

UC Santa Cruz

UC Santa Cruz Electronic Theses and Dissertations

Title

Biotic and Abiotic Determinants of Fish Behavior and Habitat Use Along a River Continuum

Permalink

<https://escholarship.org/uc/item/7b4364sj>

Author

McElroy, Katherine Nicole

Publication Date

2016

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA

SANTA CRUZ

**BIOTIC AND ABIOTIC DETERMINANTS OF FISH BEHAVIOR AND
HABITAT USE ALONG A RIVER CONTINUUM**

A thesis submitted in partial satisfaction

of the requirements for the degree of

MASTERS OF ARTS

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Katherine McElroy

December 2016

The Thesis of Katherine McElroy

is approved:

Professor Mark Carr, chair

Joe Merz, Ph.D., co-chair

Professor Eric Palkovacs

Sue Sogard, Ph.D.

Tyrus Miller
Vice Provost and Dean of Graduate Studies

Copyright © by
Katherine McElroy
2016

Table of Contents

Abstract.....	iv
Acknowledgements.....	vi
Introduction.....	1
Methods.....	5
Results.....	15
Discussion.....	18
Figures.....	29
Appendices.....	37
Bibliography.....	43

Abstract

BIOTIC AND ABIOTIC DETERMINANTS OF FISH BEHAVIOR AND HABITAT USE ALONG A RIVER CONTINUUM

by

Katherine McElroy

Association with physical structure or conspecifics can impact the survival and growth of individuals. The necessity and strength of these associations can change with environmental conditions and ontogeny, acting in concert or in opposition to influence an individual's behavior and ultimate success. To test the hypotheses that affinity for physical structure and aggregating behavior changes along a dynamic river gradient and with development of a migratory fish, I conducted a field experiment on the San Joaquin River, California with juvenile Chinook salmon (*Onchorynchus tshawyscha*). I created orthogonal combinations of turbidity, fish size, and structural cover by manipulating the presence of artificial structure within net pens at three locations along the river continuum. I recorded the affinity of juvenile Chinook salmon to physical structure and propensity to aggregate with conspecifics with video cameras. I used generalized linear models and model selection to evaluate the effects of turbidity, size (fork length), density, and structure level on proximity of individuals to structure and conspecifics. First, I found there was no difference in the total number of salmon in structure or no-structure levels. Second, I found the number of aggregating observations increases with increasing density and fork length. When structure was present, aggregating behavior was low

across turbidities. In contrast, when structure was absent, aggregating behavior increased in low turbidities. Ultimately, I found both ontogeny and a changing environmental gradient influenced the number of aggregating observations. These results indicate how environmental conditions (turbidity and availability of physical structure), size, and density interact to determine fish behavior and increase understanding of the complicated interactions surrounding fish habitat use.

Acknowledgements

I would like to thank my advisor Dr. Joe Merz for the intellectual and personal support necessary for the completion of this project. Thank you to my committee members Dr. Mark Carr, Dr. Eric Palkovacs, and Dr. Sue Sogard for their insightful feedback throughout this entire process. Special thanks go to Kirsten Sellheim, Dr. Mike Beakes, Dr. Steve Zeug, and Jesse Anderson for the immense amount of logistical support and statistics advice. Furthermore, thank you to the technical staff of Cramer Fish Sciences for the many long, hot days on the San Joaquin River; the project would not have happened without you. Thank you to my volunteers Raul Almanza, Emily Cassaretto, Rebecca White, and Saniesa Thomas for watching video after video of salmon behavior. I am very grateful to have been associated with the Palkovacs and RC labs throughout my graduate experience. I have learned so much from all of you and thank you for your friendship and advice. Finally, thank you to my family and friends; you are the best support system and continue to inspire me to do my best. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE1339067 and the United States Bureau of Reclamation San Joaquin River Restoration Program under Contract No. R13AC20015.

Introduction

The quality and function of habitats are important features of behavioral and population dynamics (Mysterud and Ims 1998, Krausman 1999, Urabe and Nakajima 2010). Species often exhibit considerable habitat selection and it has been shown that these decisions are important to overall fitness and survival (Werner et al. 1983, Poff et al. 1997, Valeix et al. 2009). However, habitat requirements are not static; how an organism perceives the value of specific habitat variables can change over the life of the organism (ontogeny) and across environmental gradients (Stamps 1983, Raleigh et al. 1986, Valeix et al. 2009). Thus, an understanding of how, when, and why habitat needs change is necessary to evaluate the role habitat plays for a species.

Cover, anything that veils, conceals, shelters or protects an organism, is a necessary aspect of habitat that exists in many forms (Dasmann 1971, Mysterud and Østbye 1999, Allouche 2002). Cover provided by physical features, such as vegetation or topography, hereby defined as “structure”, has three primary benefits to the fitness and survival of organisms. First, structure can create physical protection from abiotic stressors such as direct sunlight, extreme temperatures, wind, and current (Loveless 1964, McMahon and Hartman 1989, Naiman et al. 2005). Second, structure can aid in energy conservation, allowing individuals to seek refuge from stressful habitats and improve feeding success (Gurnell et al. 1995, Mysterud and Østbye 1999, Vehanen and Bjerke 2000). Third, structure can reduce negative inter and intraspecific interactions like predation and competition (Turner 1979, Stamps 1983, Keeley 2001, Vehanen and Hamari 2004).

Another source of cover is created when individuals associate with others of the same or different species, forming behavioral aggregations (e.g. schooling, flocking, herding; Savino and Stein 1989). The behavior of aggregating can impart similar benefits as association with structure (Emlen 1952, Partridge 1982). Individuals in aggregations can experience increased predator avoidance, greater prey detection, more efficient movement, and ameliorate the effects of stressful abiotic conditions (Springer et al. 1981, Lima 1995, Grand and Dill 1997, Grant et al. 2005, Zheng et al. 2005, Liao 2007). Individuals also aggregate because of changes in hormones and life history associated with development, indicating the behavioral propensity to aggregate is not fixed and often changes with time (Davis 1970, Katz et al. 2011). Aggregations can thus be seen as another type of cover, behavioral cover, and species may transition between behavioral and structural types of cover use throughout their lifetime (Savino and Stein 1989, Hosn and Downing 1994, Villafuerte and Moreno 1997). Because of the theorized survival and fitness benefits of either cover form, quantifying how these relationships change is critical to understand the ecology and behavior surrounding habitat use.

Environmental conditions often change along natural gradients. Temperature and precipitation can change predictably across a landscape, structuring plant communities and influencing habitat ranges of terrestrial species (Prentice et al. 1992). These environmental gradients cause changes in an individual's choice to use structure or aggregate with conspecifics as demonstrated by Stamps (1983) and Grant et al. (2005). Stream-dwelling fishes, such as migratory salmon in their freshwater

life stages, are excellent study subjects for exploring these choices in types of cover use. Salmon exhibit behavioral and physiological changes during their juvenile stage and migrate downstream along a dynamic environmental gradient referred to as the river continuum (Grand and Dill 1997, Merz et al. 2013). The River Continuum Concept (RCC) is a framework for conceptualizing how changing physical variables (velocity, width, temperature, depth) predict the occurrence of aquatic species (Vannote et al. 1980). This concept can also be applied to predict and explain how cover requirements and use change as juvenile salmon migrate downstream. Under the RCC, low order streams are relatively clear, cool, high velocity headwaters, whereas high order streams are relatively turbid, warm, low velocity waters near river deltas. Species inhabiting the river continuum encounter the extremes of velocity and turbidity, creating dynamic stressors that could influence their choice to use structure or aggregate with other individuals (McMahon and Hartman 1989, Schlosser 1991, Allouche 2002).

In this study, I investigated the influence of ontogenetic change along an environmental gradient on the affinity for physical structure and aggregating behavior of an anadromous fish, the Chinook salmon (*Oncorhynchus tshawytscha*). Salmon (Salmonidae) are exothermic fish that travel vast distances, utilize numerous habitats (including the river continuum), are exposed to dramatic ranges in climate and water quality conditions, and make marked physiological and behavioral transformations over the life of an individual (Bjornn and Reiser 1991, Quinn 2011). Juvenile salmon also vary in their densities along the river continuum, creating a dynamic population

landscape (Brandes and McLain 2001). Consequently, Chinook salmon should demonstrate detectable changes in the forms of cover they use throughout their life cycle and in different environmental conditions.

To investigate how environmental gradients and early ontogenetic shifts influence use of alternative forms of cover (structure versus aggregation), I tested three hypotheses. First, juvenile salmon affinity for structure and propensity to aggregate are both influenced by the perceived risk of predation (Werner et al. 1983, Hugie and Dill 1994, Vehanen and Hamari 2004); juvenile salmon should be in closer proximity to structure and conspecifics when predators are present compared to their absence. Thus, I expect increased association with structure and increased aggregating behavior in areas of low turbidity where visibility to avian and fish predators is higher (Gregory 1993, Abrahams and Kattenfeld 1997). Second, juvenile salmon distribution is influenced by caloric optimization, as individuals must occupy locations that enhance feeding opportunities and reduce energy expenditure (Werner et al. 1983, Fausch 1984). Juvenile salmon should be in closer proximity to structure in areas of increased energy expenditure with high prey potential, whereas proximity to other individuals should be closer in areas of low prey potential. Thus, I expect increased use of structure in high velocity conditions; high velocities deliver greater quantities of drift and structures concentrate prey while providing flow refuge (Gurnell et al. 1995, Vehanen and Bjerke 2000). I expect increasing tendency to aggregate in low velocities when prey is more difficult to find as schools have greater prey detection ability (Partridge 1982). Third, perceptions of cover will change as the

ability to avoid predators and swim in flow improves with growth and development of the juveniles, likely causing decreased association with structure and decreased aggregating behavior (Fausch 1984).

This study aims to quantify how physical habitat characteristics (governed by the RCC) and ontogeny change the decision to use structure or aggregate with conspecifics in a dynamic river gradient. I first demonstrated the environmental variables (turbidity, velocity, temperature, dissolved oxygen, substrate size) on the San Joaquin River varied predictably with river gradient according to the RCC. I then investigated whether this environmental gradient, ontogeny, and availability of structure influences whether individuals aggregate or associate with structure. I conducted a field experiment on a California Central Valley river and monitored fish behavior with video observations to address these questions.

Methods

Study System

The study was conducted on the San Joaquin River, a snow and rain-fed river that drains 82,362 km² of the Central Sierra Nevada Mountains in California, USA. The study reach was located on the lower San Joaquin River between Friant Dam, a non-passable flood and water storage reservoir located at river kilometer 430 (37°00'02"N, 119°42'19"W), and the Merced Wildlife Refuge located at river kilometer 589 (37°10'45"N, 120°38'12"W). The river has a Mediterranean climate with two distinct seasons, defined primarily by the precipitation regime: a relatively

mild, wet winter season (November through April) and a warm, occasionally foggy, dry season (May through October). Flow is much less predictable than climate due to high water consumption and regulated pulse flows from Friant Dam associated with agricultural demand (Brown 2000). Within the study reach, the river has a relatively open canopy with minimal shading, so shade from riparian vegetation is unlikely to play a significant role in fish behavior (San Joaquin Valley Drainage Program 1990). My study sites were Scout Island, Gragnani, and Merced Wildlife Refuge, located 26km, 63km, and 159km downstream from Friant Dam (Figure 1). These sites captured a range in substrate (gravel to clay), temperature (16-25°C), turbidity (0-40 NTU), dissolved oxygen (2.51 to 14.80 mg/L) and relative velocity (0-1m/s) along the San Joaquin River (Figure 2). Fieldwork reported in this paper was conducted during the wet season of February to May of 2016.

The San Joaquin River supports 25 native and 30 introduced fish species including wild and hatchery-produced Chinook salmon (Brown and Moyle 1993, Brown 1996). In North America, Chinook salmon are distributed along the West Coast from the Bering Strait of Alaska to the Central Valley of California (Merz et al. 2013). They exhibit an anadromous life cycle; adults return to their natal freshwater stream to reproduce after maturing at sea. Juvenile Chinook rear in freshwater for less than 2 months and up to 2 years before undergoing smoltification and migrating to the ocean (Bjornn 1998, Quinn 2011). San Joaquin River fall-run juveniles spend the months of January through June rearing in the system, developing from fry (under 60mm) to parr (over 60mm). There are two pulses of out-migrating fish that exit

through San Francisco Bay; fry stages, which reach peak emigration rates between February and March, and smolt stages, which reach peak emigration rates between April and May (Miller et al. 2010).

Environmental Variables along the River Continuum

To assess how physical variables and ontogeny change a juvenile salmon's use of structure and aggregating behavior along the river continuum, I used a net pen field experiment to manipulate availability of structure at three different locations that varied in environmental conditions. Following the methods of Jeffres et al. (2008), four net pens of 3-mm polypropylene aquaculture mesh (Memphis Net and Twine Co., Memphis, TN) were installed at three sites for a total of 12 pens: Scout Island, Gragnani, and Merced Wildlife Refuge (Figure 1). Each pen was 3.67m x 6m x 1.52m (LxWxH) to ensure fish densities of approximately 0.11 g of fish/L at an average water depth of 0.5m for 200 smolt-sized individuals (fork length=80mm). This value was chosen to minimize negative effects of caging associated with fish living at unnaturally high densities, such as, increased competition, decreased growth rates, and increased disease (Oikari 2006). Net pens were weighted to the substrate using long tube and pillow sandbags (The Sand Bag Store, Las Vegas, NV), anchored using t-posts, and covered with raptor netting to prevent avian predation (1.5 cm mesh; Easy Gardener Inc., Waco, TX). Scout Island had two main channel pens and one floodplain pen (the second floodplain pen was invaded by fish predators in the first week and was discarded), Gragnani had two main channel and two floodplain

pens, and Merced Wildlife Refuge had four floodplain pens (main channel habitat was absent at this site). Pen locations were chosen at suitable depths (10-80cm) on the fry/smolt habitat suitability curve (Beakes et al. 2014).

Artificial structure was installed in each pen. Structure consisted of a 0.4m² cube of twenty-eight 1cm diameter bamboo stalks suspended in a PVC frame to mimic a stand of willows (*Salix* sp.), a natural source of physical cover on the San Joaquin River, and was anchored to the substrate using a light weight t-post (Sellheim et al. 2015). The structure was anchored 1m across from another light weight t-post that held a Go Pro Hero 3 Silver Edition (Go Pro, Inc.) for video monitoring. Structure was positioned closer to the camera t-posts (0.5m and 0.8m) at the two pen locations at the Merced Wildlife Refuge due to high turbidities and lack of video clarity. Each pen also contained a no-structure control t-post and camera t-post with the same spacing, located 3.6m away from the structure. I refer to these two camera vantage points as structure and no-structure levels; however, these areas are not isolated from one another within a pen. I assume the distance between the structure and no-structure levels (3.6m) is sufficient to detect the effect of structure presence and absence on fish behavior (Hardin et al. 2005). The locations of the structure and no structure levels within pens were switched weekly (Appendix 1).

Each week for 10 weeks, I collected information on environmental conditions and fish behavior at all three sites. I took turbidity measurements using a Lutron Turbidity Meter, Model TU-2016 (Lutron Electronic Enterprise Co., Taipei, Taiwan) in front of the two camera stands in each pen, reporting the average of three

measurements. I measured temperature and dissolved oxygen (DO) using an YSI Handheld DO Instrument, Model ProODO (YSI Inc., Yellow Springs, OH) in the center of each pen at mid depths. Velocity and depth measurements were taken directly upstream, downstream, to the right, to the left, and in the center of the structure and no-structure treatments with a top setting rod (Rickly 1.2 meter USGS Top Setting Wading Rod; Rickly Hydrological Company, Columbus, OH) and Hach FH950 Handheld Flow Meter (Hach Company, Loveland, CO) following the methods of Merz et al. (2004) (Appendix 1).

Surface substrate data were taken at each pen during installation. Substrate samples were collected by pebble count at three randomly selected transects within the pen area. Surveyors collected one sample by hand every 0.1m along the 5m transect and used a round-hole template to measure size (categories: <8.0, 8.0, 16.0, 22.2, 31.8, 44.5, 63.5, 89.0, 127.0, 177.8, 254.0, and >254.0mm). Categorization was based on the largest slot through which an individual pebble could not be passed (Merz et al. 2004). These data were transformed into D_{50} , the value of the particle diameter at 50% in the cumulative distribution, by taking the median diameter or the medium value of the particle size distribution (Merz et al. 2004). Distance downstream from Friant Dam was measured by tracing the center of the San Joaquin River channel using the path function in Google Earth (7.1.5.1557, 2015, Google Inc.).

Affinity for Structure and Propensity to Aggregate along the River Continuum

Each net pen was stocked on 25 February 2016 with 80 Chinook fry (46.3 ± 2.8 mm SD) from the Mokelumne River Hatchery (Clements, CA). Fish were transported from the hatchery to the sites in a 113.6-liter cooler. Coolers were monitored every hour to ensure temperature did not exceed 15°C and DO did not drop below 7 mg/L (Maule et al. 1988). Ice and oxygen were added as needed. Fish were anesthetized using AQUI-S and fork length (FL) was taken to the nearest millimeter (mm) before they were stocked into the pens. Each week, 10 fish were removed from each pen, measured, and sacrificed for growth measurements. On 14 April 2016, the fish from the first size class were removed. On 21 April 2016, the pens were restocked with 80 Chinook parr (68.1 ± 4.3 mm SD), the second size class. I subsampled 10 fish weekly until the end of the experiment on 5 May 2016.

To collect information on fish structure use and aggregating behavior, paired 35-minute videos were collected simultaneously at the structure and no-structure locations in each pen. This was done first at each site to minimize disturbance to study fish. At the conclusion of video recording, environmental data were collected (as outlined above) and ten fish were subsampled for growth measurements using a combination of dip netting and seining.

Videos were initially sorted by image quality to prioritize editing to improve light conditions and video clarity. If I was unable to see the structure/no-structure t-post, I edited the video using Adobe® Premiere® Pro to manipulate saturation, white balance, and contrast to expand the field of view to see the structure/t-post clearly.

Videos in which the field of view could not be improved to see the structure/t-post were discarded (Appendix 2). Twenty-eight videos were discarded because of bad quality and 10 videos were discarded because the Go Pro malfunctioned and did not record a full trial (Appendix 2).

Videos were watched to extract data on fish structure usage and aggregating behavior. Videos were subsampled to 20 minutes, the longest sampling effort possible with the most videos. The observer began watching videos at time 7:00 minutes to allow fish adequate time to acclimate following video installation and concluded video observation after 20 minutes at time 27:00 in the video. Previous observations of hatchery fish in an artificial flume demonstrated most fish resume normal behavior (horizontal body position, regular tail beats) following a stressor within seven minutes (McElroy 2015, unpublished data). Observers recorded the length of time a fish or group of fish were within the video frame, the number of fish in that observation, and whether aggregating occurred. If the number of fish changed at any point within the observation, the observer would record the end time of the original group and begin a new observation for the new numbers of fish. Aggregations were defined as two or more fish within 4 FLs from each other, swimming in the same direction and at the same speed (Partridge 1982, Katz et al. 2011) (Appendix 3).

Total fish number and aggregating data were summarized by individual video using the *dplyr* package in program R (R Core Team 2016). Fish number was summed during each video to create a total number of fish observations for each video. Aggregating observations were coded as a 1, regardless of the number of

individuals aggregating in them, and non-aggregating observations were coded as a 0 in a separate “Aggregations” column. The number of aggregating observations was summed for each video using the “Aggregations” column and the turbidity, estimated FL, and estimated fish density were reported. Thus, each data point represents a single video, or weekly sample, and contains the total number of observations of aggregations. Estimated FL for each time period was calculated by averaging the FLs of the ten subsampled fish in that week at each pen. Estimated fish density was calculated by dividing the pen population by the area of the net pen. Pen population was calculated by subtracting the total number of fish removed prior to video sampling and applying an estimate of weekly mortalities and escapees based on the number of fish recovered at the end of the experiment (Appendix 4).

Analysis

Environmental Variables along the River Continuum

I used Principal Components Analysis (PCA) in R to visualize differences in environmental parameters, summarized by weekly samples, among sites and along the river continuum to demonstrate the San Joaquin River followed the predictions of the RCC. Environmental data included temperature, dissolved oxygen (DO), average velocity, distance downstream from the dam (distance DS), D_{50} , and turbidity. The PCA distilled the variation contained in the environmental data into a reduced number of uncorrelated dimensions, or principal component axes (Wold 1987, King and

Jackson 1999). This allowed me to determine those environmental variables that were most important for describing environmental differences between sites.

Affinity for Structure and Propensity to Aggregate along the River Continuum

To demonstrate that fish FL changed throughout the study duration, I conducted a linear regression in R of estimated FL by week, site, and the interaction between week and site. To test for use of structure, I used an independent two-sample t-test in R to compare the total number of fish observations at each structure level. The t-test combined the total number of fish data from all three sites across the 10-week study duration.

I evaluated the relative effects of turbidity, FL, fish density, and structure level on the propensity of fish to aggregate (i.e. the number of observations of aggregations in each video) using a generalized linear model (GLM) with a Poisson distribution and model selection via Akaike's information criterion corrected for small sample sizes (AIC_c). Poisson regressions have been used in similar studies on count data (Filipe et al. 2002). This family of regression models assumes the logarithm of the expected response variable value can be modeled by a linear combination of unknown parameters. I assumed fish modify their behavior on short temporal and spatial scales as environmental parameters and population dynamics change. The models combined all three sites' data across the 10-week study duration for a total of 136 data points (the number of videos analyzed). I reported the mean, standard error, and coefficient of variation (standard deviation/mean) of the number

of observations of aggregations for each pen in Appendix 5. Parameters were chosen to address the a priori hypotheses: propensity to aggregate will be highest in areas of greater perceived predation risk (low turbidity, absence of structure) and high energetic demand (high velocity) and will change with fish population structure (mean FL, fish density). I included fish density because it varied throughout the study duration and has been demonstrated to affect fish behavior and habitat use (Hosn and Downing 1994, Grant et al. 1998, Imre et al. 2002). These parameters initially included velocity, but it was dropped from the model because the structure of the net pens reduced velocities within the pens to comparable levels among sites that were within the preference range for juvenile Chinook (Beakes et al. 2014).

I generated a candidate set of generalized linear models using all possible combinations of the four parameters as well as all possible two-way interactions between FL, fish density, and turbidity with structure level (presence/absence). I used AIC_c scores to rank models based on parsimony (Akaike 1974, Anderson 2008). The most parsimonious model, with the best balance between model complexity and explanatory power, received the most quantitative support and lowest AIC_c score (Burnham and Anderson 2002, Swain et al. 2014). The top model with the lowest AIC_c score was reported; differences greater than 4 AIC_c units indicate model superiority (Burnham and Anderson 2002). To compare the relative effects of the parameters and interactions and interpret the main effects of the top model, I ran the model after standardizing the continuous explanatory variables (Harding and

Reynolds 2014). I centered the data by subtracting global means from each value and scaled the data by dividing two times the standard deviation (Gelman 2008).

Results

Between 1 March and 11 May 2016, 136 videos were recorded and 2,720 minutes of video were analyzed (Appendix 2). Environmental variables varied throughout the experiment: temperature 13.4 to 21.3°C, DO 2.51 to 14.80 mg/L, water velocity <0.01 to 0.14 m/s, substrate size (D_{50}) 0.15 to 30.66 cm, turbidity 0.93 to 23.94 NTU (Figure 2). Fish FL varied from 45mm in the first week of the experiment to 88mm in the sixth week (Figure 3). Fish densities declined from 3.6 to 0.3 fish per m^2 throughout the experiment due to removals for growth analysis and mortalities/escapees (Appendix 4).

Environmental Variables along the River Continuum

Component 1 of my PCA explained 45.8% of the total variation in my environmental data and component 2 explained 21.3% for a combined total of 67.1% (Figure 4). The variables on component 1 with the highest loadings were D_{50} (0.567) and distance DS (-0.571). The variables with the highest loadings on component 2 were temperature (0.695) and turbidity (0.616). In general, D_{50} , DO, and velocity decreased with distance DS while temperature and turbidity increased (Figure 2, 4). The three sites demonstrate relatively high separation among environmental parameters, moving from upstream to downstream (Figure 4). There is some overlap

between the Scout Island and Gragnani points, but these sites are much closer (23km) than the Gragnani and Merced Wildlife Refuge sites (60km). Using the PCA and my a priori hypotheses, I selected turbidity as a proxy for location on the RCC because it increased with distance downstream, reflecting the predictions of the RCC.

Affinity for Structure and Propensity to Aggregate along the River Continuum

The linear regression indicated that average weekly FL increased with time throughout the duration of the experiment and the rate of growth was significantly different between sites ($df=2$, $R^2=0.7529$, $p<0.001$; Figure 3). Week had a significant effect on the average FL ($p<0.001$) although the interaction between week and site did not ($p=0.226$). Site, when comparing Gragnani or Scout Island against Merced Wildlife Refuge, had a significant effect ($p<0.001$), indicating fish at Merced Wildlife Refuge were significantly larger.

The two-sample t-test indicated there was no significant difference in the number of fish observations in the structure and no-structure levels ($df=2$, $t=0.403$, $p=0.688$). Both structure levels contained an average of around 50 fish observations although there were similarly distributed outliers in both levels (Appendix 6). This result indicates the presence of structure by itself did not significantly change the number of fish observations across videos.

For the analysis of aggregating behavior, there were three candidate models that had similar AIC_c scores ($\Delta AIC_c < 4$). However, the top ranked model received the majority of the support with an AIC_c weight of 0.61 or 61% of the relative support.

The top ranked model included fixed effects for turbidity, FL, fish density, and structure level (presence/absence) as well as interactions between structure level and turbidity, and structure level and fish density (Table 1). The second and third ranked models had AIC_c weights of 0.24 and 0.09 respectively. All three models included an interaction of at least one parameter with structure level (Table 1). Below I focus on results from the top ranked model that received highest AIC_c weight.

Results from the top ranked GLM indicate the effect of turbidity on the number of fish aggregations was dependent on structure level (Table 2); the interaction between structure level and turbidity had a significant effect. Specifically, when structure was absent, I observed significantly more observations of aggregated fish in low turbidities. In a low turbidity of 2 NTU, I saw 53% more aggregating observations if structure was absent. At high turbidities of 10-12 NTU, there were few aggregating observations in the presence or absence of structure (Figure 5). The number of aggregating observations decreased with increasing turbidity when structure was absent, or along the RCC.

Fork length had a significant effect on the number of aggregating observations (Table 2). When structure was unavailable, I observed more aggregating observations across the range of FLs. In general, aggregating increased with FL (Figure 5); there were 80% more aggregating observations of large smolt-sized fish (85mm) in both treatments than small fry-sized fish (45mm). Aggregating increased with increasing FL, or as fish developed and experienced ontogenetic change.

Fish density had both a significant fixed effect and significant interaction with structure level (Table 2). At low densities of 1 n/m², I observed 76% more aggregating observations in the absence of structure than in the presence of structure. Aggregating generally increased with fish density and fish in the absence of structure aggregated more than fish in the presence of structure up to a fish density of roughly 3 n/m² (Figure 5). At 3 n/m², the upper end of my fish densities, I observed more aggregating observations in the presence of structure than in its absence.

After centering and scaling the data, I found fish density had the largest effect on the number of aggregating observations, although the absence of structure and FL had strong positive effects (Figure 6). Fish density and turbidity had strong negative effects on aggregating in the absence of structure (Figure 6). The fixed effect of turbidity did not have a significant effect on the number of aggregating observations.

Discussion

The purpose of my study was to discover how the use of structural and behavioral mechanisms of cover changes along an environmental gradient and with ontogeny to increase understanding of the factors influencing habitat use. I chose a migratory fish inhabiting a dynamic river continuum to test my predictions. I predicted that use of both physical structure and aggregating behavior would increase in areas of high-perceived predation risk and energetic cost, and these behaviors would decrease as individuals developed. I used the RCC as a natural environmental gradient and expected the propensity of individuals to aggregate would be highest in

areas of high velocity and low turbidity. I used the development of juvenile Chinook salmon from fry to parr to smolts to investigate the impact of ontogeny, predicting that propensity to aggregate would decrease as fish develop. This study connected ontogeny and a changing environment as factors influencing forms of cover use to improve the understanding of the ecology surrounding habitat use.

First, I found the San Joaquin River fit the predictions of the RCC through a PCA on turbidity, temperature, DO, velocity, D_{50} , and distance downstream for my three sites. Principal component axis one (PC1) was dominated by distance downstream from the dam and D_{50} , a measure of substrate size. As the RCC predicts, substrate size decreased downstream, marking a transition from large gravel appropriate for spawning and incubation to fines and clay associated with river deltas (Vannote et al. 1980, Schlosser 1991). The second principal component axis (PC2) correlated with water quality parameters; turbidity and temperature increased downstream. As gravel size and velocity decreased downstream, small particles remained suspended in the water column and water temperatures remained high due to lack of water circulation (Vannote et al. 1980). Although the San Joaquin River has been altered by anthropogenic disturbance, the river generally followed the predictions of the RCC, allowing me to test the effects of environmental gradient on cover use.

Although my PCA showed velocity inside the pens was highest upstream and decreased downstream, my measurements did not reflect the magnitude of velocity change the RCC predicts (Vannote et al. 1980). My net pen experiment was limited in

its ability to capture true velocity measurements for two reasons. First, velocities inside the pens were lower than those outside because the pen created a flow obstruction and caused velocities to decrease. Pens often clogged with drift material, further blocking flow from moving into the pen. Second, net pen placement was limited to a range in velocities in which they were structurally sound. At Scout Island and Gragnani, I could not install pens in the true main channel because the flow was too swift and would compromise the structural integrity of the pen. Because my velocity measurements did not reflect the true magnitude of those experienced in the RCC, I dropped velocity from my model and chose to use only turbidity as a proxy for the RCC. Turbidity fit the predictions of the RCC and reflected the magnitude of values expected.

I found that fish grew over the duration of the experiment at all three sites. Fish growth was faster throughout the experiment at the Merced Wildlife Refuge site, the farthest downstream on the RCC, than at the Scout Island and Gragnani sites, which did not differ from each other. Merced Wildlife Refuge supported faster growth rates due to increased prey levels from productivity associated with a long flooding period of off-channel habitats created by refuge managers. Gragnani would normally be expected to have larger fish than Scout Island due to higher water temperatures; however, drought conditions, in combination with reduced velocities inside the pen, appeared to have decreased velocities and drift at Gragnani, making it comparable to the upstream Scout Island site. Fish FL and growth data indicated study fish transitioned between fry, parr, and smolt life stages at all three sites,

reflecting the distribution of all juvenile life stages along the length of the RCC (Brandes and McLain 2001). Generally, fry are found in the upstream sections of the RCC while smolts are found in the downstream sections (Merz et al. 2013). However, this reflects only the dominant juvenile life history. Alternate life histories include fry that are pushed (by rain events) or move downstream shortly after emerging from the gravel to rear in the downstream floodplains and reaches, and parr that remain upstream guarding territories and growing large before they emigrate later in the season (Quiñones and Mulligan 2005, Zeug et al. 2014). Thus, my experimental design mirrored the actual distribution of juvenile salmon along the RCC.

Through a two-sampled t-test, I found there was no significant difference in the total number of fish observations near structure and away from structure. This does not align with my original hypotheses that affinity for structure should increase with decreasing turbidity, increasing velocity, and decreasing FL (Werner et al. 1983, Fausch 1984, Gregory 1993). My results instead show fish observations were constant between structure levels, indicating they did not demonstrate affinity for structure. This is likely because fish preferred using another type of cover to physical structure, like aggregating with conspecifics.

I found both the RCC and ontogeny had an effect on the number of aggregating observations. The interaction between turbidity and structure level had a significant effect on the number of aggregating observations. In the absence of structure, aggregating behavior declined as turbidities increased; however, when structure was present, aggregating was low across the range of turbidities. Turbidity

has been demonstrated to affect an individual's perceived risk of predation, with fish exhibiting anti-predator behavior, such as hiding or aggregating with conspecifics, in clear waters, but generally not in turbid waters (Gregory 1993, Abrahams and Kattenfeld 1997). Gregory (1993) found juvenile salmon exhibited anti-predator behavior in the presence of avian and fish predators in clear waters of 1-6 NTU, but were randomly distributed in turbid waters of around 20 NTU. My data reflected the results of Gregory (1993); fish aggregated more in turbidities of 0-6 NTU when structure was absent, but aggregating decreased regardless of structure availability in high turbidities of 6-12 NTU. The small range of turbidity experienced in this study was similar to the ranges in Abrahams and Kattenfeld (1997), in which they found high proportions of minnows in risky habitat when predators were present in high turbidities of around 11 NTU. It was also similar to the ranges of Barrett et al. (1992), where reaction distances of trout decreased by 80% in high turbidities of 15 NTU in comparison to low turbidities of 4-6 NTU. Based on these findings, I concluded the environmental gradient of the RCC caused aggregating behavior to decrease downstream with increasing turbidity.

Fork length had a significant effect on the number of aggregating observations; as fish developed and their swimming abilities increased, they tended to aggregate more. Aggregating increased with FL regardless of the presence of structure, indicating smaller fish aggregated less and may have associated with structure to escape stressful conditions, while larger fish preferred to aggregate. This is consistent with the findings of Liao (2007), which indicated salmonid fry (under

55mm) were generally more solitary and dove under gravel or hid behind structure to escape stressful conditions or predators. Parr (over 55mm), in contrast, were stronger and faster swimmers that began to aggregate in preparation for the smoltification process (Quiñones and Mulligan 2005). Hoar (1976) found the dominant feeding and predator avoidance strategy for smolts in the pelagic marine environment is aggregating, suggesting parr begin aggregating in preparation for this ontogenetic shift. There are also instances in which it is beneficial for fry to aggregate and for parr to use structural cover. Fry will aggregate as they emigrate downstream at night for protection from predators (McDonald 1960). Parr will associate with structure in high velocities to conserve energy (Grand and Dill 1997). In pulse flows or after rain events, the magnitude of velocity drastically increases, causing multiple sizes of fish to associate with structure to avoid displacement (Liao 2007). However, based on the general trends in my data, I concluded ontogeny affects the decision to aggregate, with fry aggregating significantly less than parr.

Fish density also had an effect on the number of aggregating observations. It has been widely documented that fish density has important effects on behavior and growth of juvenile fish (Keeley 2001), so I predicted that density of juvenile salmon would influence their propensity to aggregate. My model found aggregating increased significantly with fish density. In low fish densities, around 1 n/m^2 , aggregations were close to zero when structure was present, but occurred at low levels when structure was absent. At high fish densities, around 3 n/m^2 , aggregations occurred regardless of the presence of structure, indicating there is a threshold in

which it is preferred to aggregate than associate with structure. This could be because other individuals were already using structure at high densities leaving their conspecifics vulnerable and forcing them to aggregate. The fish densities in my pens were low enough to give individuals the opportunity to avoid aggregating, always offering the choice of structure or aggregating with conspecifics. Brandes and McLain (2001) demonstrated Chinook density varies with the RCC on the San Joaquin River, with higher densities upstream where fry emerge from gravel and densities declining downstream as predation and mortality occur. Because I used a net pen experiment with weekly fish removals, fish densities declined relatively constantly among my pens, preventing me from explicitly comparing against Brandes and McLain (2001). However, it is likely that fish density, turbidity, and other reasons to aggregate (e.g., hormonal changes, development) interplayed to influence the number of observations of aggregations along the RCC. In particular, I had larger fish in my most downstream site; the high turbidities experienced there were predicted to decrease aggregations, although I found increased aggregating due to FL. This is because the environmental gradient and ontogenetic change affected aggregating behavior in opposite directions, and in this case developmental desires to aggregate predominated (Hoar 1976).

My model targeted specific a priori hypotheses, but other environmental parameters likely have an effect on affinity for structure and propensity to aggregate. I left these environmental parameters out of my model to test my specific hypotheses and avoid over-parameterization. Temperature and dissolved oxygen likely interact to

influence both of these behaviors because they directly affect the stress levels of fish (Cech and Myrick 1999). High temperature and low dissolved oxygen may push juveniles to exhibit bold behavior to find food to satisfy their increased metabolisms (Vogel and Beauchamp 1999). Increased substrate size could reduce the likelihood of aggregating, as smaller fish will alternatively dive into or hide behind large gravel as a form of cover (Liao 2007). Aggressive behaviors and competition with conspecifics could increase the use of structure and decrease the propensity to aggregate. Structure visually isolates individuals and causes a reduction in further aggressive behavior that aggregating does not provide (Allouche 2002). These relationships should be addressed and tested to increase the understanding of the ecology surrounding cover use.

My original question included the effect of velocity on the number of aggregating observations. I dropped velocity from my model because my measurements were greatly reduced in comparison to the velocities outside the pen, as stated above. Although I could not test velocity with my net pen experimental design, I predict it has significant effects on both the propensity to aggregate and affinity to structure. As velocity increases so do the energetic costs of remaining in that area, pushing individual fish to aggregate or associate with structure to conserve energy (Werner et al. 1983, McMahon and Hartman 1989, Vehanen and Bjerke 2000). I also expect velocity to interact with FL as larger fish have greater swimming abilities (Liao 2007). The relationships between velocity, structure, aggregations, and

fish size should be explored to better understand the decision to aggregate or associate with structure.

The nature of my net pen experimental design excluded predators and non-salmon competitors from interacting with juvenile Chinook. In the presence of interspecies competition for food and other resources, Chinook could have demonstrated stronger use of structure (by defending habitat and setting up a territory) or an increased propensity to aggregate (to improve prey finding abilities) (Keeley 2000, 2001). Similarly, Chinook may have behaved differently if the actual threat of predation was increased (Hugie and Dill 1994). The net pens did not allow the actual threat of predation, so both behaviors could increase markedly in any conditions if predators were introduced into the net pens.

Through my net pen study I found number of aggregating observations changed along the RCC and with ontogeny. The limitations of my experimental design prevented me from testing the effects of velocity and inter and intra-species interactions because the net pens excluded high flows and non-study organisms. Rivers and streams are complicated systems to study due to their length and diversity of habitats, making it difficult to capture multiple areas at once (Fausch et al. 2002). I recommend snorkel surveys and habitat characterizations as potential avenues to pursue to allow a range of velocities and interactions with other species.

The results from this study are highly applicable to terrestrial and aquatic animals that exhibit aggregating behavior and experience ontogenetic changes throughout their lifetime. My study suggests changing environmental gradients and

ontogeny interact with density to influence the type of cover organisms use, structural or behavioral. In the case of juvenile salmon, environmental parameters and ontogenetic change acted in concert to create a gradient in aggregating behavior as the fish moved downstream in the river continuum. This pattern could be similar in other species or environmental gradient and ontogenetic change could interact with other pressures, predation and competition, to influence cover use.

Due to numerous anthropogenic disturbances, California Chinook salmon populations have become stressed, altered, and depleted, resulting in a listing under the Endangered Species Act for spring and winter runs in California (Yoshiyama et al. 2001, Kondolf et al. 2007, Zeug et al. 2010, Moyle et al. 2011). Salmon are an integral part of California's culture and economy, providing recreational and commercial fishing, and nutrient subsidies in the form of marine-derived nitrogen to the terrestrial environment (Merz and Moyle 2006, Wipfli and Baxter 2010). Numerous restoration projects have been funded to help revive these populations and the habitats they rely upon, including placement of structure to benefit salmonid production. The results from my study increase the understanding surrounding the forms of cover use (structure or aggregating behavior) in different locations along the river continuum. Ultimately I found that aggregating behavior was affected by the RCC, ontogeny, and fish density. Managers could use this information to prioritize structure installation by reach based on river conditions, fish densities, and average size of juveniles. This study could help implement the most economically and ecologically beneficial restoration practices along the river continuum with its

increased understanding of the complex interactions that influence the ecology and behavior surrounding habitat use.

Figures

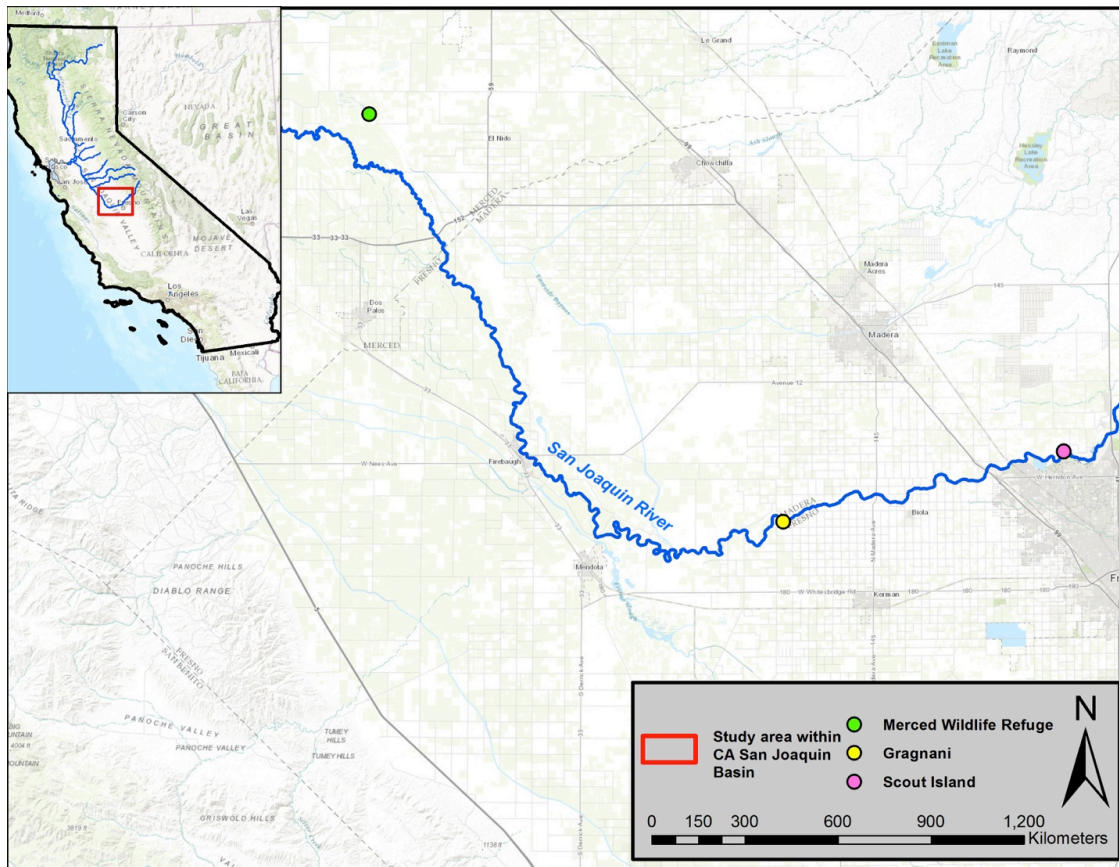


Figure 1: Map of my study locations along the San Joaquin River: Scout Island, Gragnani, and the Merced Wildlife Refuge.

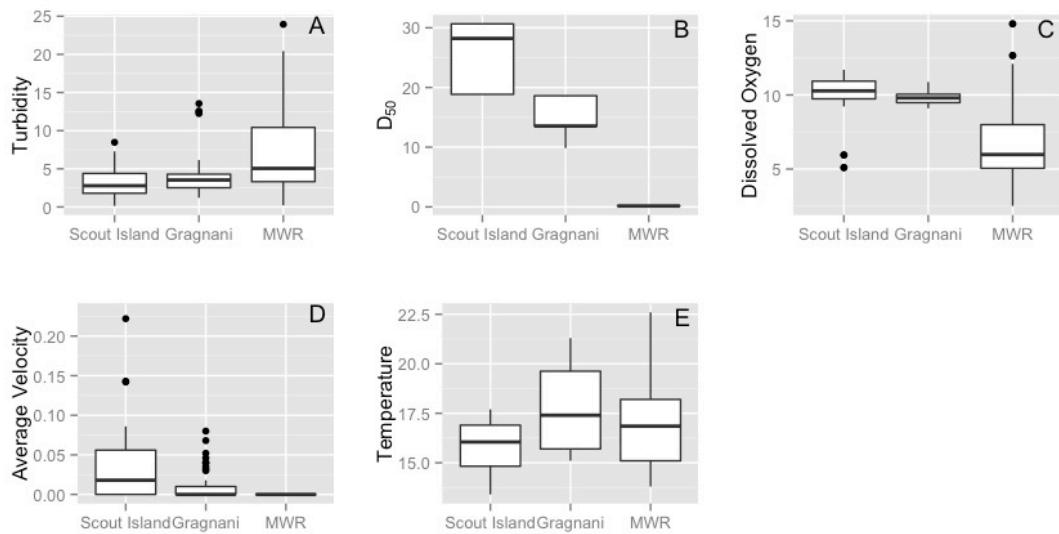


Figure 2: The distribution of environmental parameters by site: Scout Island, Gragnani, and Merced Wildlife Refuge (MWR). Boxplots display data from 1 March 2016 to 11 May 2016 and show the mean, 25th percentile, 75th percentile, and 95% confidence intervals of the data. (A) Turbidity (NTU) increased from my most upstream site, Scout Island, to my most downstream site, MWR. (B) D₅₀ (mm) decreased downstream. (C) Dissolved oxygen (mg/L) was similar at Scout Island and Gragnani, but significantly lower at MWR. (D) Average velocity (m/s) decreased downstream. (E) Temperatures (°C) were highest at Gragnani, but were not significantly different among sites.

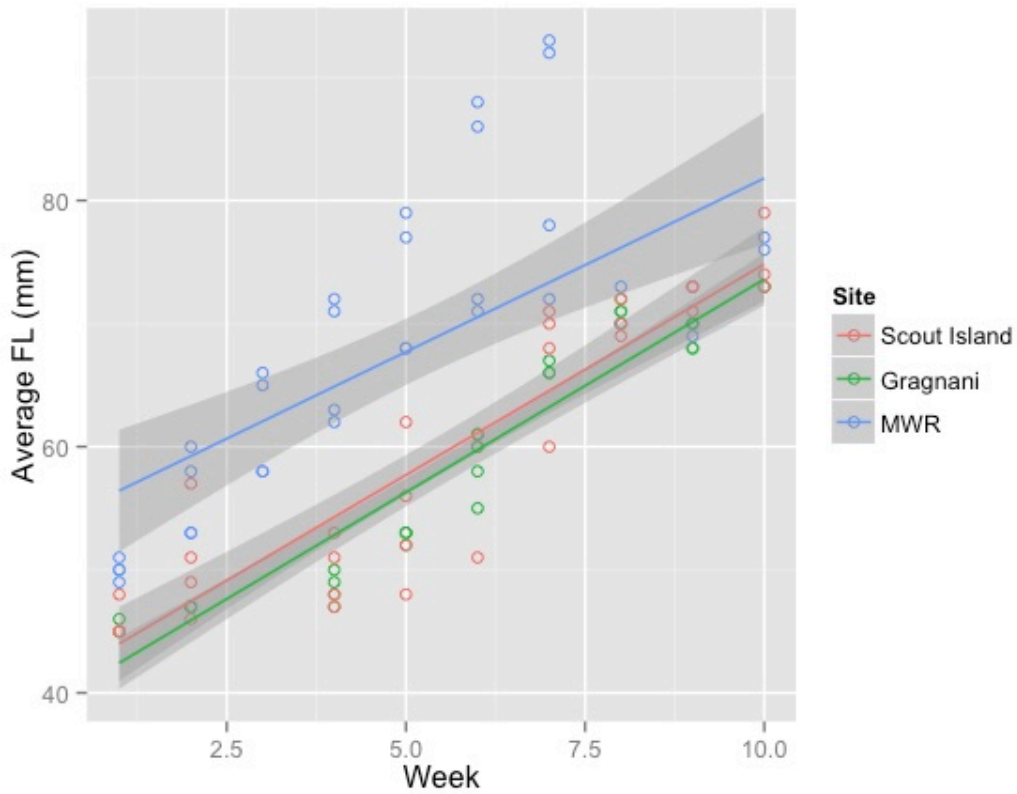


Figure 3: The linear regression of average FL (in mm) by week of the three sites. Each symbol represents an average estimated FL of a pen. Merced Wildlife Refuge (MWR) has significantly larger fish than Scout Island and Gragnani. Scout Island and Gragnani had similarly sized fish throughout the experiment.

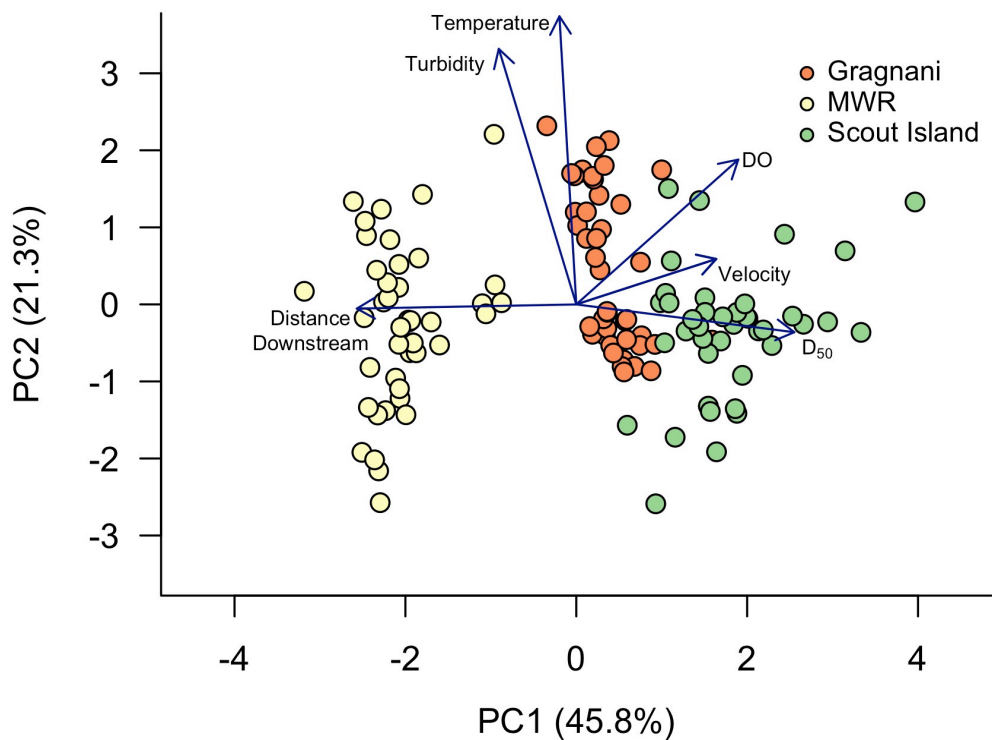


Figure 4: The principal components graph of environmental variables on the San Joaquin river: Turbidity (NTU), distance downstream from the dam (km), temperature (°C), DO (mg/L), velocity (m/s), and d50 (cm). Sites are color-coded: green as Scout Island, orange as Gragnani, and yellow as the Merced Wildlife Refuge (MWR). Each symbol represents an individual weekly sample of a pen.

Table 1: AIC_c candidate model set and corresponding AIC_c scores and AIC_c weights (W_i) for models testing the number of aggregating observations. A change of greater than 4 units in AIC_c indicates model superiority. W_i is a proportional measure representing the relative support of the model.

Model Rank	Parameters	AIC _c	Δ AIC _c	W_i
1	T+D+FL+S+S:T+S:D	1443.42	0	0.61
2	T+D+FL+S+S:T+S:D+S:FL	1445.31	1.89	0.24
3	T+D+FL+S+S:D	1447.24	3.82	0.09
4	T+D+FL+S+S:D+S:FL	1447.80	4.38	0.07
5	T+D+FL+S+S:T+S:FL	1481.94	38.52	0
6	T+D+FL+S	1482.11	38.69	0
7	T+D+FL+S+S:T	1482.46	39.04	0
8	T+D+FL+S+S:FL	1483.00	39.58	0
9	T+D+FL	1499.77	56.35	0
10	D+FL+S	1500.62	57.20	0
11	D+FL	1516.24	72.82	0
12	T+D+S	1561.51	118.09	0
13	D+S	1563.16	119.74	0
14	T+D	1581.92	138.50	0
15	D	1582.84	139.42	0
16	T+FL+S	1596.13	152.71	0
17	FL+S	1618.07	174.65	0
18	T+FL	1620.39	176.97	0
19	T+S	1620.80	177.38	0
20	S	1629.75	186.33	0
21	FL	1643.18	199.76	0
22	T	1644.88	201.46	0

T, turbidity; D, fish density; FL, fork length; S, structure level.

Table 2: The output of the top model. Significant values ($p < 0.05$) are in bold.

Parameter	Estimate	Standard Error	Z Value	$p > z $
Intercept	-3.48	0.47	-7.46	<0.001
Turbidity (NTU)	-0.02	0.04	-0.51	0.61
Fork Length (mm)	0.04	0.01	9.74	<0.001
Fish Density (n/m^2)	1.10	0.10	10.95	<0.001
Structure Level (No Structure)	2.75	0.34	6.95	<0.001
Turbidity: Structure Level	-0.13	0.05	-2.51	0.01
Fish Density: Structure Level	-0.08	0.12	-6.32	<0.001

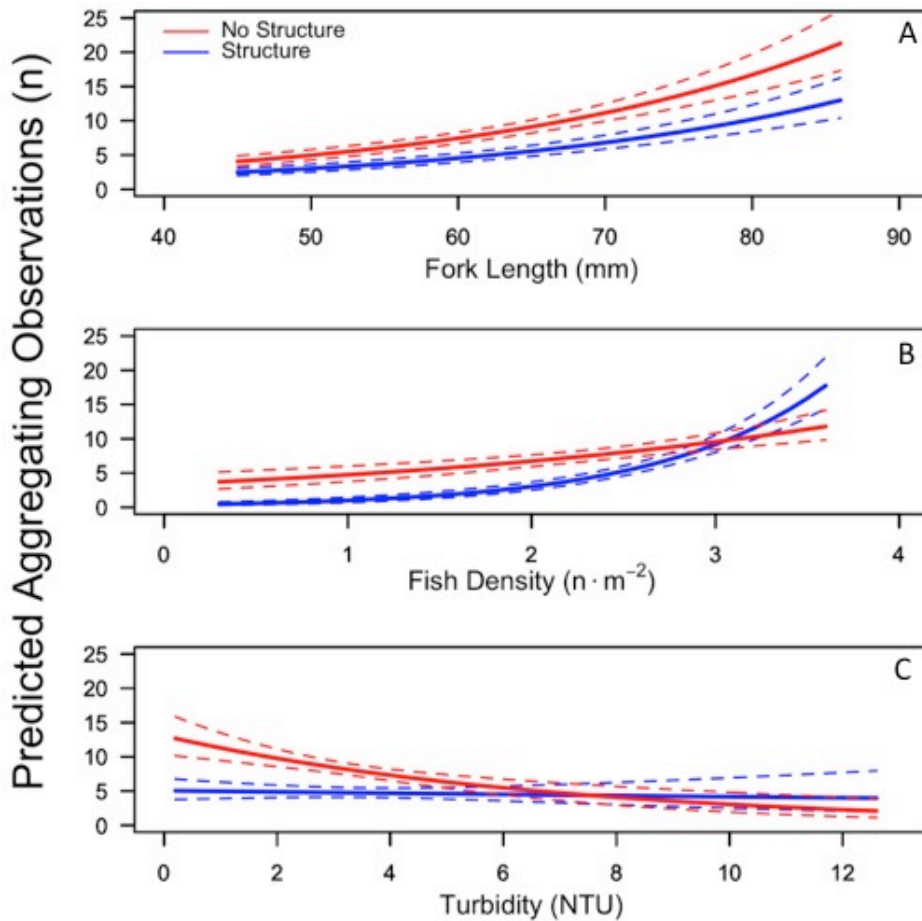


Figure 5: The top model predictions of how aggregating behavior varies with FL, fish density, turbidity, and structure level (blue=structure, red=no structure). Model predictions were generated for FL, fish density, and turbidity by holding all other parameters constant at their mean level while varying the targeted parameter for both “structure” and “no structure” levels. (A) Aggregating behavior increased with FL in both structure levels. (B) Aggregating behavior increased with fish density in both structure levels. (C) Aggregating behavior decreased with turbidity in the absence of structure, but was constant when structure was present.

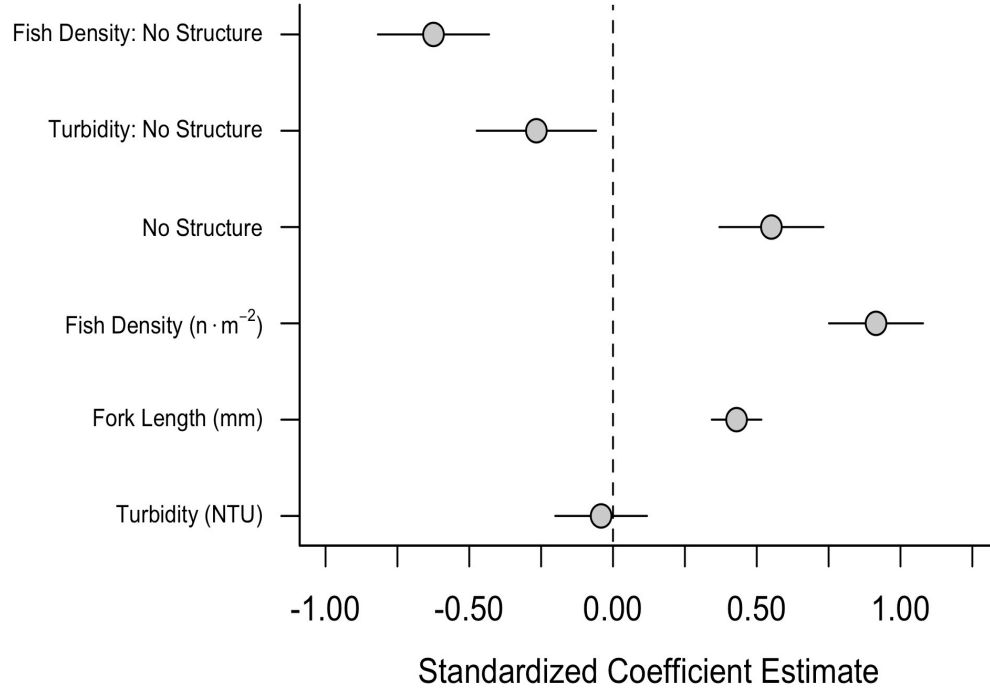
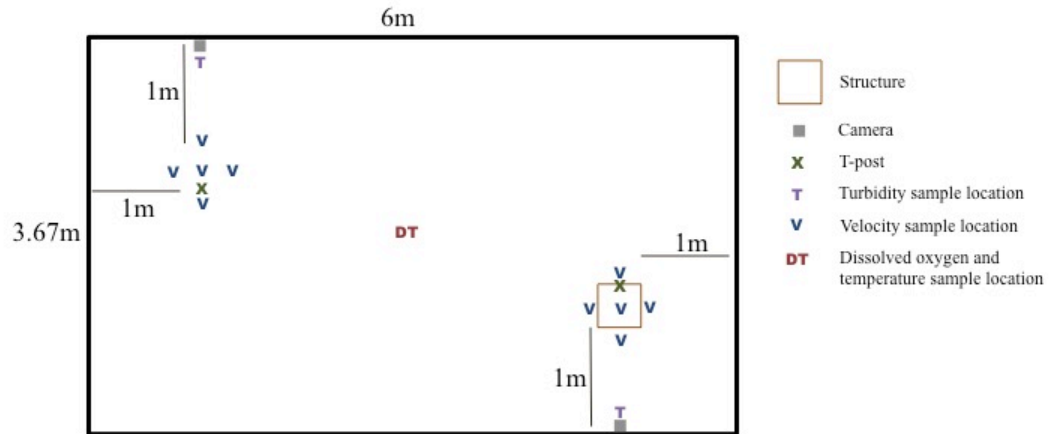


Figure 6: The standardized coefficient estimates for the parameters of the scaled top model predicting the number of aggregating observations. Colons represent interactions between two parameters. Turbidity is not a significant parameter. The interactions between fish density and structure absence, and turbidity and structure absence have significant negative effects on aggregating behavior, while the structure absence, fish density, and FL have significant positive effects.

Appendices

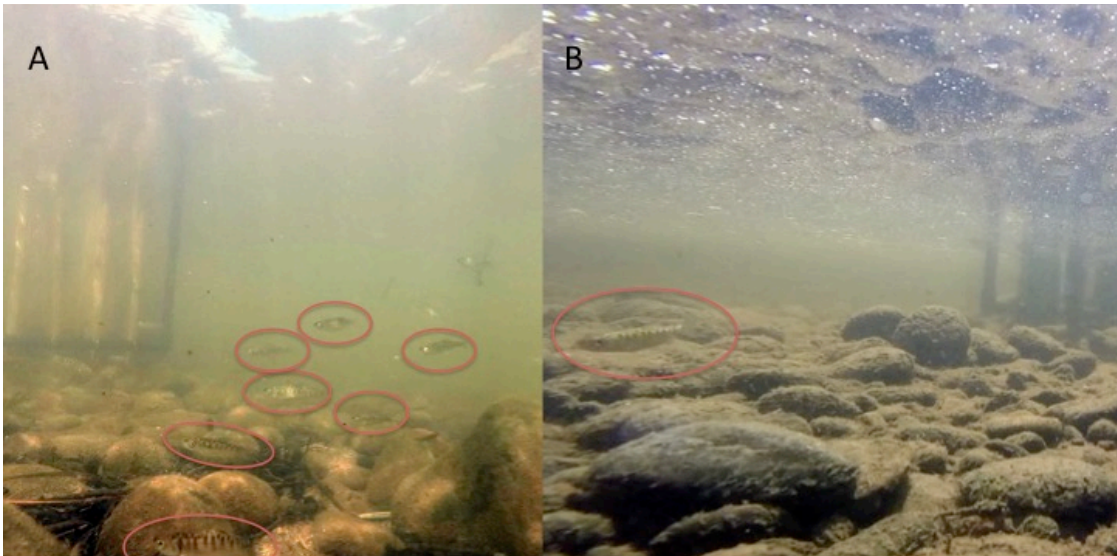


Appendix 1: A diagram of the layout of each pen and environmental sampling locations to scale. Flow entered the pen through the right side. The structure location switched weekly between the two t-posts.

Site	Pen	Structure Level	Week										
			1	2	3	4	5	6	7	8	9	10	
Scout Island	FP1	Structure	DP	DP	DP	DP	DP	DP	DP	DP	DP	DP	
		No Structure	DP	DP	DP	DP	DP	DP	DP	DP	DP	DP	
	FP2	Structure		NV	NV								
		No Structure		NV	NV								
	MC1	Structure		NV	NV								
		No Structure		NV	NV					DT			
MC2	Structure	DT	NV	NV									
	No Structure		NV	NV							DT		
Gragnani	FP1	Structure		NV	NV							NV	
		No Structure		NV	NV				DQ			NV	
	FP2	Structure		NV	NV			NV	NV			DT	
		No Structure	DT	NV	NV			NV	NV				
	MC1	Structure		NV	NV			DQ		DT			
		No Structure		NV	NV				DQ				
MC2	Structure		NV	NV				NV			NV		
	No Structure		NV	NV				NV			NV		
Merced Wildlife Refuge	CS1	Structure		DQ							DQ	NV	
		No Structure				DT			DQ	DQ		NV	
	CS2	Structure		DQ							DQ	NV	
		No Structure							DQ	DQ		NV	
	ESB1	Structure		DT	DQ					DQ	DQ	DQ	NV
		No Structure		DQ	DT					DQ	DQ	DQ	NV
ESB2	Structure			DQ	DT				DQ	DQ	DQ	NV	
	No Structure			DQ				DQ	DQ	DQ	DQ	NV	

DP=Discarded for predator; DQ=Discarded for poor quality; DT=Discarded for time; NV=No Video

Appendix 2: The distribution of discarded videos throughout the 10-week experiment by site and pen. Scout Island FP1 was discarded due to a predator invasion in the first week (DP). Videos were discarded if the Go Pro did not record a full trial (DT), or the structure/no structure t-post was not visible after video editing (DQ). There were no videos (NV) recorded at Scout Island and Gragnani during Week 2 and 3 because a rain event blew out the pens. Other NV classifications occurred if fish experienced high mortalities (at MWR) or rain events compromised pen integrity (Gragnani).



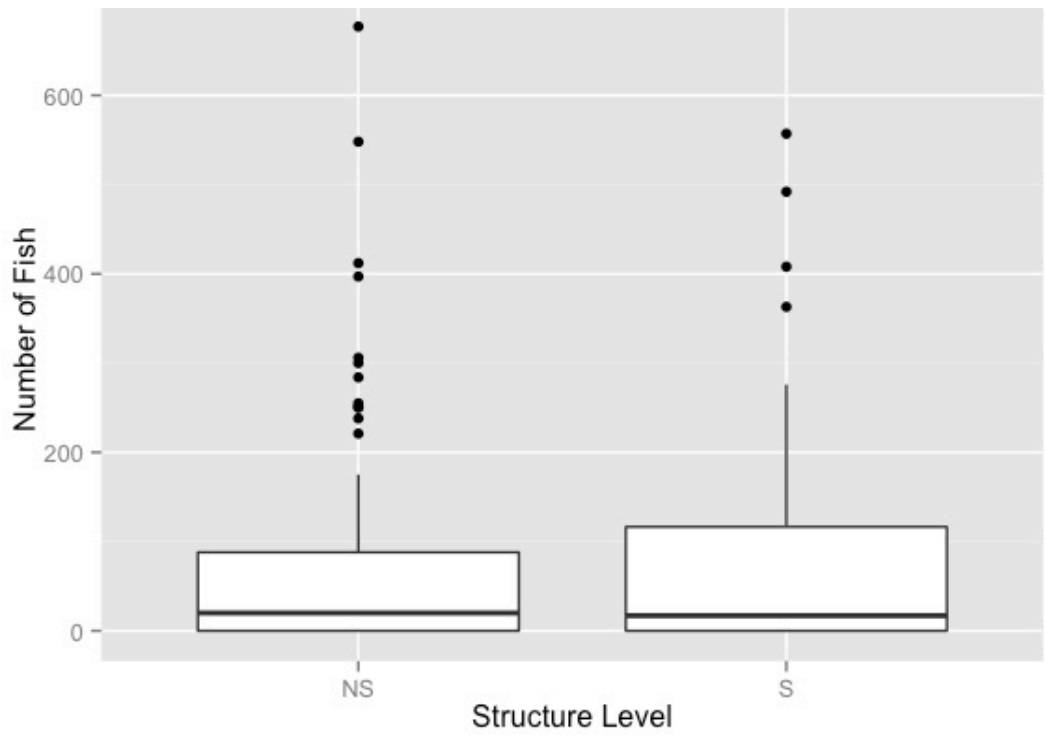
Appendix 3: Screen shots from the videos that show (A) aggregating behavior in the presence of structure and (B) an individual in the presence of structure. Photos were cropped to show target individuals and individuals were circle with red.

Site	Pen	Week									
		1	2	3	4	5	6	7	8	9	10
Scout Island	FP2	0			5	5	5	16	17	18	35
	MC1	0			4	4	4	18	8	8	16
	MC2	0			1	1	1	4	2	2	4
Gagnani	FP1	0			0	0	0	0	63	0	
	FP2	0			0	0	0	0	24	24	34
	MC1	0			0	0	0	1	13	13	44
	MC2	0			8	8	8	22	59	0	
Merced Wildlife Refuge	CS1	1	1	1	1	1	1	4	0	0	
	CS2	1	1	1	1	1	1	4	11	11	
	ESB1	2	2	2	2	2	2	11	8	35	
	ESB2	2	2	2	2	2	2	12	0	5	

Appendix 4: The distribution of mortalities/escapes over the 10-week experiment in each pen. These numbers were estimated by assuming constant mortality/escapement rates and applying an estimate of weekly mortalities/escapes based on the number of fish recovered at the end of the experiment. Blank cells indicate no fish were in the pen at that time. The second round of fish was added at Week 8.

Site	Pen	Mean	Standard Deviation	Coefficient of variation
Scout Island (SI)	FP2	18.50	25.52	1.38
	MC1	5.30	9.94	1.88
	MC2	6.92	14.58	2.11
SI Average		10.97	19.28	1.76
Gragnani	FP1	2.58	2.61	1.01
	FP2	4.60	9.94	2.16
	MC1	3.58	5.66	1.58
	MC2	2.56	4.75	1.86
Gragnani Average		3.33	6.03	1.81
Merced Wildlife Refuge (MWR)	CS1	2.00	2.00	1.00
	CS2	0	NA	NA
	ESB1	0	NA	NA
	ESB2	16.20	11.21	0.69
MWR Average		7.91	10.71	1.35

Appendix 5: The mean, standard deviation, and coefficient of variation of the number of aggregating observations for each pen.



Appendix 6: The distribution of the total number of fish observed at each structure level (NS=No structure, S=Structure).

Bibliography

- Abrahams, M. V., and Kattenfeld, M.G. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behav. Ecol. Sociobiol.* **40**(3): 169–174. doi:10.1007/s002650050330.
- Akaike, H. 1974. A new look at the statistical model identification. *Autom. Control. IEEE Trans.* **19**(6): 716–723. doi:10.1109/TAC.1974.1100705.
- Allouche, S. 2002. Nature and functions of cover for riverine fish. *Bull. Fr. La Pech. La Piscic.* **365**: 297–324. doi:10.1051/kmae:2002037.
- Anderson, D.R. 2008. *Model based inference in the life sciences: a primer on evidence.* Springer Science, New York.
- Barrett, J. 1992. Turbidity-induced changes in reactive distance of rainbow trout. *Trans. Am. Fish. Soc.* **121**(4): 437–443. doi:10.1577/1548-8659(1992)121<0437:TICIRD>2.3.CO;2.
- Beakes, M., Moore, J., Retford, N., Brown, R., Merz, J.E., and Sogard, S.M. 2014. Evaluating statistical approaches to quantifying juvenile Chinook salmon habitat in a regulated California river. *River Res. Appl.* **30**: 180–191. doi:10.1002/rra.
- Bjornn, T. 1998. Upstream: Salmon and society in the Pacific Northwest. *Ecology* **79**(4): 1471–1473. doi:10.2307/176763.
- Bjornn, T., and Reiser, D. 1991. Habitat requirements of salmonids in streams. *In* Influences of forest and rangeland management on salmonid fishes and their habitat. *Edited by* W.R. Meehan. American Fisheries Society Special Publication. pp. 83–138.
- Brandes, P.L., and McLain, J.S. 2001. Juvenile Chinook salmon abundance, distribution, and survival in the Sacramento-San Joaquin estuary. *In* Contributions to the Biology of Central Valley Salmonids. *Edited by* L.R. Brown. California Department of Fish and Game, Sacramento, CA. pp. 39–138.
- Brown, L.R. 1996. Aquatic biology of the San Joaquin-Tulare basins: analysis of available data through 1992. No. 2471. U.S. Geological Survey, Water-supply Paper 2471, Denver, CO.
- Brown, L.R. 2000. Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. *Environ. Biol. Fishes*

- 57: 251–269. doi:10.1023/A:1007660914155.
- Brown, L.R., and Moyle, P.B. 1993. Distribution, ecology, and status of the fishes of the San Joaquin River drainage, California. *Calif. Fish Game* **79**: 96–114.
- Burnham, K., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. *In* 2nd edition. Springer Science, New York.
- Cech, J.J., and Myrick, C.A. 1999. Steelhead and Chinook salmon bioenergetics: temperature, ration, and genetic effects. University of California Water Resources Center, Technical Completion Report 885, Davis, CA.
- Dasmann, W. 1971. If deer are to survive. Wildlife Management Institute, Stackpole, Harrisburg, Pennsylvania.
- Davis, J.G. 1970. Seasonal changes in flocking behavior of starlings as correlated with gonadal development. *Wilson Bull.* **82**(4): 391–399.
- Emlen, J.T.J. 1952. Flocking behavior in birds. *Auk* **69**(2): 160–170.
- Fausch, K.D. 1984. Profitable stream positions for salmonids: Relating specific growth rates to net energy gain. *Can. J. Zool.* **62**: 441–451. doi:10.1139/z84-067.
- Fausch, K.D., Torgersen, C.E., Baxter, C. V., and Li, H.W. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *Bioscience* **52**(6): 483–498. doi:10.1641/0006-3568(2002)052[0483:LTRBTG]2.0.CO;2.
- Filipe, A.F., Cowx, I.G., and Collares-Pereira, M.J. 2002. Spatial modelling of freshwater fish in semi-arid river systems: A tool for conservation. *River Res. Appl.* **18**(2): 123–136. doi:10.1002/rra.638.
- Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* **27**: 2865–2873. doi:10.1002/sim.
- Grand, T.C., and Dill, L.M. 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): Ideal free distribution theory applied. *Behav. Ecol.* **8**(4): 437–447. doi:0.1093/beheco/8.4.437.
- Grant, J., Hopcraft, C., Sinclair, A.R.E., and Packer, C. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *J. Anim. Ecol.* **74**(3): 559–566. doi:10.1111/j.1365-2656.2005.00955.x.

- Grant, J.W.A., Steingrímsson, S.Ó., Keeley, E.R., and Cunjak, R.A. 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. *Can. J. Fish. Aquat. Sci.* **55**: 181–190. doi:10.1139/d98-018.
- Gregory, R.S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* **50**: 241–246. doi:10.1139/f93-027.
- Gurnell, A.M., Gregory, K.J., and Petts, G.E. 1995. The role of coarse woody debris in forest aquatic habitats: implications for management. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **5**(2): 143–166. doi:10.1002/aqc.3270050206.
- Hardin, T.S., Grost, R.T., Ward, M.B., and Smith, G.E. 2005. Habitat suitability criteria for anadromous salmonids in the Klamath River, Iron Gate Dam to Scott River, California. Stream Evaluation Report.
- Harding, J.N., and Reynolds, J.D. 2014. Opposing forces: Evaluating multiple ecological roles of Pacific salmon in coastal stream ecosystems. *Ecosphere* **5**(12): 157. doi:10.1890/es14-00207.1.
- Hoar, W.S. 1976. Smolt transformation: Evolution, behavior, and physiology. *J. Fish. Res. Board Canada* **33**: 1233–1252. doi:10.1139/f76-158.
- Hosn, W.A., and Downing, J.A. 1994. Influence of cover on the spatial distribution of littoral-zone fishes. *Can. J. Fish. Aquat. Sci.* **51**: 1832–1838. doi:10.1139/f94-185.
- Hugie, D., and Dill, L. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. *J. Fish Biol.* **45**: 151–169. doi:10.1111/j.1095-8649.1994.tb01090.x.
- Imre, I., Grant, J., and Keeley, E. 2002. The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* **59**(2): 303–309. doi:10.1139/f02-010.
- Jeffres, C.A., Opperman, J.J., and Moyle, P.B. 2008. Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. *Environ. Biol. Fishes* **83**(4): 449–458. doi:10.1007/s10641-008-9367-1.
- Katz, Y., Tunstrom, K., Ioannou, C.C., Huepe, C., and Couzin, I.D. 2011. Inferring the structure and dynamics of interactions in schooling fish. *Proc. Natl. Acad.*

- Sci. **108**(46): 18720–18725. doi:10.1073/pnas.1107583108.
- Keeley, E. 2000. An experimental analysis of territory size in juvenile steelhead trout. *Anim. Behav.* **59**(3): 477–490. doi:10.1006/anbe.1999.1288.
- Keeley, E.R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. *Ecol. Soc. Am.* **82**(5): 1247–1259. doi:10.1890/0012-9658(2001)082[1247:DRTFAS]2.0.CO;2.
- King, J.R., and Jackson, D.A. 1999. Variable selection in large environmental data sets using principal components analysis. *Environmetrics* **10**(1): 67–77. doi:10.1002/(SICI)1099-095X(199901/02)10:1<67::AID-ENV336>3.0.CO;2-0.
- Kondolf, G.M., Anderson, S., Lave, R., Pagano, L., Merenlender, A., and Bernhardt, E.S. 2007. Two decades of river restoration in California: What can we learn? *Restor. Ecol.* **15**(3): 516–523. doi:10.1111/j.1526-100X.2007.00247.x.
- Krausman, P.P.R. 1999. Some basic principles of habitat use. *In* Idaho Forest, Wildlife & Range Exp. Sta. Bull. #70.
- Liao, J.C. 2007. A review of fish swimming mechanics and behaviour in altered flows. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **362**(1487): 1973–1993. doi:10.1098/rstb.2007.2082.
- Lima, S.L. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. *Anim. Behav.* **49**(1): 11–20. doi:10.1016/0003-3472(95)80149-9.
- Loveless, C.M. 1964. Some relationships between wintering mule deer and the physical environment. *Trans. North Am. Wildl. Nat. Resour. Conf.* **29**.
- Maule, A.G., Schreck, C.B., Bradford, C.S., and Barton, B. a. 1988. Physiological effects of collecting and transporting emigrating juvenile Chinook salmon past dams on the Columbia River. *Trans. Am. Fish. Soc.* **117**: 245–261. doi:10.1577/1548-8659(1988)117<0245:PEOCAT>2.3.CO;2.
- McDonald, J. 1960. The behaviour of Pacific salmon fry during their downstream migration to freshwater and saltwater nursery areas. *J. Fish. Board Canada* **17**(5): 655–676. doi:10.1139/f60-051.
- McMahon, T.E., and Hartman, G. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **46**: 1551–1557. doi:10.1139/f89-197.
- Merz, J.E., and Moyle, P.B. 2006. Salmon, wildlife, and wine: Marine-derived

- nutrients in human-dominated ecosystems of Central California. *Ecol. Appl.* **16**(3): 999–1009. doi:10.1890/1051-0761(2006)016[0999:SWAWMN]2.0.CO;2.
- Merz, J.E., Setka, J.D., Pasternack, G.B., and Wheaton, J.M. 2004. Predicting benefits of spawning-habitat rehabilitation to salmonid (*Oncorhynchus* spp.) fry production in a regulated California river. *Can. J. Fish. Aquat. Sci.* **61**(8): 1433–1446. doi:10.1139/f04-077.
- Merz, J.E., Workman, M., Threlhoff, D., and Cavallo, B. 2013. Salmon lifecycle considerations to guide stream management: Examples from California's Central Valley. *San Fr. Estuary Watershed Sci.* **11**(2).
- Miller, J.A., Gray, A., and Merz, J. 2010. Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon *Oncorhynchus tshawytscha*. *Mar. Ecol. Prog. Ser.* **408**: 227–240. doi:10.3354/meps08613.
- Moyle, P.B., Katz, J.V.E., and Quiñones, R.M. 2011. Rapid decline of California's native inland fishes: A status assessment. *Biol. Conserv.* **144**(10): 2414–2423. Elsevier Ltd. doi:10.1016/j.biocon.2011.06.002.
- Mysterud, A., and Ims, R. 1998. Functional responses in habitat use: Availability influences relative use in trade-off situations. *Ecology* **79**(4): 1435–1441. doi:10.2307/176754.
- Mysterud, A., and Østbye, E. 1999. Cover as a habitat element for temperate ungulates: Effects on habitat selection and demography. *Wildl. Soc. Bull.* **27**(2): 385–394. Available from <http://www.jstor.org/stable/3783905>.
- Naiman, R.J., Bechtold, J.S., Drake, D.C., Joshua J. Latterell, T.C.O., and Balian, E. V. 2005. Origins, patterns, and importance of heterogeneity in riparian systems. *In* *Ecosystem function in heterogenous landscapes*. Springer, New York. pp. 279–309.
- Oikari, A. 2006. Caging techniques for field exposures of fish to chemical contaminants. *Aquat. Toxicol.* **78**(4): 370–381. doi:10.1016/j.aquatox.2006.03.010.
- Partridge, B.L. 1982. The structure and function of fish schools. *Sci. Am.* **246**(6): 114–123. doi:10.1038/scientificamerican0682-114.
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B.D., Sparks, R.E., and Stromberg, J.C. 1997. A paradigm for river conservation and

- restoration. *Bioscience* **47**(11): 769–784. doi:10.2307/1313099.
- Prentice, C., Cramer, W., Harrison, S.P., Leemans, R., Robert, R.A., and Solomon, A.M. 1992. A Global Biome Model Based on Plant Physiology and Dominance, Soil Properties and Climate. *J. Biogeogr.* **19**: 117–134. doi:10.2307/2845499.
- Program, S.J.V.D. 1990. Fish and wildlife resources and agricultural drainage in the San Joaquin Valley. Sacramento.
- Quinn, T.P. 2011. The behavior and ecology of Pacific salmon and trout. UBC Press.
- Quiñones, R.M., and Mulligan, T.J. 2005. Habitat use by juvenile salmonids in the Smith River estuary, California. *Trans. Am. Fish. Soc.* **134**(5): 1147–1158. doi:10.1577/T04-092.1.
- R Core Team 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Savino, J.F., and Stein, R.A. 1989. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. *Environ. Biol. Fishes* **24**(4): 287–293. doi:10.1007/BF00001402.
- Schlosser, J. 1991. Stream fish ecology: A landscape perspective. *Bioscience* **41**(10): 704–712. doi:10.2307/1311765.
- Sellheim, K.L., Watry, C.B., Rook, B., Zeug, S.C., Hannon, J., Zimmerman, J., Dove, K., and Merz, J.E. 2015. Juvenile salmon utilization of floodplain habitat after gravel augmentation in a regulated river. *River Res. Appl.*: 1085–1095. doi:10.1002/rra.
- Springer, S.D., Gregory, P.A., and Barret, G.W. 1981. Importance of social grouping on bioenergetics of the golden mouse, *Ochrotomys nuttalli*. *J. Mammal.* **62**(3): 628–630.
- Stamps, J.A. 1983. The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). *Behav. Ecol. Sociobiol.* **12**(1): 19–33. doi:10.1007/BF00296929.
- Swain, N.R., Hocking, M.D., Harding, J.N., and Reynold, J.D. 2014. Effects of salmon on the diet and condition of stream-resident sculpins. *Can. J. Fish. Aquat. Sci.* **71**(4): 521–532. doi:10.1139/cjfas-2013-0159.
- Turner, D.C. 1979. An analysis of time-budgeting by roe deer (*Capreolus capreolus*) in an agricultural area. *Behaviour* **71**(3): 246–290.

doi:10.1163/156853979X00188.

- Urabe, H., and Nakajima, M. 2010. Evaluation of habitat quality for stream salmonids based on a bioenergetics model. *Trans. Am. Fish. Soc.* **139**(6): 1665–1676. doi:10.1577/T09-210.1.
- Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., and Macdonald, D.W. 2009. Behavioural adjustments of African herbivores to predation risks by lions: spatiotemporal variations influence habitat use. *Ecology* **90**(1): 23–30. doi:10.1890/08-0606.1.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* **37**: 130–137. doi:10.1139/f80-017.
- Vehanen, T., and Bjerke, P. 2000. Effect of fluctuating flow and temperature on cover type selection and behaviour by juvenile brown trout in artificial flumes. *J. Fish Biol.* **56**(4): 923–937. doi:10.1006/jfbi.1999.1215.
- Vehanen, T., and Hamari, S. 2004. Predation Threat Affects Behaviour and Habitat Use by Hatchery Brown Trout (*Salmo Trutta* L.) Juveniles. *Hydrobiologia* **525**(1–3): 229–237. doi:10.1023/B:HYDR.0000038869.60894.20.
- Villafuerte, R., and Moreno, S. 1997. Predation risk, cover type, and group size in European rabbits in Donana (SW Spain). *Acta Theriol. (Warsz.)* **42**(2): 225–230. doi:10.4098/AT.arch.97-23.
- Vogel, J., and Beauchamp, D. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. *Can. J. Fish. Aquat. Sci.* **56**(7): 1293–1297. doi:10.1139/f99-071.
- Werner, E.E., Gilliam, J.F., Hall, D.J., and Mittelbach, G.G. 1983. Experimental tests of optimal habitat use in fish: The role of relative habitat profitability. *Ecology* **64**: 1540–1548. doi:10.2307/1937507.
- Wipfli, M.S., and Baxter, C. V. 2010. Linking ecosystems, food webs, and fish production: Subsidies in salmonid watersheds. *Fisheries* **35**(8): 373–387. doi:10.1577/1548-8446-35.8.373.
- Wold, S. 1987. Principal Component Analysis. *Chemom. Intell. Lab. Systms* **2**: 37–52. doi:10.1007/b98835.
- Yoshiyama, R.M., Gerstung, E.R., Fisher, F.W., and Moyle, P.B. 2001. Historical and

present distribution of Chinook salmon in the Central Valley drainage of California. *Contrib. to Biol. Cent. Val. Salmonids Fish Bull.* 179 **1**: 71–176. Available from <http://escholarship.org/uc/item/58g617zq.pdf>.

- Zeug, S.C., Albertson, L.K., Lenihan, H., Hardy, J., and Cardinale, B. 2010. Predictors of Chinook salmon extirpation in California's Central Valley. *Fish. Manag. Ecol.*: 61–71. doi:10.1111/j.1365-2400.2010.00769.x.
- Zeug, S.C., Sellheim, K., Watry, C., Wikert, J.D., and Merz, J. 2014. Response of juvenile Chinook salmon to managed flow: lessons learned from a population at the southern extent of their range in North America. *Fish. Manag. Ecol.* **21**(2): 155–168. doi:10.1111/fme.12063.
- Zheng, M., Kashimori, Y., Hoshino, O., Fujita, K., and Kambara, T. 2005. Behavior pattern (innate action) of individuals in fish schools generating efficient collective evasion from predation. *J. Theor. Biol.* **235**(2): 153–167. doi:10.1016/j.jtbi.2004.12.025.