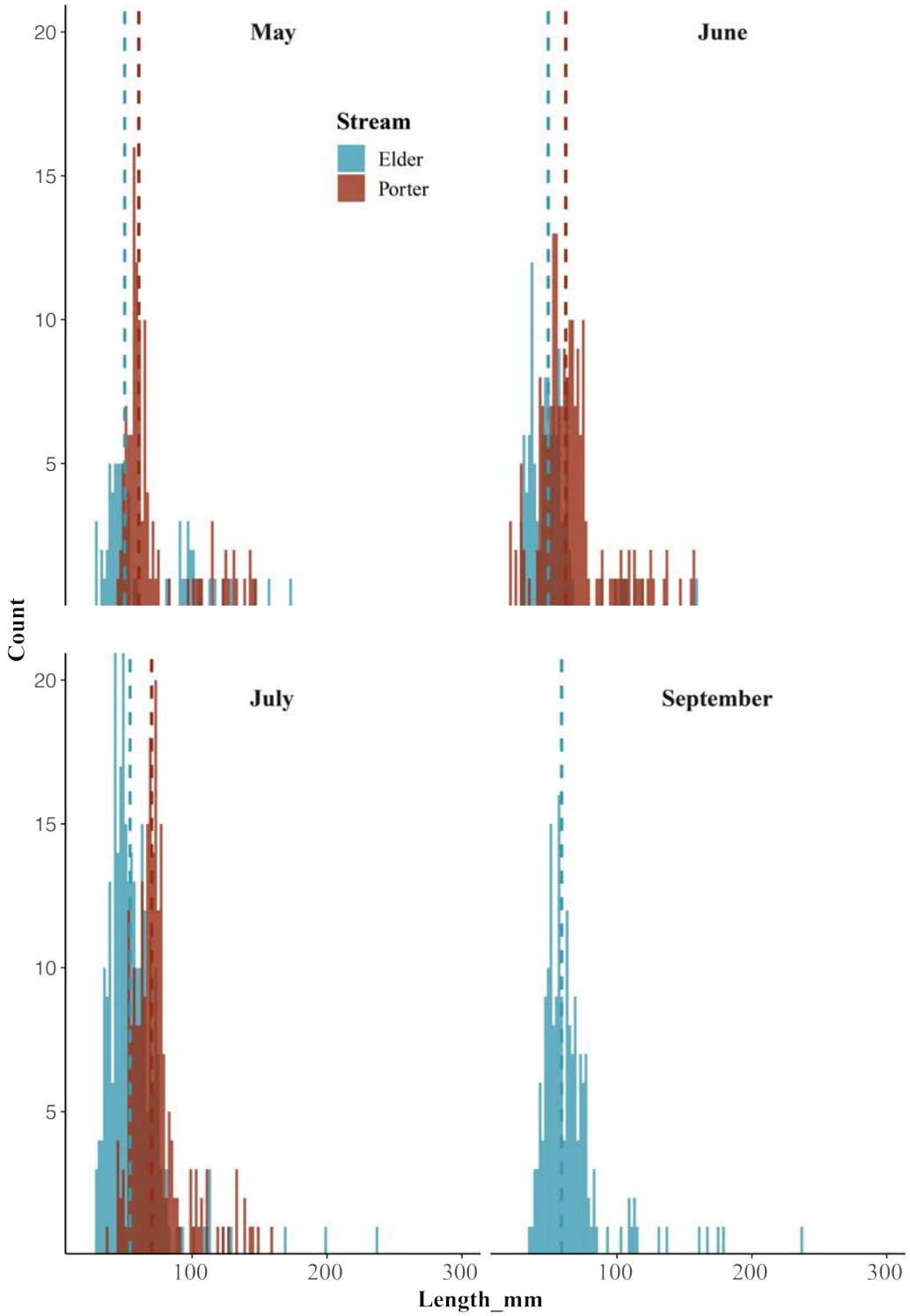
Size_Age	Behavior	Stream	Behavioral Observations	Total Observations	Prop. of Obs for
Small YOY < 60 mm	Benthic Foraging	Elder	96	605	16%
Large YOY 60 to 80 mm		Elder	7	900	1%
Small Parr 80 to 120 mm		Elder	6	771	1%
Large Parr > 120 mm		Elder	0	461	0%
Small YOY < 60 mm	Drift Foraging	Elder	291	605	48%
Large YOY 60 to 80 mm		Elder	459	900	51%
Small Parr 80 to 120 mm		Elder	635	771	82%
Large Parr > 120 mm		Elder	404	461	88%
Small YOY < 60 mm	Non-Foraging	Elder	8	605	1%
Large YOY 60 to 80 mm		Elder	18	900	2%
Small Parr 80 to 120 mm		Elder	31	771	4%
Large Parr > 120 mm		Elder	3	461	1%
Small YOY < 60 mm	Search Foraging	Elder	210	605	35%
Large YOY 60 to 80 mm		Elder	416	900	46%
Small Parr 80 to 120 mm		Elder	99	771	13%
Large Parr > 120 mm		Elder	54	461	12%
Small YOY < 60 mm	Benthic Foraging	Porter	38	445	9%
Large YOY 60 to 80 mm		Porter	29	728	4%
Small Parr 80 to 120 mm		Porter	4	373	1%
Large Parr > 120 mm		Porter	2	174	1%
Small YOY < 60 mm	Drift Foraging	Porter	210	445	47%
Large YOY 60 to 80 mm		Porter	285	728	39%
Small Parr 80 to 120 mm		Porter	291	373	78%
Large Parr > 120 mm		Porter	153	174	88%
Small YOY < 60 mm	Non-Foraging	Porter	70	445	16%
Large YOY 60 to 80 mm		Porter	140	728	19%
Small Parr 80 to 120 mm		Porter	15	373	4%
Large Parr > 120 mm		Porter	3	174	2%
Small YOY < 60 mm	Search Foraging	Porter	127	445	29%
Large YOY 60 to 80 mm		Porter	274	728	38%
Small Parr 80 to 120 mm		Porter	63	373	17%
Large Parr > 120 mm		Porter	16	174	9%



Supplemental Figure 1. Observations of surface strikes (A) and aggressive interactions (B) in Elder (black) and Porter (gray) creeks.



Supplemental Figure 2. Observed growth for recaptured *O. mykiss* during the summer of 2018 from Elder and Porter creeks.



Supplemental Figure 3. Size -frequency distributions for Elder Creek and Porter Creek (all pools combined) in May, June, July, and September. Note that Porter Creek pools were nearly dry in September and salmonid occupancy was zero. Vertical line shows median size of fish in each stream on each date.

CONCLUSION AND FUTURE RESEARCH

My dissertation research explored how interactions between stream habitat and prey phenology affected the behavior, growth, and performance of rearing Pacific salmon — with a focus on *O. mykiss* in Mediterranean streams along the Pacific Coast of California. Each chapter of my dissertation emphasized a different, but related aspect of these interactions. Chapter 1 focused on *O. mykiss* foraging behavior and movement in response declining streamflow, hydraulic habitat, and invertebrate drift in Elder Creek. In Chapter 2 I investigated how human management – specifically dry season flow enhancement, could affect foraging profitability for over-summering *O. mykiss* in an intermittent stream (Porter Creek). And in Chapter 3 I reported my quantification and model predictions of seasonal differences in *O. mykiss* growth potential, foraging behavior, and intraspecific interactions in Elder Creek (perennial, shaded, cold) *vs.* Porter Creek (intermittent, sunny, and seasonally warm).

Collectively, this research produced some core findings (1-8), which have application for the ecology and management of Pacific salmon and also lead to proposals for areas of future research (see **Areas of Future Research** below).

1. *O. mykiss* foraging movement and foraging mode followed strongly seasonal patterns across changing contexts of flow and prey phenology (Ch 1), and between stream types (Ch 3). The seasonal streamflow recession in these Mediterranean streams produced more diversity of juvenile *O. mykiss* foraging behavior than previously reported for this species.
2. *O. mykiss* foraging mode shifts could be predicted from simple hydraulic indicators, but not well predicted from drift concentration alone (Ch1). This led us to speculate about hydraulic cues for foraging mode (Gowan 2007), and the importance of non-drifting prey fluxes (e.g. benthic standing crop and aerial in-fall) in the late summer, as well as increasing predation risk once pools become shallow and still.
3. Prey concentration and modeled energetic intake (NREI) for drift foraging was a poor predictor of foraging mode at the pool scale (Ch1) but a reasonable predictor of drift foraging behavior, specifically for larger parr (Ch 3).
4. Dry season flow enhancement (Ch 2) in an intermittent stream (Porter Creek) caused significant increases in dissolved oxygen, riffle width, depth and velocity, as well as increased invertebrate drift and benthic invertebrate standing crop. But augmentation had negligible effects pool volume and water temperature. Across three fish species (Coho salmon, steelhead and adult Roach), these changes led to increased proportions of drift foragers, increased forager density in riffle-pool transition zones, and increased movement relative to a non-augmented control reach in Porter Creek.
5. However, the effects of augmentation (Ch 2) on wetted habitat varied seasonally and in response to ambient streamflow and channel characteristics (especially hyporheic conductivity).
6. The timing of peak prey concentration and modeled drift foraging profitability (Ch 3) was at least two months earlier in intermittent Porter Creek then perennial Elder Creek (between April and August, 2018), and the seasonal change in spring-summer growth potential followed different patterns in these two streams. The severity of Porter Creek's late summer abiotic conditions (drying pools, low dissolved oxygen and high

temperature), was also much greater. However Porter Creek *O. mykiss* had nearly twice the stored body fat – which has been linked to early outmigration in other salmonids.
7. While modeled growth potential was driven by interacting stream habitat and prey concentration, *realized* foraging opportunity was strongly mediated by intraspecific competition and foraging mode shifts, which also varied seasonally in both streams.
8. Observed growth was likely *underestimated* by the drift foraging NREI model in Porter Creek and behavioral observations suggest that young-of-year salmonids (and possibly small parr) were energetically benefiting from benthic and surface prey, particularly in mid-summer.

Areas of Future Research

Bioenergetics modeling in streams with seasonally low flow and invertebrate drift

The bioenergetics of non-drift related foraging behaviors for stream rearing salmonids has received little treatment (but see Harvey and Railsback 2014 and Caldwell et al. 2018), yet my research suggest those foraging behaviors are important factors affecting both realized foraging profitability and biotic interactions in streams with seasonally low flow and drift. Efforts to model and predict the energetic profitability of search, surface, and benthic foraging, and link these foraging modes to non-drift related prey fluxes (Nielson 1992) would greatly improve the capacity of resource managers and ecologists to understand and steward these systems. This would require refinements in measuring non-drifting prey flux and concentration. For example, measuring the renewal rate (mass/area/time) of benthic prey in pools is necessary to model the energetic profitability of this prey resource for consumers like salmonids. In addition, movement data computed from programs like VidSync (Neuswanger 2016) could be used to refine swimming cost equations in energetic models, particularly for search foraging fish, actively swimming through the water column. Most NREI models currently assume swimming costs are proportional to focal point velocity (Rosenfeld and Taylor 2009), which is incorrect for actively swimming animals. VidSync data can provide critical information on occupied foraging volumes, a key area of uncertainty in search foraging models (Harvey and Railsback 2014). Finally, my research strongly suggests that the consequences of intra-specific competition for the *realized* NREI of foragers should also be integrated into future bioenergetics modeling.

Expanding the interaction between habitat and prey phenology: the Salmonid Foodscape.

Pointing out that if our aim is to understand the fate of wild salmon populations in changing watersheds, Fausch et al. (2002) enjoined fisheries biologists and managers to move beyond short-term studies of local reaches to a "riverscape" perspective. The riverscape framework stresses that assessment of watershed conditions and practices that will affect juvenile salmon populations must track states of "all the diverse habitats needed to complete a life history." However, the riverscape's focus on structure and dynamics of physical habitats for salmonids is necessary but not sufficient for their protection and recovery (Wiplfi and Baxter 2010). The fates of salmon rearing in river networks also depend on the states and dynamics of their "resource sheds" (Power and Rainey 2000, Wiplfi and Baxter 2010): areas of habitat that impart energy, elements or nutrients to fuel activity or support production of consumers. The resource sheds of mobile consumers like salmon include habitat traversed during their foraging and migrations, as well as spatial sources of incoming foods external to occupied habitat. These source areas must be linked to consumers' foraging range by fluxes, known as trophic subsidies (Polis et al. 2004). Trophic fluxes between river habitats and linked food webs in upstream,

terrestrial, and marine environments, as well as *in situ* food production have all been shown to be important to salmonids rearing in heterogenous habitats down river networks (Nielsen 1991, Cederholm et al. 1999, Piccollo and Wiplfi 2002, Baxter et al. 2005, Wiplfi and Baxter 2010, Bellmore et al. 2013, Kaylor et al. 2019, Naman et al. 2018, Jeffres et al. 2019), Figure C1. Resource sheds have time-space dimensions. They expand spatially with time—the spatial source volumes that nourish a consumer over its lifetime are larger and likely more diverse than those feeding it over a briefer period (Power and Rainey 2000).

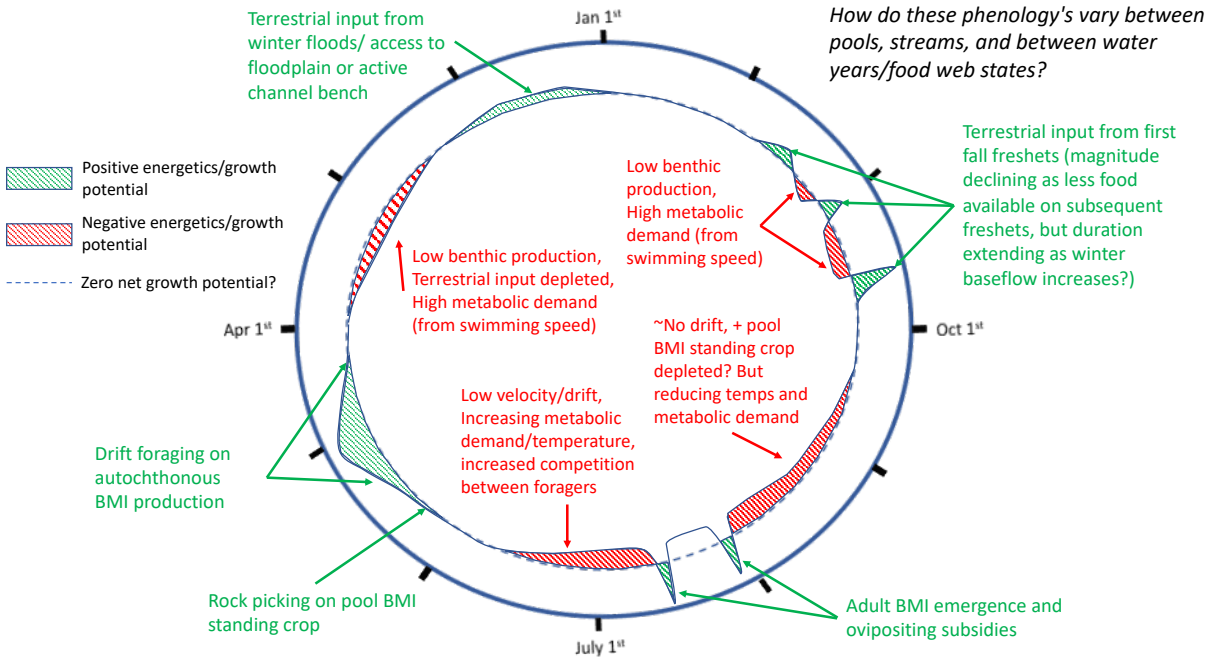


Figure C1. A hypothesized mandala of annual growth opportunity (energetic value from zero line), for rearing salmonids in a Mediterranean tributary stream. The author wonders…is this figure correct in fall and winter? How would this figure look for a mainstem river, a floodplain, or an estuary? How can we use this information to better manage salmon living in food webs?

In my third chapter I proposed a conceptual model for how stream hydraulics and secondary production interact to affect foraging profitability for juvenile salmon during the streamflow recession in Mediterranean coastal streams (Figure 1 from Chapter 3). This model can be generalized to encompass the entire salmon bearing watershed from headwaters to the ocean and the entire annual cycle. In future work, I will build on this conceptual model to develop more explicitly how seasonal hydraulics and food phenology control growth potential for salmonids and other mobile riverine consumers in in habitats from headwater streams (as I studied in this dissertation) to mainstem rivers, floodplains, estuaries, and the near marine environment and across the entire year (not just spring-fall). Following Power and Rainy (2000) and Wiplfi and Baxter (2010), I introduce the concept of a "Foodscape" which I define as a mosaic of linked source habitats that supply food to foraging habitats within a river network through time and mediate salmonid growth potential and life history decisions. The interaction of Riverscapes and Foodscapes affects the spatial and seasonal dynamics of food concentration, energy expenditure and prey capture success for foragers in a habitat, determining the net profitability of that habitat (Fausch 1984; Hughes and Dill 1990, Piccolo et al. 2014, Naman et al. 2018 and 2019). When

and where seasonal pulses of prey concentration coincide with suitable hydraulically-mediated habitat quality and connectivity, salmon enjoy opportunities for growth (as in Fig. 1 from Chapter 3 of my dissertation). The availability of prey items to foraging salmonids depends on food phenology in the habitat, and its match or mismatch with the timing of their foragers' arrival and foraging success in habitats. Thus the third determinant of watershed potential for salmon is the portfolio of life histories in a river network (Hillborn 2003, Schindler et al. 2010, Carlson and Satterthwaite 2015), which can strongly affect whether some consumers will be "at the right place at the right time" to profit from peaking feeding opportunities. These are the "three legs of a stool" that are all needed to realize the potential of a given watershed to sustain salmonid growth, production, and resilience.

Finally - Following Mobrand (1997), and Wiplfi and Baxter (2010) and others, I hope to study how an integrated "riverscape – foodscape – life history diversity" perspective can inform salmon population recovery efforts. Human alteration of rivers and watersheds (e.g. flow modification, deforestation, gravel harvesting, isolation of channels from floodplains, climate change) have changed each of the elements a productive salmon bearing watershed: Reducing the *size, and quality and arrangement of physical habitats*; the duration of *habitat connectivity*; and the timing, quality and strength of resources fluxes between *linked river, upland, and coastal food webs*.

My dissertation began with the observation that our recovery actions are heavily weighted towards the first element – *in-situ* physical habitat quality. With the Foodscape concept, I hope to integrate seasonal hydrology, prey phenology and ecosystems linkages down drainage networks (headwaters the ocean) to understand how salmon life history diversity can track and exploit resources at the watershed scale. This perspective may reveal new approaches to salmon recovery –by identifying and protecting the trophic pathways and ecosystem linkages that feed rearing salmon and promote a stabilizing portfolio of juvenile salmon life history diversity within watersheds.

Literature Cited

Baxter, C. V., K. D. Fausch, and W. Carl Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones: Prey subsidies link stream and riparian food webs. Freshwater Biology 50:201–220.

Bellmore, J. R., C. V. Baxter, K. Martens, and P. J. Connolly. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. Ecological Applications 23:189–207.

Caldwell, T. J., G. J. Rossi, R. E. Henery, and S. Chandra. 2018. Decreased streamflow impacts fish movement and energetics through reductions to invertebrate drift body size and abundance: Reduced streamflow changes drift, fish behavior and fish energetics. River Research and Applications 34:965–976.

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

Cederholm, C. J., M. D. Kunze, T. Murota, and A. Sibatani. 1999. Pacific Salmon Carcasses: Essential Contributions of Nutrients and Energy for Aquatic and Terrestrial Ecosystems. Fisheries 24:6–15.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–451.
Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes. BioScience 52:483.
Gowan, C. 2007. Short-term cues used by foraging trout in a California stream. Environmental Biology of Fishes 78:317–331.
Harvey, B. C., and S. F. Railsback. 2014. Feeding modes in stream salmonid population models: is drift feeding the whole story? Environmental Biology of Fishes 97:615–625.
Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences 100:6564–6568.
Hughes, N. F., and L. M. Dill. 1990. Position Choice by Drift-Feeding Salmonids: Model and Test for Arctic Grayling (Thymallus arcticus) in Subarctic Mountain Streams, Interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:2039–2048.
Jeffres, C. A., E. J. Holmes, T. R. Sommer, and J. V. E. Katz. 2019. Detrital Food Web Drives Aquatic Ecosystem Productivity in a Managed Floodplain. preprint, Ecology.
Mobrand, L. E., J. A. Lichatowich, L. C. Lestelle, and T. S. Vogel. 1997. An approach to describing ecosystem performance “through the eyes of salmon” 54:10.
Naman, S. M., J. S. Rosenfeld, P. M. Kiffney, and J. S. Richardson. 2018. The energetic consequences of habitat structure for forest stream salmonids. Journal of Animal Ecology 87:1383–1394.
Neuswanger, J. R., M. S. Wipfli, A. E. Rosenberger, and N. F. Hughes. 2016. Measuring fish and their physical habitats: versatile 2D and 3D video techniques with user-friendly software. Canadian Journal of Fisheries and Aquatic Sciences 73:1861–1873.
Nielsen, J. L. 1992. Microhabitat-Specific Foraging Behavior, Diet, and Growth of Juvenile Coho Salmon. Transactions of the American Fisheries Society 121:617–634.
Piccolo, J. J. & M. S. Wipfli, 2002. Does red alder (Alnus rubra) along headwater streams increase the export of invertebrates and detritus from headwaters to fish-bearing habitats in southeastern Alaska? Canadian Journal of Fisheries and Aquatic Sciences 59: 503–513.
Polis G.A., Power M.E., Huxel G.R. editors. 2004. Food Webs at the Landscape Level. Chicago: University of Chicago Press.
Power, M. E., and W. E. Rainey. 2000. Food webs and resource sheds: towards spatially delimiting trophic interactions. Page 24 Ecological Consequences.
Rosenfeld, J. S., and J. Taylor. 2009. Prey abundance, channel structure and the allometry of growth rate potential for juvenile trout. Fisheries Management and Ecology 16:202–218.
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.
Wipfli, M. S., and C. V. Baxter. 2010. Linking Ecosystems, Food Webs, and Fish Production: Subsidies in Salmonid Watersheds. Fisheries 35:373–387.