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Investigating Environmental Drivers of Migratory Habitat Selection in Adult Chinook Salmon with Implications for Homing and Straying Dynamics

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Investigating Environmental Drivers of Migratory Habitat Selection in Adult Chinook Salmon
with Implications for Homing and Straying Dynamics

By

SEAN MICHAEL LUIS
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

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2022

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This dissertation is dedicated to my incredible wife Jillian, and beautiful daughters Juniper and Penelope. They supported and inspired me every step of the way.

1 *Overall Abstract*

Anadromous salmonids utilize a combination of physical, chemical, and biological cues when migrating from ocean foraging grounds as mature adults to freshwater spawning grounds to complete their lifecycle. The biological processes behind homing behavior (migrating to their stream of natal origin to spawn) and straying behavior (migrating to non-natal habitats) have been well studied since the 1950's. However, the abiotic environmental factors that partially drive these behaviors have received comparatively less attention. One aspect that is particularly understudied is the influence of localized channel hydraulics on habitat selection in migrating adults. The first chapter of this dissertation includes an investigation into migratory microhabitat selection at a major river confluence by California Central Valley fall-run Chinook salmon in response to localized hydraulic conditions, as well as temperature and turbidity. Conveyance (depth*velocity magnitude) was found to be the strongest hydraulic predictor of micro-scale habitat selection, and acts in conjunction with temperature to facilitate rheotactic swimming behavior. Chapter 2 includes modeled simulations of migratory movement under varying drought conditions, utilizing the same confluence used in Chapter 1 as a study system. These simulations indicate that both discharge magnitude in each river, as well as the ratio of discharge magnitudes between them, are significant drivers of the availability and distribution of preferred hydraulic microhabitats at the confluence, potentially influencing migratory routing. These findings support observed patterns in Chinook salmon escapement data in response to historical flows at this confluence. Chapter 3 includes a literature review and meta-analysis assessing the extent to which abiotic factors have been investigated in the existing literature on homing and straying behavior in anadromous salmonids. Only 70 out of 169 articles included at least one abiotic study component. This phenomenon was surprisingly consistent across study method types, study locations, and study species, with none of these attributes having statistically significant differences in frequency of abiotic components among attribute classes. The research presented in this dissertation provides valuable advancements in the field of fisheries ecology, particularly with respect to the topic of homing and straying in anadromous salmonids. Novel approaches to both field data collection and riverine habitat modeling

were developed, and key results link open channel hydraulic processes to adult migratory behavior, filling an existing knowledge gap in the basic life history of salmonids.

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2.1 Abstract

Migratory habitat selection in adult anadromous salmonids occurs in response to a combination of physical, chemical, and biological cues. Migratory behavioral responses to localized hydraulics are not well understood and hydraulic flow features can be particularly complex at confluence junctions. In some cases, hydraulics may play a partial role in migratory routing, with implications for population structure where wild- and hatchery-origin fish hybridize. This study investigated two questions about such confluences: (1) Can patterns in migratory microhabitat selection or migratory swimming behavior in adult Chinook salmon be attributed to micro-scale hydraulic conditions driven by discharge magnitude and ratio at a confluence? (2) What is the relative influence of selectivity for hydraulic conditions compared to temperature and/or turbidity in micro-scale habitat selection or migratory swimming behavior at a confluence? The 2019 migration of California Central Valley fall-run Chinook salmon (*Oncorhynchus tshawytscha*) at the confluence of the Feather and Yuba Rivers in northeastern California served as a study system. Using two dual-frequency identification sonars, 12 monitoring sites representing distinct physical microhabitats upstream of, within, and downstream of the confluence were repeatedly sampled during two four-day flow periods (mean flow ratios between the Feather and Yuba Rivers were 8.66 and 4.02, respectively). Temperature magnitudes and ratios flipped between sampling periods. We used a multiple regression analysis using the F test for significance and a corrected Akaike information criteria (AICc) analysis to identify predictors of both detection rate (# individuals/m^3/min) and percent occurrence of directing, milling, and backtracking swimming behaviors. A combination of conveyance (depth*velocity magnitude), temperature, and turbidity was found to perform best in predicting detection rate ($p < 0.001$). No suitable model was found to predict directed behavior. Milling was best predicted by a combination of all hydraulic variables ($p < 0.001$) and although temperature alone was found to best predict backtracking ($p < 0.01$), we identified a candidate model including conveyance and temperature as predictors (ΔAICc = 3.66, $p = 0.02$)

which aided in the interpretation of our results. This study provides evidence that channel hydraulics play an active role in the sum of navigation cues that are utilized by migrating adult salmon en route to spawning grounds and should be considered in future investigations of homing and straying patterns in anadromous salmonids.

2.2 Introduction

Salmon have long been a focal point in aquatic resource management at all scales where such anadromous fish occur. Conservation goals for maintaining healthy populations include sustainable harvest, ecosystem benefits, and cultural significance (Larkin, 1979; Bottom et al. 2009; Cote et al. 2021). The nature of salmon migrations has been studied extensively, as it is a critical facet of their life history strategy (Dittman and Quinn, 1996; Keefer and Caudill, 2014; Putman et al., 2013). In many cases, anadromous fish habitat in regulated rivers experiences altered flow regimes to accommodate agricultural, municipal, and industrial water use throughout the year (Brown and Ford, 2002; Buddendorf et al., 2017; Marchetti and Moyle, 2001; Tsuboi et al., 2010) as well as riverscape narrowing and simplification to accommodate adjacent land use (Jacobson and Galat, 2006).

River confluences can be hydraulically and geomorphologically complex features of regulated fluvial channel networks and represent critical points for successful homing. Understanding of their dynamics (including hydraulic flow features, sediment flux, and channel geometries) has become increasingly more sophisticated since the mid-20th century (Best 1986, Gualtieri et al. 2017, Miller, 1958, Richards 1980). For salmon migrating upstream, each confluence that is encountered represents a critical navigational step in a sequence of decisions that must be made between entering the estuary and reaching spawning grounds. In many rivers, the physical, chemical, and biological attributes of migratory habitat at a confluence are dictated by environmental drivers that occur in a spatial hierarchy, from landscape-scale processes down to micro-scale processes.

2.2.1   Study purpose and scientific questions

This study investigated microhabitat-scale drivers of migratory habitat selection at a regulated river confluence by addressing the following questions: (1) Can patterns in migratory microhabitat selection or migratory swimming behavior in adult Chinook salmon be attributed to micro-scale hydraulic conditions driven by discharge magnitude and ratio at a confluence? (2) What is the relative influence of selectivity for hydraulic conditions compared to temperature and/or turbidity in micro-scale habitat selection or migratory swimming behavior at a confluence? Our study design does not explicitly account for microhabitat selection based on homing fidelity to natal water. It is impossible to disentangle micro-scale preference for temperature and/or turbidity purely based on those physical characteristics from selectivity of natal source water having some thermal/optical characteristics at the time of our observation. In our study, we consider the degree to which temperature and turbidity play a role in micro-scale habitat preference as a potential sign of homing fidelity and our results are discussed in that context. The experimental design concept and tested hypotheses are included below in Section 2.2 and summarized in Table 1.1.

Table 1.1. Hypotheses and test methods used in this study. Predictor variables a-g are each tested as a separate hypothesis in the analysis. Directed, milling, and backtracking behaviors are defined in section 2.3.3.

Hypothesis

	a	Velocity magnitude
	b	Depth
	c	Conveyance
H_1: Detection rate* correlates with…	d	Froude number
	e	Temperature
	f	Turbidity
	g	Multiple Predictors
Percent of _____ swimming behavior correlates with…	a	Velocity magnitude
	b	Depth
H_2: Directed**	c	Conveyance
	d	Froude number
H_3: Milling**	e	Temperature
	f	Turbidity
H_4: Backtracking**	g	Multiple Predictors

*Nonlinear (exponential) regression **Linear regression. Hypothesis testing utilizes the F test for multiple regression coefficients being non-zero (95% confidence).

2.2.2   Conceptual model background

Figure 1.1 presents a conceptual model of migratory habitat attributes for adult Pacific salmon that occur within a spatial hierarchy of physical, chemical, and biological processes which directly or indirectly drive habitat selection at river confluences. An expanded literature review and synthesis supporting the conceptual model is included in Section 5.1 of Appendix A. It is important to consider the potential roles of landscape-, reach-, and micro-scale phenomena that affect fish migratory decision-making and/or behavior instincts when a fish arrives at a confluence.
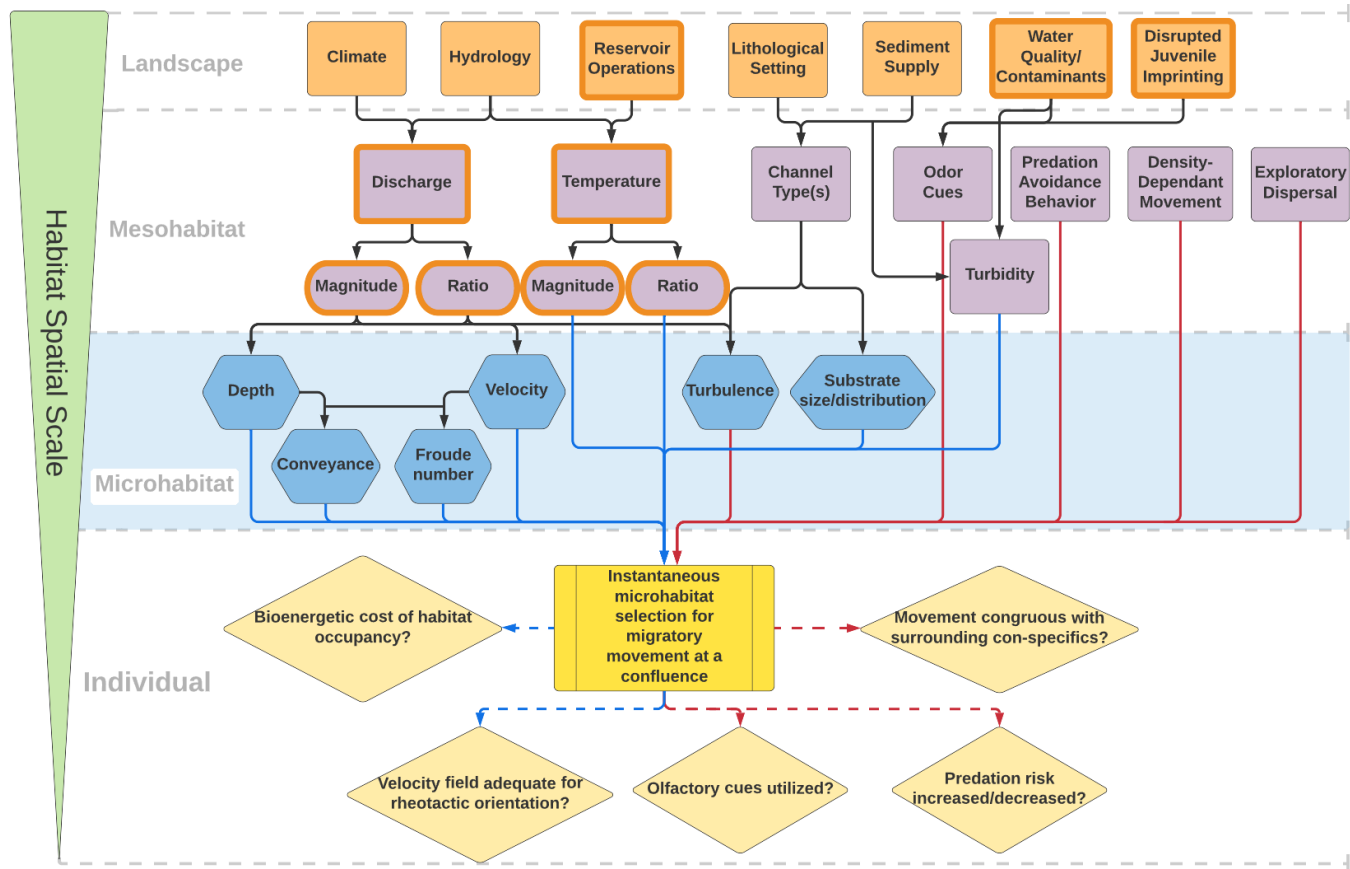
Figure 1.1. Conceptual model diagram summarizing physical and biological drivers involved in multi-scale habitat selection by anadromous migrating adult salmonids at river confluences. Black lines indicate indirect drivers of habitat selection. The area shaded in blue includes microhabitat attributes that are investigated in this study (with the exception of turbulence). Blue lines indicate direct drivers that are quantified and analyzed in this study, while red lines indicate direct drivers that are not measured. Items outlined in orange indicate physical and biological drivers that are actively managed, either partially or fully. Yellow diamonds describe the physiological and behavioral implications for a given movement by an individual. Dotted blue arrows are ecological implications that could be accounted for using the results of this study, and red dotted lines cannot.

2.2.2.1 Landscape-scale habitat attributes

Landscape-scale hydrologic and sediment supply regimes act as top-down controls on local flow magnitude, frequency, duration, timing, and rate of change, including interannual variation of these attributes (Edwards et al., 2015). River discharge at a catchment or reach scale has been used to partially explain the timing of population-level adult salmon migratory movements with implications for flow management in the context of accommodating or facilitating migration (Anderson and Beer, 2009; Dahl et al., 2004; Peterson et al., 2017). In catchments with regulated rivers, many dam operation schedules are partially planned to control downstream discharges (Acreman et al., 2009; Bradford et al., 2011; Gendaszek et al., 2018; Saltveit et al., 2019), as well as temperatures (Ahmad and Hossain, 2020; Nichols et al., 2014; Rheinheimer et al., 2015) to accommodate specific salmonid life-cycle stages and their habitat requirements. Along with climate and precipitation patterns, regional orogeny, epeirogeny, and lithology act as major drivers of sediment transport dynamics, drainage pattern, and spatial distribution of channel types (Dietrich et al., 2003; Howard et al., 1994; Massong and Montgomery, 2000; Sklar and Dietrich, 2001). These landscape-scale processes ultimately determine amount and type of habitat available to a salmon population by dictating spatial extent and distribution of alluvial channel forms (Church, 2006).

Hatchery production facilities can induce population-level effects when juveniles are reared to the parr/smolt stage and released off site to avoid mortality associated with downstream migration (Huber et al., 2015; Murdoch et al., 2009). This dynamic is thought to result in increased rates of straying in returning adults due to interruption of olfactory imprinting at early life stages (Jonsson et al., 2003; Keefer and Caudill, 2014; Sturrock et al., 2019). In addition to hatchery release practices, some pollutants are known to disrupt olfaction via toxicity to olfactory physiology by multiple biochemical pathways (Tierney et al., 2010). Many salmon populations occur in regions that experience extensive agricultural land use and large-scale application of pesticide compounds that enter waterways via agricultural runoff.

2.2.2.2   Reach-scale habitat attributes

With the exception of some Alaskan chum salmon (*O. keta*) runs (known to occasionally spawn in intertidal areas of river mouths, see Johnson et al. 1997), most adult Pacific salmon undergo some degree of upstream migration into a catchment, encountering a sequence of tributary confluences. The distance travelled along a migration route can vary intra- and inter-specifically (Quinn, 2018). Thus, types of riverine habitats occupied by Pacific salmon species throughout their range are highly variable as well. As salmon progress through upstream migration, fish experience variations in channel discharge, geometry, and local features, such as deposited wood, boulders, bank outcrops, man-made structures, etc. This dynamic combination of flow and channel shape dictates the hydraulic conditions that each individual experiences. Hydraulic connectivity and passage capability at knickpoints are major factors that determine how far into a channel network an individual fish can swim. Confluences within a catchment can be important drivers of reach-scale geomorphic features and resultant physical migratory habitat structure (Blettler et al., 2016; Penna et al., 2018). In a review of "confluence effects" (meaning the formation of fluvial landforms associated with confluences such as fans, bars, and terraces) in drainage networks, Benda et al. (2004) found a correlation between the ratio of tributary and mainstem drainage area and probability of confluence effects occurring. In certain cases, sediment aggradation at channel confluences may interrupt downstream sediment supply, disrupting alluvial processes that facilitate physical habitat heterogeneity downstream of the confluence. The extent to which this occurs within a basin is largely driven by drainage area and stream network length (Rice, 2017).

Because acute injury to olfactory organs has been demonstrated in presence of certain pesticide compounds (Tierney et al., 2008), it is possible that non-point source contamination may have some influence in migratory routing at confluences above a concentration threshold for acute toxicity. Point source contamination may also have reach-scale impacts to adult salmon migratory habitat via contaminant spills, poor pesticide management practices, or concentrated discharge of agricultural runoff during dry periods (Holvoet et al., 2007; McKnight et al., 2015).

It is also important to note that some amount of straying occurs naturally across Pacific salmon species. Exploratory dispersal as an innate behavior appears to be an expression of the portfolio effect in their life history strategy and in some cases may be related to thermoregulation (Goniea et al. 2006, High et al. 2006, Peterson et al. 2016, Schindler et al. 2010, Keefer et al., 2018). Beyond biological cues at the individual level, recent evidence has demonstrated density-dependent movement of spawning cohorts (Berdahl et al., 2017, 2016). Further investigation is needed before a density threshold for aggregated group movement can be identified across salmonid taxa. Finally, little is known about predator avoidance dynamics in migrating adult salmon, though it is thought to be most important on or near spawning grounds (Quinn, 2018; Quinn et al., 2001).

2.2.2.3 *Micro-scale habitat attributes*

Channel discharge, geometry, and sediment composition act together to produce micro-scale physical habitat conditions commonly referred to as "microhabitats". The microhabitat spatial scale is defined by Baldes and Vincent (1969) as "the physical conditions immediately surrounding an animal at a given time and place". This spatial scale has been utilized in investigations into life stage-specific habitat requirements (Carnie et al., 2016; Moir and Pasternack, 2010; Nielsen, 1992; Shirvell, 1994), restoration design and planning applications (Brown and Pasternack, 2009; Fangue et al., 2021; Favrot et al., 2018), and evaluation of passage infrastructure (Li et al., 2021; Nestler et al., 2008; Weber et al., 2006). To date, influence of confluence hydraulics on species-specific microhabitat distribution in space and time has not yet been studied.

2.3 Materials and Methods

2.3.1 Study area and management context

The Feather and Yuba River catchments lie adjacent in the northeastern area of the California Central Valley (Figure 1.2). Both experienced intensive hydraulic gold mining activity during the 19th century. Differences in early river engineering approaches resulted in contrasting channel evolution processes, particularly with

regard to levee width (James et al., 2009). The Yuba drainage area is 3480 km^2 and the lower Yuba River (LYR) is a 37.1 km segment between Englebright Dam to the confluence with the lower Feather River (LFR). It is dominated by gravel/cobble substrate, transitioning to a sand-dominant channel at the confluence. The Feather drainage area is 16,050 km^2 and the LFR extends 117 km from Oroville Dam to its confluence with the Sacramento River. The LFR is dominated by finer sediment and has experienced significant channel avulsion. The Oroville spillway collapse in 2017 resulted in the rapid mobilization of approximately 1 million metric tons of debris that was deposited in adjacent floodplain areas (Nalin and Kotulla, 2018). The LFR is also heavily influenced by Thermalito Afterbay, a series of hydraulically connected shallow reservoirs adjacent to the main channel that result in increased water temperatures. Both rivers are regulated and experience annual flow regimes that are altered from historical conditions, though the LYR has a relatively natural flood regime (Gervasi et al., 2021).
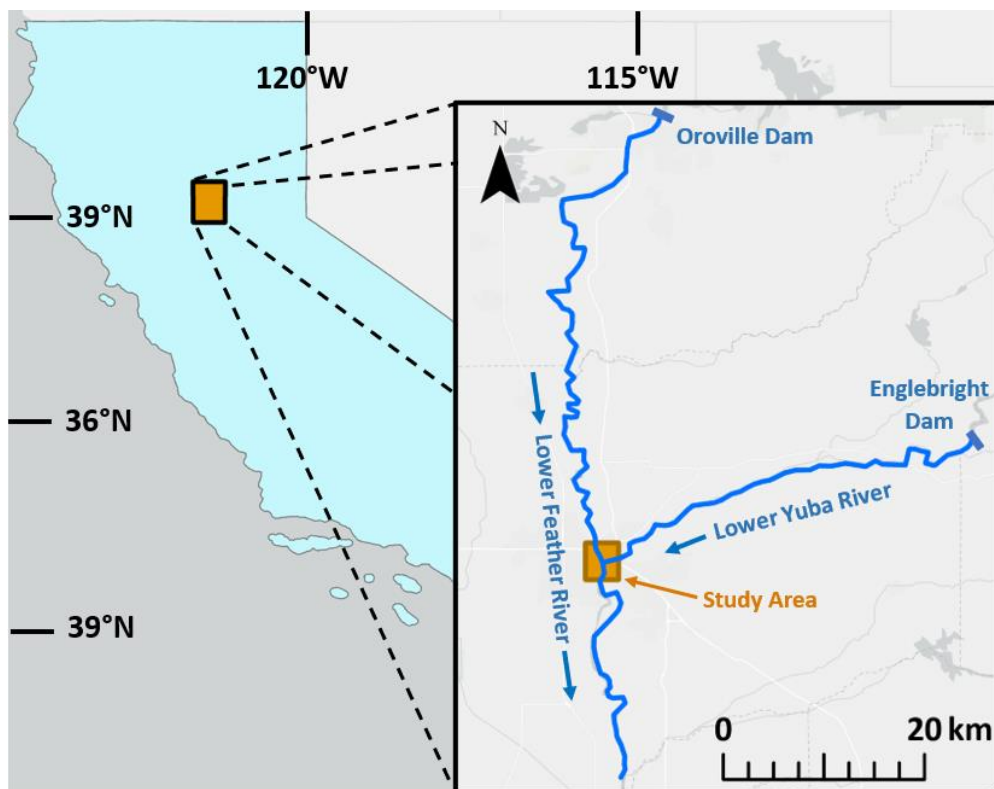
Figure 1.2. Location of the study area. The state of California is shaded in blue in the main panel. The inset identifies the lower Feather River, lower Yuba River, and the dams that create total fish passage barriers upstream of the study area. Blue arrows indicate flow direction. Base map image sources: ESRI, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS user community.

The location of the study area is the immediate confluence of the LFR and LYR. Specifically, it includes approximately 1.42 km of the LFR and 0.85 km of the LYR upstream of the confluence and 1.13 km of the LFR downstream of the confluence (Figure 1.3). The study area is dominated by sand-sized substrate with small patches of coarser material in fast-moving riffles (see Table A.A.1 in Appendix A for grain size distribution by sample site). Topographic surveys and aerial imagery indicate that the study area is subject to significant interannual changes in channel geometry due to mobilization of fine sediment during winter high flow periods. In-stream wood is present along the banks and can be submerged. More wood occurs in the LYR, because the west bank of the LFR has a sandy levee and that bank is subject to maintenance and clearance.

The Feather River Fish Hatchery is located at the base of Oroville Dam and is one of the largest production facilities for fall-run Chinook in the Central Valley. In 2019, spring- and fall-run Chinook produced by Feather River Fish Hatchery accounted for 43.6% of adult hatchery-origin Chinook collected in the Sacramento and San Joaquin basins during the fall-run escapement period (CDFW, 2021). The hatchery is located ~ 61.9 RKM upstream of the study site. In 2019 (the year that our field surveys took place), 27,103 Chinook salmon returned to the hatchery with 51,967 in-river returns, totaling 79,070 fish (CDFW 2022). The LYR has no hatchery production facility and extant naturally spawning populations of spring- and fall-run Chinook persist. In 2019, the LYR experienced 3,446 in-river returns (CDFW 2022).

The Yuba Accord River Management Team (YARMT) found that discharge magnitudes differing between the two rivers appear to influence navigational choice at the LFR-LYR confluence (YARMT 2013). Correlative patterns have emerged in the two rivers between escapement rates for spring- and fall-run Chinook and discrepancies in the magnitude of flow and temperature between the rivers in certain years. Monitoring data show that in years with higher discharge and lower temperature in the LYR relative to the LFR, high rates of straying of Feather-origin fish can be seen in the LYR.

In surveys conducted from 2004–2011, YARMT counted the number of Feather-hatchery origin fish passing a low-head dam on the LYR and, using a fitted logistic model, found 72% of the variation in the

proportion of hatchery- and wild-origin adults entering the LYR could be attributed to the ratio of discharge magnitude between the two rivers and the ratio of water temperature between the two rivers. As a result, the National Marine Fisheries Service's California Central Valley Salmonid Recovery Plan includes a recovery action to "evaluate whether salmonid straying between the Feather and Yuba rivers can be minimized through flow management" (NMFS 2014). It may be necessary to co-manage the LFR and LYR to a degree to address this.

Based on the results of YARMT's monitoring efforts and the extent to which migratory behavioral cues in adult salmon are characterized in the literature, there is a clear need to go beyond simple empirical correlations to investigate potential mechanisms of straying behavior at the LFR/LYR confluence driven by local physical processes that convert general drivers like discharge and temperature into sensory experiences fish use to make decisions or respond to instinctually. Beyond the direct management implications for hatchery-origin fish occupying these watersheds, such an investigation would aid in filling a critical knowledge gap in the migratory physiology and behavior of anadromous salmonids.

It may be that the cue is simply magnitude of discharge, but how can that be possible mechanistically? Specifically, how can a fish experience an instantaneous total volume of water passing a cross-section that is ~ 300 times wider than their body length? That is unlikely. Instead, it is most likely that discharge is a distal "black box" governing variable inducing the ecohydraulic mechanism by which a proximal physical template is presented to fish for their behavioral response. The risk of relying on empirical analysis of only one governing variable without investigating underlying mechanisms is that important, yet unaccounted for other governing variables (e.g. topography, substrate, vegetation, stream wood, etc.) could change independently of managers tuning flow releases, resulting in a poor or ambiguous outcome from controlled actions. Further, there remains ~ 30% of the behavioral decisions that are not explained by YARMT's empirical analysis, and that constitutes a sizable population-level effect that needs to be understood (YARMT 2013).

2.3.2 Experimental design concept

As shown conceptually in Figure 1.1, this study investigated drivers of migratory microhabitat selection at a regulated river confluence. Depths and velocities throughout the study site experienced top-down control by discharge magnitude and ratio (referred to as "discharge condition") between the LFR and LYR. Discharge condition changed significantly between September and October sampling periods in 2019. Fixed DIDSON sampling sites were selected to capture the broadest possible range of depth and velocity magnitude values to identify one or both of those attributes as drivers of selection ("deep" and "shallow" site type designations, see Figure 1.3 Figure 1.4). The study area was divided into three zones that experienced different overall velocity conditions depending on their orientation to the confluence. The three zones include the LYR portion upstream of the confluence, referred to as the "Yuba" zone; the LFR portion upstream of the confluence, referred to as the "Feather" zone; and the LFR portion downstream of the confluence, referred to as the "downstream" zone.
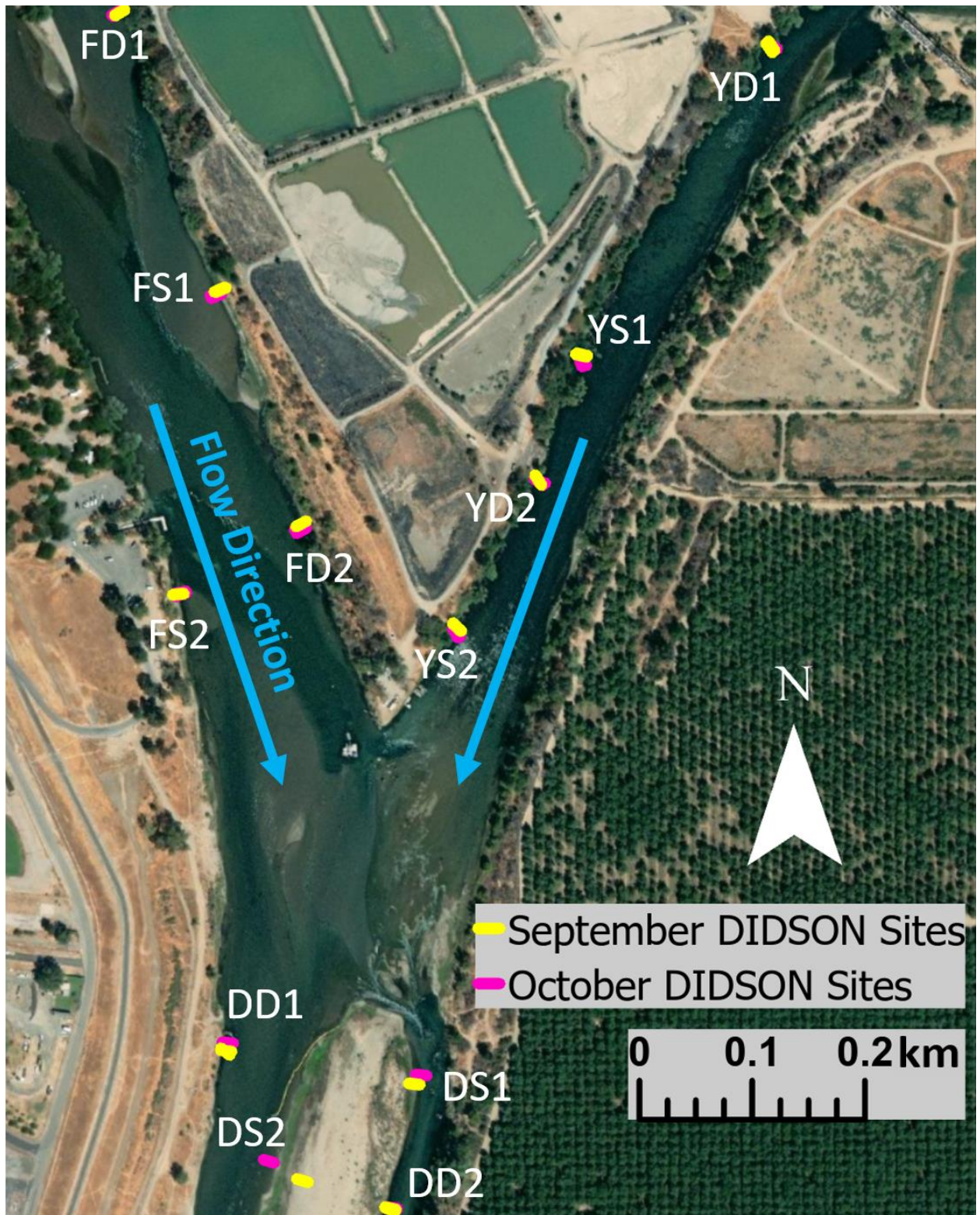
Figure 1.3. DIDSON deployment sites with centerlines indicating orientation (colors indicate sampling period). Sites are classified as being in the Feather, Yuba, or downstream zones (F, Y, and D), and whether it was a deep or shallow site (D or S, two in each zone). Base map image sources: ESRI, Maxar, Earthstar Graphics, and the GIS user community.
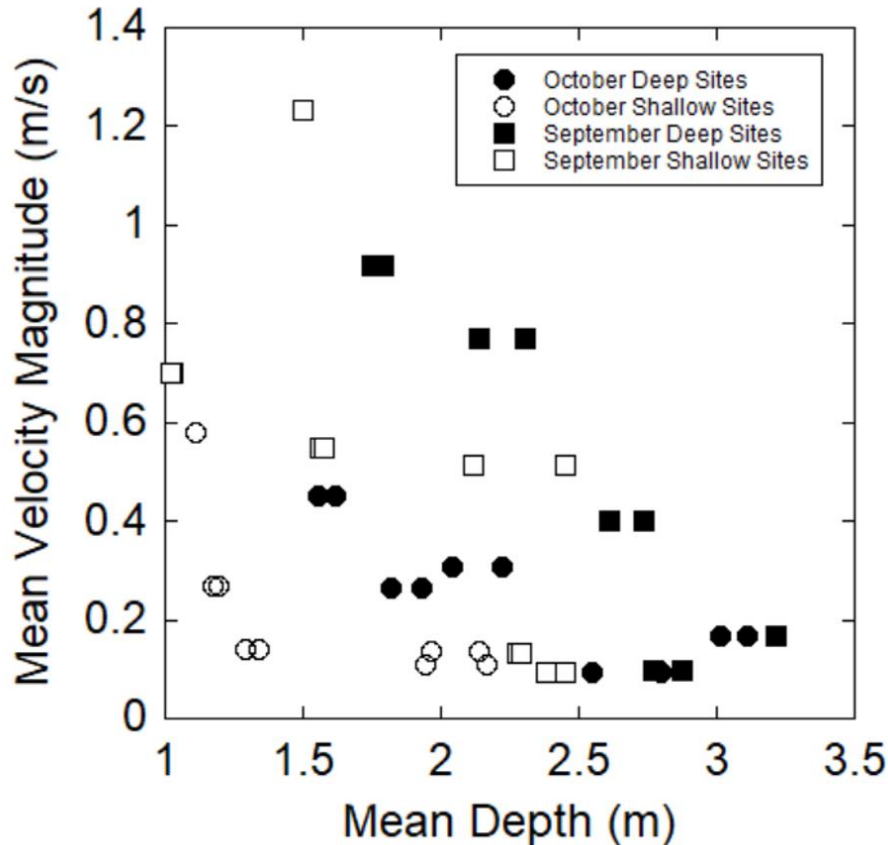
Figure 1.4. Mean depths are plotted against mean velocity magnitude for each DIDSON deployment site in both sampling periods. Some overlap occurs between "deep" and "shallow" sites as they were selected based on relative depths within each zone of the sampling scheme.

Detection rate data from our DIDSON surveys were fit to a set of multiple non-linear regression models to investigate the strength of four hydraulic variables (velocity magnitude; depth; Froude number, a dimensionless quantity that represents the ratio of inertial forces to gravitational forces; and conveyance, a representation of the flow per unit-width that an individual fish experiences at a given point along their migratory pathway) as well as temperature and turbidity, as predictors of micro-scale habitat selection. The sediment grain size distribution within the study area is dominated by sand and therefore would not serve as a useful predictor of habitat selection (see Table A.A.1 in Appendix A). Candidate models as well as the regression function (exponential) were selected based on preliminary exploration of the detection rate data. Additionally, we analyzed migratory swimming behavior type by measuring a combination of rheotactic orientation and progress over ground. This yielded a Eularian-based indicator of upstream migration, and it cannot be used to truly characterize Lagrangian-based movement (Doyle and Ensign 2009; Willis 2011).

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Swimming behavior types were designated as "directed", "milling", and "backtracking" as detailed below and depicted in Figure 1.5. The same set of multiple regression models was used to predict percent occurrence of each of these swimming behaviors, but these models were instead fit using a linear regression type. An Akaike information criteria analysis corrected for small sample sizes (AICc) was used to score and rank the suitability of the models for predicting each response variable. F tests for statistical significance in each regression fit served as a test metric for our stated hypotheses in Table 1.1.
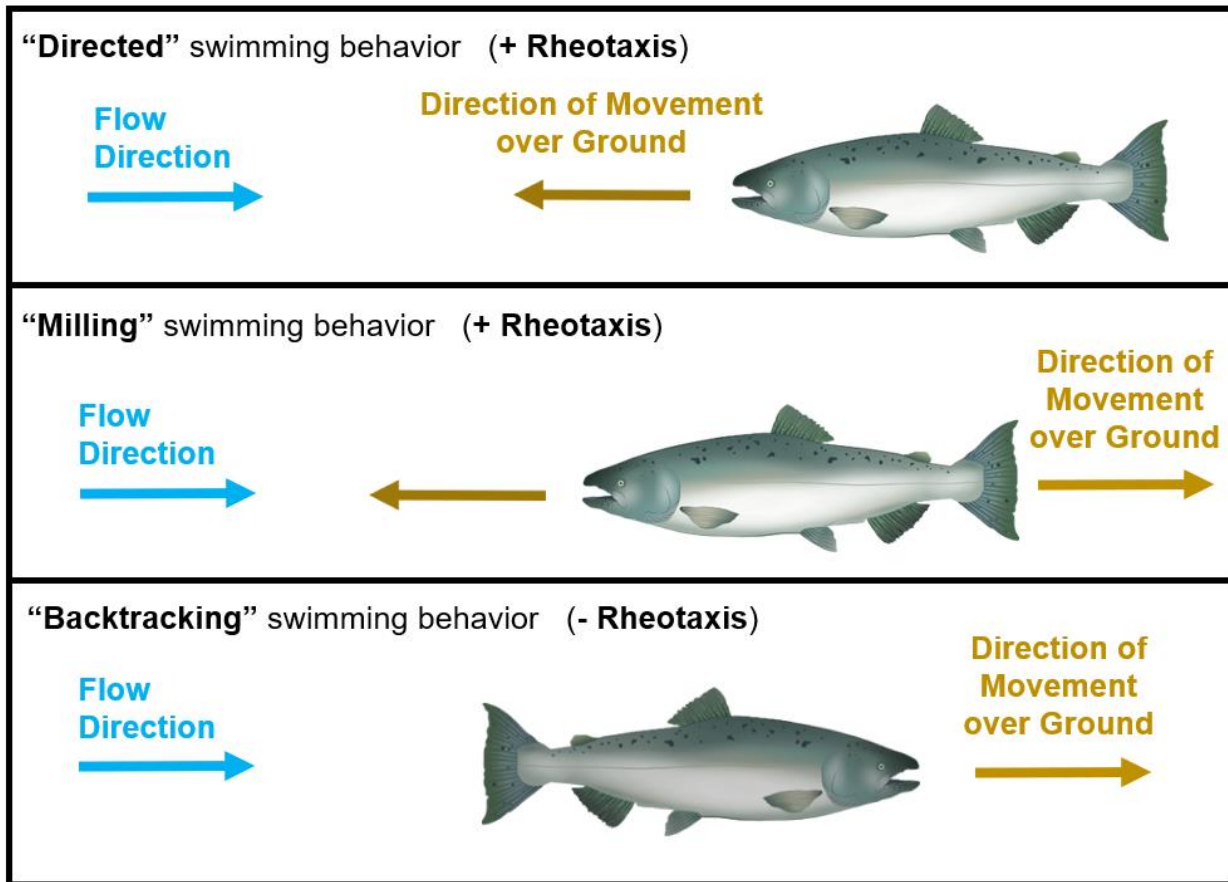
Figure 1.5. Description of swimming behaviors analyzed in this study. Behaviors are defined by rheotaxis and movement over ground relative to the flow direction. Chinook salmon image credit: Emily Nastase, Integration and Application Network (ian.umces.edu/media-library).

2.3.3 DIDSON surveys

2.3.3.1 DIDSON sonar

The potential utility of dual-frequency identification sonars (DIDSON) technology for biological research applications has been noted for settings in which optical underwater imaging equipment may be limited by light, turbidity, or suspended particulate matter (Belcher et al., 2002, 2001). Moursund et al. (2003) first assessed feasibility of DIDSON technology in fisheries research applications. Since then, it has been used to monitor salmon passage rates in Alaska (Faulkner and Maxwell, 2009; Maxwell and Gove, 2004, 2007) and fish behavioral responses to passage infrastructure in Australia (Baumgartner et al., 2006). It has also been used for steelhead (*Oncorhynchus mykiss*) population assessments in coastal California watersheds (Pipal et al., 2012) and green sturgeon (*Acipenser medirostris*) abundance estimates in the Sacramento River (Mora et al., 2015).

To assess fine-scale hydraulic habitat selection at the LFR/LYR confluence, two DIDSON systems were deployed to observe migratory behavior and quantify rates of habitat selection within the immediate area of the confluence. A DIDSON system (Sound Metrics Corp.) features a multibeam transducer that emits 48 beams spaced 0.4° apart when operated at the 1.0 MHz frequency and 96 beams spaced 0.3° apart with two operating at the 1.8 MHz frequency. The beams are emitted through an "acoustic lens" that can shape the resultant sonar images to focus on a particular field of view.

2.3.3.2 DIDSON sampling scheme

Migratory behavioral observations via DIDSON occurred over the course of two 4-day sampling periods in 2019, representing markedly different discharge conditions at the confluence due to the scheduled decrease in Feather River flows for salmon spawning in mid-October (CDWR and CDFG 1983, NMFS 2016). The first period occurred from September 23-26 and the second from October 22-25. During the first sampling period, mean discharges on the LFR and LYR were ~ 213 and 24 m^3/s, respectively. During the second period, discharges on the LFR and LYR were ~ 68 and 17 m^3/s, respectively (CDWR 2021). Discharge decreased because of a scheduled annual flow decrease in the LFR to prevent anadromous fish

from spawning in overbank areas that may be dewatered (CDWR and CDFG 1986, NMFS 2016). LYR discharge also decreased, but not by as much, yielding a lower flow ratio. Scheduled facility maintenance typically yields the lowest discharge out of Englebright Dam in September. However, actual released discharge may be higher than scheduled depending on carryover storage, natural autumn runoff, and water demand by Yuba County farmers. Further, the timing of LYR flow reduction is earlier than it is for the LFR, so the main effect on the flow ratio in late September is driven by the LFR. Independently of releases, minimum flow requirements on the LYR close to the confluence with the LFR are identical for September and October regardless of water year type used to define the operational schedule in the Yuba Accord. Therefore, the primary control on discharge ratios at the confluence is LFR flow operations.

We established four DIDSON deployment sites in three zones, in both the LFR ("Feather" sites) and LYR ("Yuba" sites) upstream of the confluence and an additional four in the LFR downstream of the confluence ("Downstream" sites). Each of these three zones included two "deep" and two "shallow" sites, relative to surrounding channel topography. Site selection was somewhat limited by availability of shoreside area for equipment set up and deployments were limited to normal daylight working hours due to logistical constraints and safety concerns. The goal of the sampling scheme was to capture a range of depths and velocities that were representative of the study area. These sites and their physical attributes are shown in Figure 1.4 and summarized in detail in Table A.A.2 in Appendix A.

All 12 DIDSON deployment sites were sampled twice for a duration between 30-60 min within each 4 d period at a fixed range of 10 m. Deployment locations during the second sampling period were moved laterally into the wetted channel to accommodate the stage drop. DIDSON transducers were suspended in stationary PVC cages and both sonar and laptop equipment were powered by 12v deep cycle marine batteries. For all deployments, a handheld Trimble GeoHX GeoExplorer 2008 Series GPS was used to obtain a position fix for the transducer. A handheld compass and angle measuring device were used to obtain the compass heading and downward (pitch) angle orientation of the transducer. Roll angle was minimized to the maximum extent possible. From the digital elevation model (DEM, described below) and

the transducer position information for each deployment, volumes sampled were estimated using a geometric solution scheme (details included in Figure A.A.1 in Appendix A). Sampling bias was not found to influence detection rates with regards to volume sampled, deployment time, deployment duration, or mean body length estimate. This is discussed further in Section 5.2.5 of Appendix A. A thorough discussion of the species identification criteria used in this study is included in Section 5.2.6 of Appendix A with body length estimates being the primary metric used to identify adult Chinook salmon in the DIDSON footage.

2.3.3.3 *Detection rates and swimming behavior*

Individual DIDSON files (recorded at 8 frames per second) were reviewed manually at 30 frames per second and processed to obtain migratory behavioral data for adult Chinook salmon. Footage at the beginning and end of each file that contained camera movement was discarded. Each time a fish entered the field of view that fit the species identification criteria, it was measured three times using the DIDSON software's measuring tool to obtain a mean body length. The time of entry and exit was recorded as well as its rheotactic orientation to the flow. Detection rates for each deployment were calculated by summing the number of individual detections and dividing those by the minutes of footage analyzed multiplied by the volume of water sampled by the DIDSON:

$$D = \frac{\sum(I)}{t_A V} \tag{1}$$

where D is the detection rate, I is the number of individual detections per site, t_A is the time of footage analyzed in minutes, and V is the total volume of water sampled by the DIDSON in m^3.

Migratory swimming behavior was identified for each detection based on both rheotactic orientation to the flow and movement over ground at each DIDSON site (Figure 1.5). Fish that showed positive rheotaxis (body oriented against the flow direction) are said to exhibit either "directed" movement if their path of travel over ground was only upstream, or "milling" if their path over ground included both upstream and downstream movement. Fish were said to be "backtracking" if they exhibited negative rheotaxis (body oriented with the flow direction).

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2.3.3.4   Bathymetric mapping

A DEM was constructed using topo-bathymetric point data from GPS and echosounding. Bathymetric mapping of the wetted channel occurred several weeks prior to the behavioral surveys in August 2019 using a Hydrolite single beam echosounder (minimum depth of 0.3 m; depth accuracy of 1 cm; sampling frequency of 200 Hz; Seafloor Systems, Inc.) in sync with a Trimble R8 real-time kinematic GPS (horizontal and vertical accuracies of ~ 1 and 2 cm, respectively) receiving corrections over the internet from a regional base station network on the fly at 1 Hz. Several cross-sectional transects were mapped at each DIDSON deployment site. Additional cross-sectional transects were mapped approximately one channel width apart as well as 8-12 longitudinal transects that spanned the length of each zone in the study area. Bare-Earth topography was collected in January 2020 on an island at the confluence junction using the Trimble R8.

ESRI ArcGIS software was used to process survey data and produce a DEM. Erroneous survey data points were manually identified and removed. Additional augmented points were added along known contours from the field work to smooth any artifacts in the digital terrain that resulted from topographic data gaps. A triangulated irregular network was produced from the point data and then this was converted into a 0.3-m resolution raster. Raster resolution was selected based on the overall density of topographic data points and especially considering point density in the vicinity of DIDSON deployments.

2.3.4   Hydraulic data

On September 19th and 20th, one week prior to the first behavioral observation period, and again on October 30th, one week following the second behavioral observation period, velocity measurements were taken at each of the DIDSON deployment sites using a boat-mounted Sontek M9 acoustic doppler current profiler. At each DIDSON cross section, six lateral velocity transects were performed, capturing column-wise velocity measurements in succession across the channel. Transects extended the full width of the wetted channel for each sampling period. Mean velocity magnitude values were computed for each column over a

1-second time step and positions were recorded using a Sontek DGPS antenna. The points that were taken from these data in GIS to represent each DIDSON site occurred adjacent to the centerline of the DIDSON beams, within the lateral length of the DIDSON beams in the up or downstream direction. Points included in this search area were then averaged to generate one mean velocity magnitude value for each DIDSON site. During the October sampling period, two of the DIDSON sites were not accessible by boat (DS1 and DD2) and no ADCP data was collected. As a result, those DIDSON deployments were discarded and excluded from our analysis. Mean depth estimates for each DIDSON site were estimated based on the 10-m-long centerline of the DIDSON field of view, using bed elevation measurements from the DEM raster along the centerline at 0.3 m intervals and assuming a uniform transducer submergence depth of 0.9 m at all sites.

Froude number is a dimensionless quantity that represents the ratio of inertial forces to gravitational forces and has been used by others to assess habitat suitability for salmonids (Ayllón et al., 2009; Lamouroux and Souchon, 2002; Persinger et al., 2011):

$$\underline{Fr} = \frac{\underline{u}}{\sqrt{g * \underline{d}}} \tag{2}$$

where u is the mean velocity magnitude at each site in m/s, g is the gravitational acceleration constant in m/s^2, and d is the mean depth at each site in m. Conveyance is defined as follows:

$$\underline{C} = \underline{u} * \underline{d} \tag{3}$$

where u is mean velocity magnitude in m/s and d is mean depth in m. C results in units of m^2/s and is conceptually the discharge per unit width of the wetted channel. It is a representation of the flow that an individual fish experiences at a given point along their migratory pathway. This metric has been used in similar applications for assessing salmonid habitat suitability (Kammel et al., 2016; Moniz et al., 2019).

2.3.5 Hydraulic model

The overall hydraulic conditions that were available to fish at the study site could not be directly measured for a comparison against those conditions where fish were located, so they were estimated using the two-dimensional (2D) hydrodynamic model TUFLOW HPC (Build 2018-03-AE; BMT Commercial Australia Pty Ltd). The model simulated steady state hydraulics throughout the study area for the regulated, steady mean daily discharges that occurred during each sampling period. Gridded model solutions for depth and velocity magnitude were generated with a computational square cell size of 3 m x 3 m. Velocity magnitude validation found model predictions to be a good fit to the data on the basis of an r^2 value of 0.76, which is quite high compared to the literature using 2D hydrodynamic models. Details on the hydrodynamic models including inputs, topographic data, parameters, and validation can be found in Table A.A.3 in Appendix A.

2.3.6 Temperature and turbidity monitoring

Temperature and turbidity were monitored at fixed sampling locations throughout the 2019 field campaign to represent both discharge conditions (Figure 1.6). All but two DIDSON sites had a corresponding temperature/turbidity site, the remaining two were assigned averaged temperature/turbidity values from sites directly up- and down-stream. Three HOBO Water Temperature Pro V2 data loggers (Onset Computer Corp.) were permanently installed at depths of ~ 1 m at each boundary of the project area (Figure 1.6) to generate a continuous temperature time series during the two sampling periods (Figure 1.7). The purpose of the fixed loggers was to account for any changes in temperature within each 4-day DIDSON sampling period. Fixed HOBO loggers recorded water temperatures (± 0.2°C) at 30-minute intervals. To avoid dewatering during the Feather discharge decrease and stage drop between DIDSON sampling periods, the fixed loggers were vertically repositioned to achieve > 0.5 m depth submersion for the October period.
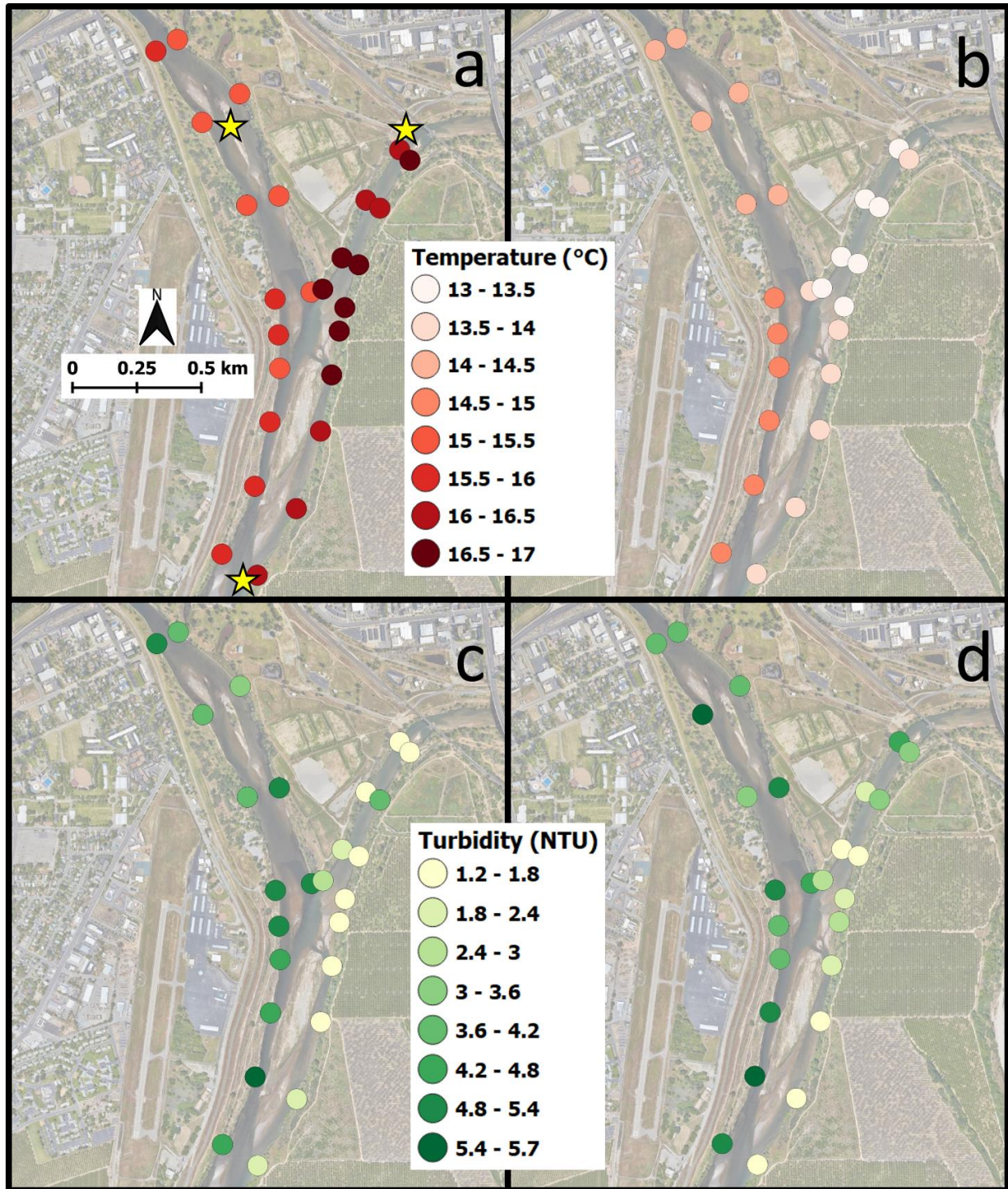
Figure 1.6. Locations and results of hand-held surface temperature and turbidity measurements for September (a,c) and October (b,d) sampling periods. The yellow stars indicate the locations of the fixed temperature loggers. Base map image is from Google Earth.
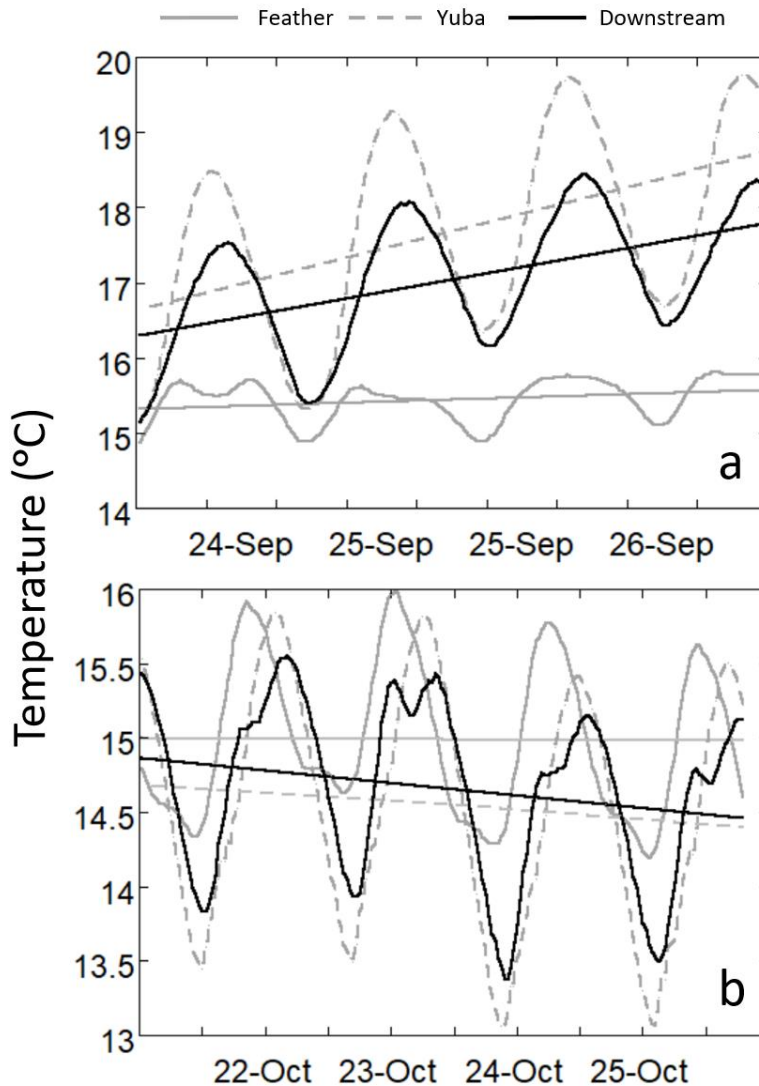
Figure 1.7. Temperature time series from each of the three fixed HOBO data loggers during both the September (panel a) and October (panel b) DIDSON sampling periods in 2019. In the September plot, slopes and intercepts for the Feather, Yuba, and downstream temperature time series trendlines are 0.0016, 0.0124, 0.0088, and 15.32, 16.65, 16.30, respectively. In the October plot, slopes and intercepts for the Feather, Yuba, and downstream temperature time series trendlines are -0.0001, -0.0014, -0.0021 and 15.01, 14.68, 14.87, respectively.

Temperature data from the loggers were supplemented with hand-held measurements taken at fixed sampling locations (Figure 1.6) before and after each DIDSON sampling period (samples taken September 20th and 27th and October 18th and 26th). A resistance temperature detector thermometer ($\pm$ 0.3°C) with a general immersion probe (Tegam Inc.) was used to take surface measurements at each station. A third HOBO logger attached to a pole was used to take temperature measurements at 1 m depth or at the bottom

(if shallower than 1 m) at each station. Surface and submerged temperatures were compared to determine if vertical temperature stratification occurred at any point in the site.

A 2100Q Portable Turbidimeter (accurate to ± 2 % of reading; HACH Company) was used to measure turbidity in nephelometric turbidity units (NTUs) at each of the handheld temperature monitoring stations. Three measurements were taken at each station and averaged. Sampling vials were rinsed with distilled water between each measurement and the instrument was calibrated at the start of each sampling day in accordance with manufacturer guidance.

2.3.7   Data analysis

A key question to address is whether the locations where fish were present are distinguishable from the overall river confluence conditions. Mann-Whitney U tests are a typical approach to answering this question, so they were performed using the base R package *stats* (McFarland and Yates 2016, R Core Team 2022b) to test (at 95% confidence) for differences in means between both velocity magnitude and depth values associated with each DIDSON detection, and randomly sampled modeled values from outside of the DIDSON sample sites, representing conditions present within the study area at the time of observation. This was performed across all detections, as well as individually for the September and October sampling periods, which is two variables times three time intervals yielding six total tests. The number of randomly sampled modeled values for velocity magnitude and depth used in each comparison was equal to the number of detections associated with that comparison (228 for all detections, 188 for the September comparison, and 40 for the October comparison).

Nonlinear regression was used to test for correlation between detection rate and four micro-scale hydraulic variables (H_{1a-d}), temperature (H_{1e}), turbidity (H_{1f}), and several combinations of these predictors that were assembled based on preliminary exploration of our data (H_{1g}). Data were fit to exponential functions using a nonlinear ordinary least squares approach (Motulsky and Ransnas, 1987; Ritz and Streibig, 2008) via the base R function '*lm*' and using the F statistic at 95% confidence to test whether at least one regression

coefficient was non-zero (Olive, 2017; R Core Team, 2022a). The same R function was used to test the same predictor variables and candidate models on our swimming behavior data using linear regressions. Percent occurrence of each behavior type was the response variable in these models (testing H_2: % directed, H_3: % milling, and H_4: % backtracking). In addition to the F test for significance, the coefficient of determination (r^2) indicated amount of variance explained by each model. The list of candidate models that was generated to test our stated hypotheses and our rationale for each are included in Table A.A.4 in Appendix A in accordance with best practices for information-theoretic data analysis described by Anderson and Burnham (2002). A preliminary examination of our DIDSON detection data helped inform this list by eliminating model candidates that would likely have poor explanatory power.

Akaike information criteria corrected for small sample sizes (AICc) was utilized to identify the most appropriate model for predicting each response variable; the R package *AICcmodavg* was used (Cavanaugh and Neath, 2019; Mazerolle, 2020). AICc produces a ranked list of candidate models with the most appropriate (lowest AICc score) striking a balance between having the best fit to the data while also having the fewest predictive parameters used to achieve that fit. A ΔAICc for a given model that is <2 indicates substantial empirical support for that model whereas values >10 offer essentially none (Cavanaugh and Neath, 2019). Finally, the AICc weight of support (*w*) can be interpreted as the probability that a given model is the most appropriate of the list under the AICc. It is computed by normalizing the likelihoods of candidate models in a list so that *w* values sum to 1. The value of *w* for model *i* is expressed as:

$$w_i = \frac{e^{-0.5\Delta AICc_i}}{\sum_{i=1}^{M} e^{-0.5\Delta AICc_i}} \tag{4}$$

where *M* is the number of candidate models in the list (Portet, 2020). Finally, the R package *car* (Fox et al., 2022) was used to generate added variable plots (AVP) for the top AICc-ranked model for each response variable (or other model of interest as in the case for backtracking behavior). Each panel in an AVP includes a single parameter from the model plotted against the response variable while holding all other parameters constant and a line is fit to the data (Johnson and McCulloch 1987). The AVP is a useful diagnostic tool in

regression applications as the degree of departure of the line from horizontal indicates the relative strength of its predictive influence in the model.

2.4   Results

Overall, DIDSON surveys yielded a total of 228 adult fall-run Chinook salmon detections (Table 1.2). Considerably more occurred during the September sampling period (188) than the October period (40). Feather sites upstream of the confluence had the most detections across both sampling periods (163), while the Yuba sites had the least (18); Downstream sites were in between (47). Finally, deep sites showed more detections across both periods (170) than shallow sites (58). Swimming behaviors among all detections occurred as follows: directed (135), milling (39), and backtracking (54). Details on detections per swimming behavior as a function of sampling period, zone, and deployment site type (deep vs. shallow) are included in Table 1.2. It is important to note that one deployment (FD2 in September) had an exceptionally high detection rate compared to all other deployments and accounted for 48% of all fish detections. We chose not to exclude this deployment as an outlier because it shared similar site attributes (i.e., mean depth and mean velocity) as other deployment sites with high detection rates.

Table 1.2. Total number of detections by sampling period, study area zone, and site type. Also included are total detections by swimming behavior type as a function of sampling period, study area zone, and site type. This information also serves as the contingency tables for the Chi-squared analysis performed in this study.

| | | Detection Summary | | | | | Swimming Behavior Summary | | |
| | Total | Sampling Period | | Sampling Zone | | | | | |
		September	October	Feather	Yuba	Downstream	Directed	Milling	Backtracking
Overall	228						135	39	54
September Period	188						120	25	43
October Period	40						15	14	11
Feather Zone	163	147	16				105	16	42
Yuba Zone	18	6	12				10	1	7
Downstream Zone	47	35	12				20	22	5
Deep Sites	170	151	19	134	5	31	107	16	47
Shallow Sites	58	37	21	29	13	16	28	23	7

Mean surface temperature and turbidity values for the hand-held surveys showed the LFR to be more turbid in both sampling periods with a notable shift in cooler temperatures between periods from the LFR to the LYR (Figure 1.6). Vertical temperature differences were measured to demonstrate that they were negligible and did not introduce potential bias based on vertical swimming positions of fish. In September, vertical temperature differences ranged from -0.54-0.77°C with a mean difference of 0.069°C and median difference of 0.065°C. In October, vertical temperature differences ranged from -0.18-1.30°C with a mean difference of 0.42°C and median difference of 0.39°C. Figure 1.7 shows 30-min temperature measurements taken by the fixed HOBO data loggers. Linear curves fit to the temperature time series indicate slight increases throughout the DIDSON sampling period in September for the Feather, Yuba, and Downstream loggers. In October, the time series show slight decreases in temperature throughout the DIDSON sampling period.

Modeled velocity magnitude values throughout the study area ranged from 0 - 1.22 m/s in September and 0 – 1.75 m/s in October. Modeled depth values throughout the study area ranged from <0.01 – 5.66 m in September and <0.01 – 4.90 m in October. Percent occurrences of binned, modeled depth and velocity magnitude values throughout the study area are summarized in Table 1.3, allowing for comparison of the range of observed mean depth and velocity magnitude values that were attributed to the DIDSON deployments (Figure 1.4) to the overall hydraulic conditions that were available to the fish.

Comparisons of means and standard deviations between observed and modeled available hydraulics revealed that differences in depths were greater than differences in velocity magnitude across both sampling periods and in September, but not October (Table 1.4). The Mann-Whitney U test resulted in statistically significant differences in fish-selected versus available hydraulic conditions (depth and velocity values) for five of six tests (Table 1.5 and Figure 1.8). Fish preferred deeper sites with slower flow. The October analysis with only 40 observations could not distinguish between the two, indicating a sample size problem. Overall, the tests with the full dataset found that physical microhabitat conditions selected by fish were

different from the overall available conditions at the river confluence, indicating a scientifically meaningful

preference which is of interest to the topic of migration in river corridors.

Table 1.3. Total areas and percent occurrence for binned values of modeled depth and velocity magnitude occurring throughout the study area during September and October DIDSON sampling periods.

	Sept		Oct	
Depth Bin	Area (km^2)	%	Area (km^2)	%
0 - 1m	0.08	12.86	0.27	46.05
1 - 2m	0.30	45.67	0.25	42.73
2 - 3m	0.22	33.38	0.06	9.64
3 - 4m	0.04	6.83	0.01	1.01
4 - 5m	0.01	0.83	<0.01	0.57
>5m	<0.01	0.43	0.00	0.00
Velocity magnitude bin	Area (km^2)	%	Area (km^2)	%
0 - 0.2 m/s	0.12	19.19	0.15	25.73
0.2 - 0.4 m/s	0.04	6.33	0.14	23.69
0.4 - 0.6 m/s	0.08	13.03	0.20	35.37
0.6 - 0.8 m/s	0.22	33.95	0.05	9.25
0.8 - 1.0 m/s	0.16	24.66	0.02	4.08
1.0 - 1.2 m/s	0.02	2.75	0.01	1.49
>1.2 m/s	<0.01	0.08	<0.01	0.38

Table 1.4. A comparison of means and standard deviations for mean depth and velocity magnitude values associated with each DIDSON detection as well as sampled values from 2D hydrodynamic model outputs. Unsigned % differences between means and standard deviations of observed and modeled values are also included.

DIDSON sampling period	Summary statistic	Mean V_{mag} (m/s)	V_{mag} sample	|% V_{mag} diff.|	Mean d (m)	d sample (m)	|% d diff.|
All (N = 228)	Mean	0.48	0.50	3.26	2.25	1.57	30.26
	SD	0.26	0.28	9.29	0.50	0.84	65.97
Sept (N = 188)	Mean	0.52	0.57	8.85	2.35	1.83	22.05
	SD	0.25	0.30	18.40	0.44	0.89	104.06
Oct (N = 40)	Mean	0.29	0.43	48.99	1.80	1.11	38.44
	SD	0.16	0.23	43.76	0.56	0.53	5.65

Table 1.5. Results from Mann-Whitney U tests comparing mean depth and velocity magnitudes associated with each DIDSON detection with values randomly sampled from 2D hydrodynamic model outputs representing conditions in the study area outside of the DIDSON sample areas. The number of observed and modeled values were equal (Comparison N), and the comparison was performed for both September and October sampling periods combined as well as each period individually. Model cell N is the number of available depth or velocity values from which random samples were taken.

	Comparison N	Model cell N	Variable	U	p value
All	228	407979	V_{mag}	23,022	0.03
			depth	41,731	<0.01
Sept	188	215515	V_{mag}	12,801	<0.01
			depth	25,542	<0.01
Oct	40	192463	V_{mag}	686	0.46
			depth	1151	<0.01
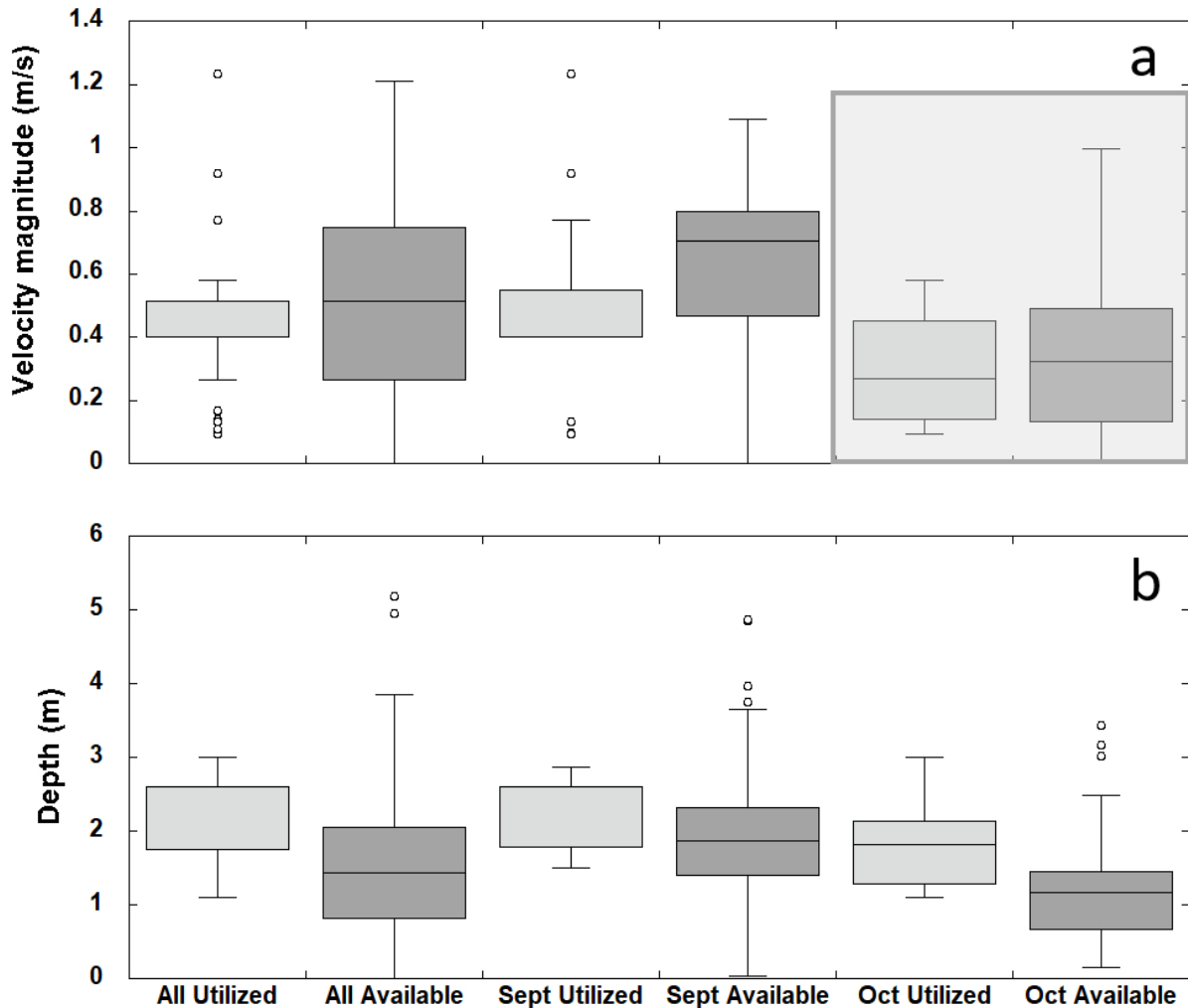
Figure 1.8. Box and whisker plot showing a comparison of velocity magnitude (panel a) and depth (panel b) values utilized in DIDSON detections and randomly sampled modeled values from 2D hydrodynamic outputs representing available conditions outside of DIDSON sample sites. The gray box indicates the Mann-Whitney U test comparison that was not statistically significant at 95% confidence.

2.4.1   Drivers of microhabitat selection

We reject H_{1b} as depth was not a statistically significant predictor of detection rate. We fail to reject any other hypothesis, as the F tests for each predictor variable and the multiple combinations yielded p values <0.05 at 95% confidence (Table 1.6). Table 1.7 includes parameter estimates for these models. The best performing model for predicting detection rate included a combination of conveyance, temperature, and turbidity, having a p value < 0.001, an adjusted r^2 value of 0.42, and a w value of 0.53; an AVP for this

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model is shown in Figure 1.9. Figure 1.10 includes graphical simulations of how this model behaves in predicting detection rate as a function of conveyance under three different temperature values while holding turbidity constant (steeper increases in D with increasing temperature, see panel a) and under three turbidity values while holding temperature constant (steeper increases in D with increasing turbidity, see panel b).

Table 1.6. Model performance summary and AICc ranking for nonlinear regression models predicting detection rate.

Rank	Model	K	d.f.	F stat	p value	AICc	ΔAICc	Adjusted r^2	w
1	D ~ C + T + TU	5	25	7.90	**< 0.001**	104.58	0.00	0.42	0.53
2	D ~ C	3	27	13.24	**< 0.01**	106.68	2.11	0.30	0.19
3	D ~ T + TU	4	26	7.54	**< 0.01**	107.70	3.12	0.32	0.11
4	D ~ C + T	4	26	7.14	**< 0.01**	108.28	3.70	0.30	0.08
5	D ~ V_{mag}	3	27	9.24	**< 0.01**	109.72	5.14	0.23	0.04
6	D ~ Fr	3	27	7.00	**0.01**	111.57	7.00	0.18	0.02
7	D ~ T	3	27	6.42	**0.02**	112.07	7.50	0.16	0.01
8	D ~ TU	3	27	4.62	**0.04**	113.68	9.11	0.11	0.01
9	D ~ V_{mag} + d + C + Fr + T + TU	8	22	3.74	**0.01**	114.09	9.51	0.37	< 0.01
10	D ~ V_{mag} + d + C + Fr	6	24	3.34	**0.02**	114.14	9.56	0.25	< 0.01
11	D ~ d	3	27	0.25	0.62	117.99	13.41	< 0.00	< 0.01

K = number of parameters, d.f. = degrees of freedom, AICc = Akaike information criterion corrected for small sample sizes, ΔAICc = increase in AICc score from the top-ranked model, Adjusted r^2 is the coefficient of determination adjusted for all predictors, w is the relative weight of support for each model among the candidate set. D = detection rate, V_{mag} = velocity magnitude, d = depth, C = conveyance, Fr = Froude number, T = temperature, TU = turbidity. P values in bold indicate statistical significance at 95% confidence.

Table 1.7. Model parameter estimates for statistically significant candidate models predicting detection rate.

AICc Rank	Model	Intercept (α)	β_{Vmag}	β_d	β_C	β_{FR}	β_T	β_{TU}
1/11	$D = e^{(\beta_C C + \beta_T T + \beta_{TU} TU + \alpha)}$	-12.87			1.27		0.41	0.51
2/11	$D = e^{(\beta_C C + \alpha)}$	-5.41			1.77			
3/11	$D = e^{(\beta_T T + \beta_{TU} TU + \alpha)}$	-17.55					0.78	0.58
4/11	$D = e^{(\beta_C C + \beta_T T + \alpha)}$	-9.75			1.46		0.31	
5/11	$D = e^{(\beta_{Vmag} Vmag + \alpha)}$	-5.14	2.57					
6/11	$D = e^{(\beta_{Fr} Fr + \alpha)}$	-4.96				8.85		
7/11	$D = e^{(\beta_T T + \alpha)}$	-14.75					0.73	
8/11	$D = e^{(\beta_{TU} TU + \alpha)}$	-5.85						0.53
9/11	$D = e^{(\beta_{Vmag} Vmag + \beta_d d + \beta_C C + \beta_{Fr} Fr + \beta_T T + \beta_{TU} TU + \alpha)}$	-13.27	26.76	0.00081	-3.55	-75.67	0.44	0.56
10/11	$D = e^{(\beta_{Vmag} Vmag + \beta_d d + \beta_C C + \beta_{Fr} Fr + \alpha)}$	-3.59	-4.35	-0.89	4.13	-0.13		

AICc Rank = #/Total, D = detection rate, V_{mag} = velocity magnitude, d = depth, C = conveyance, Fr = Froude number, T = temperature, TU = turbidity.
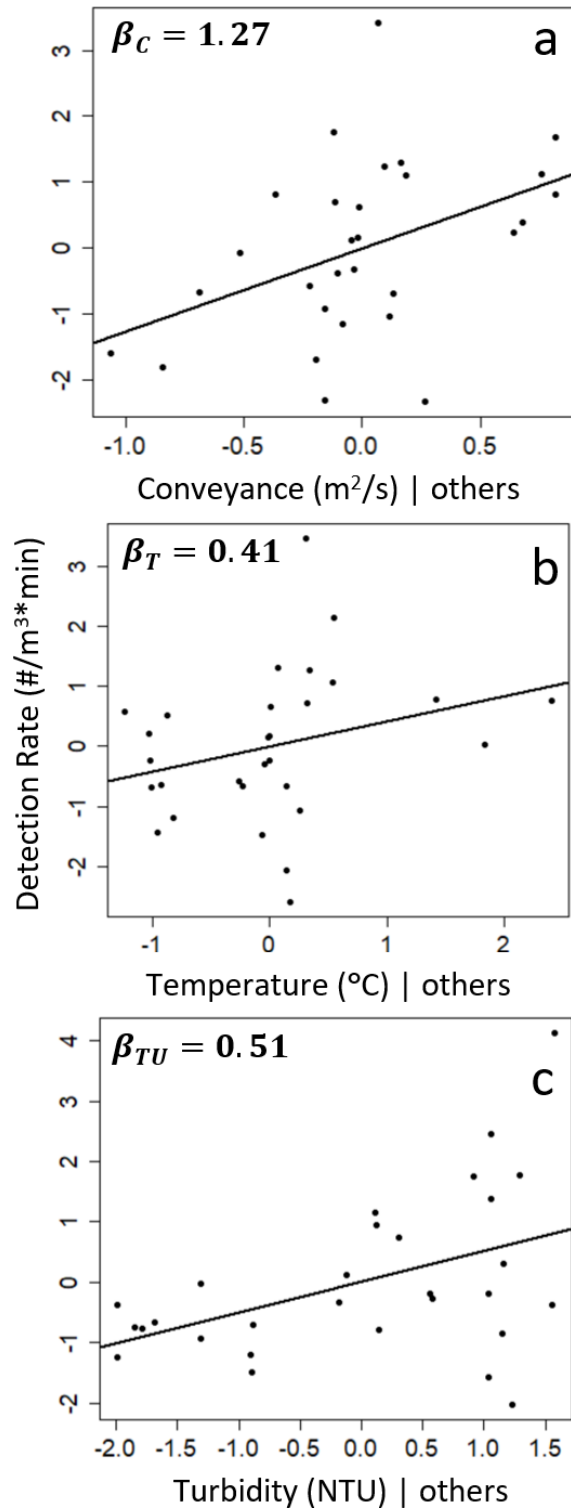
Figure 1.9. Added variable plots describing the relationship between each indicated predictive model parameter (given the magnitude of all others) with detection rate as the response variable. Panels a through c are regression coefficients for conveyance, temperature, and turbidity, respectively. Parameters belong to the highest AICc-ranked regression model for predicting detection rate. Trendlines are fit to the points in each plot. The degree to which each trendline departs from horizontal (which would mean the parameter was equal to zero) indicates its relative predictive strength in the model.
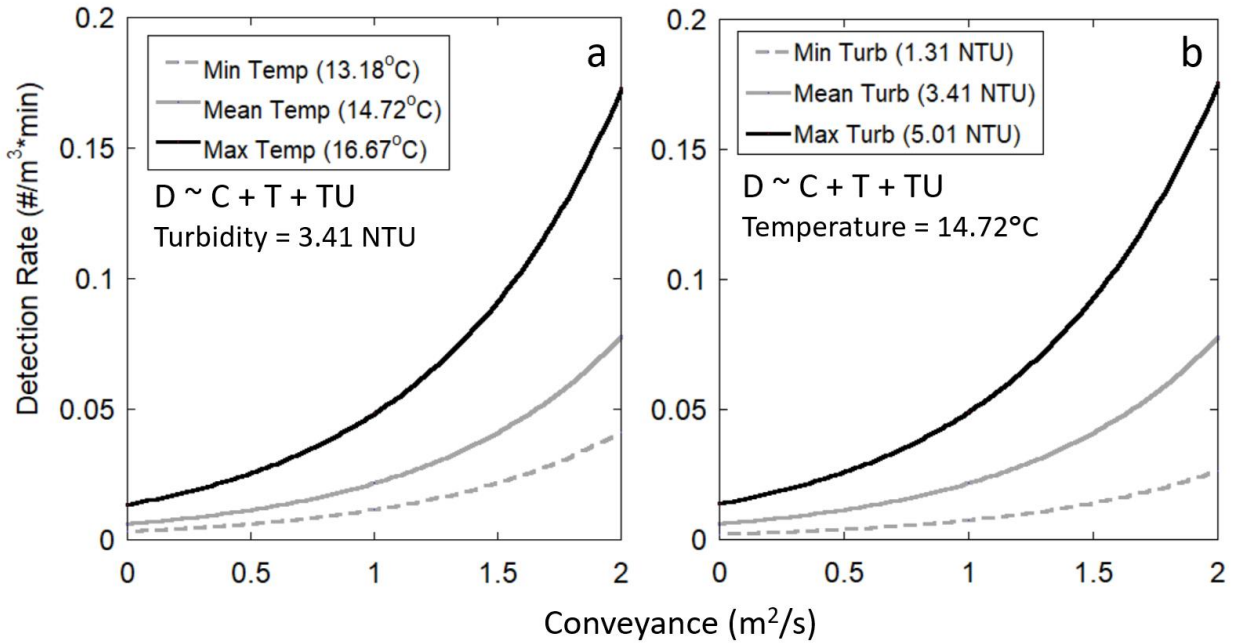
Figure 1.10. Detection rate is predicted using the highest AICc-ranked model which is fit using a nonlinear (exponential) regression and includes conveyance, temperature, and turbidity as predictors. Each panel includes continuous predictions of detection rate as a function of conveyance. Panel a includes three different temperature values that correspond to the maximum, minimum, and mean values in our observed data. Turbidity is held constant at the mean observed value in our data. Panel b uses this same scheme but with three turbidity values used and temperature held at the observed mean.

2.4.2   Drivers of migratory swimming behavior

We reject hypotheses H_{2a-g}. None of the candidate models yielded one or more statistically significant predictors of percent directed swimming behavior under the F test. We fail to reject H_{3f} and H_{3g} as turbidity as well as four combinations of predictors yielded statistically significant models for predicting percent milling behavior (see Table 1.8 for model performance metrics and Table 1.9 for parameter estimates). The best performing model for predicting percent milling behavior included all four hydraulic variables and had a p value < 0.001, an adjusted r^2 value of 0.82, and a w value of 0.83. An AVP for this model is shown in Figure 1.11.

Table 1.8. Model performance summary and AICc ranking for regression models predicting frequency of milling and backtracking swimming behaviors.

Rank	Model	K	d.f.	F stat	p value	AICc	ΔAICc	Adjusted r^2	w
				Milling					
1	$P_m \sim V_{mag} + d + C + Fr$	6	9	15.47	**< 0.001**	135.79	0.00	0.82	0.83
2	$P_m \sim TU$	3	12	11.9	**< 0.01**	139.44	3.64	0.46	0.13
3	$P_m \sim T + TU$	4	11	5.86	**0.02**	142.98	7.18	0.43	0.02
4	$P_m \sim d$	3	12	3.35	0.09	145.64	9.84	0.15	0.01
5	$P_m \sim Fr$	3	12	2.85	0.12	146.10	10.31	0.12	< 0.01
6	$P_m \sim V_{mag}$	3	12	1.65	0.22	147.28	11.49	0.05	< 0.01
7	$P_m \sim C + T + TU$	5	10	3.68	**0.05**	147.76	11.97	0.38	< 0.01
8	$P_m \sim C$	3	12	0.10	0.76	148.97	13.18	< 0.00	< 0.01
9	$P_m \sim T$	3	12	0.01	0.91	149.07	13.27	< 0.00	< 0.01
10	$P_m \sim V_{mag} + d + C + Fr + T + TU$	8	7	12.61	**< 0.01**	150.92	15.13	0.84	< 0.01
11	$P_m \sim C + T$	4	11	0.31	0.74	152.36	16.57	-0.12	< 0.01
				Backtracking					
1	$P_b \sim T$	3	10	11.64	**< 0.01**	112.12	0.00	0.49	0.38
2	$P_b \sim T + TU$	4	9	9.78	**< 0.01**	112.23	0.12	0.62	0.36
3	$P_b \sim C + T$	4	9	6.13	**0.02**	115.78	3.66	0.48	0.06
4	$P_b \sim Fr$	3	10	5.82	**0.04**	115.87	3.76	0.30	0.06
5	$P_b \sim V_{mag}$	3	10	5.52	**0.04**	116.10	3.99	0.29	0.05
6	$P_b \sim Con$	3	10	4.50	0.06	116.92	4.81	0.24	0.03
7	$P_b \sim TU$	3	10	4.10	0.07	117.26	5.14	0.22	0.03
8	$P_b \sim C + T + TU$	5	8	6.00	**0.02**	118.23	6.12	0.58	0.02
9	$P_b \sim d$	3	10	1.40	0.27	119.81	7.70	0.03	0.01
10	$P_b \sim V_{mag} + d + C + Fr$	6	7	4.78	**0.04**	125.37	13.25	0.58	< 0.01
11	$P_b \sim V_{mag} + d + C + Fr + T + TU$	8	5	3.98	0.08	155.32	43.21	0.62	< 0.01

K = number of parameters, d.f. = degrees of freedom, AICc = Akaike information criterion corrected for small sample sizes, ΔAICc = increase in AICc score from the top-ranked model, Adjusted r^2 is the coefficient of determination adjusted for all predictors, w is the relative weight of support for each model among the candidate set. P_x = percent of behavior among detections (m = milling, b = backtracking), V_{mag} = velocity magnitude, d = depth, C = conveyance, Fr = Froude number, T = temperature, TU = turbidity. P values in bold indicate statistical significance at 95% confidence.

Table 1.9. Model parameter estimates for statistically significant candidate models predicting percent milling and backtracking behaviors.

AICc Rank	Model	Intercept (α)	β_{Vmag}	β_d	β_C	β_{FR}	β_T	β_{TU}
1/11	$P_m = \beta_{Vmag}V_{mag} + \beta_d d + \beta_C C + \beta_{Fr}Fr + \alpha$	-234.44	1732.46	180.20	-693.47	-2467.93		
2/11	$P_m = \beta_{TU}TU + \alpha$	140.62						-23.23
3/11	$P_m = \beta_T T + \beta_{TU}TU + \alpha$	243.26					-6.76	-23.84
7/11	$P_m = \beta_C C + \beta_T T + \beta_{TU}TU + \alpha$	137.67			-14.19		1.60	-25.40
10/11	$P_m = \beta_{Vmag}V_{mag} + \beta_d d + \beta_C C + \beta_{Fr}Fr + \beta_T T + \beta_{TU}TU + \alpha$	80.58	630.14	129.76	-389.16	-44.56	-2.55	-11.90
1/11	$P_b = \beta_T T + \alpha$	346.60					-20.87	
2/11	$P_b = \beta_T T + \beta_{TU}TU + \alpha$	345.21					-18.35	-9.68
3/11	$P_b = \beta_C C + \beta_T T + \alpha$	305.03			-12.43		-17.35	
4/11	$P_b = \beta_{Fr}Fr + \alpha$	64.46				-233.58		
5/11	$P_b = \beta_{Vmag}V_{mag} + \alpha$	65.62	-56.42					
8/11	$P_b = \beta_C C + \beta_T T + \beta_{TU}TU + \alpha$	369.77			7.43		-19.92	-11.70
10/11	$P_b = \beta_{Vmag}V_{mag} + \beta_d d + \beta_C C + \beta_{Fr}Fr + \alpha$	16.07	4322.14	28.83	-744.25	-12729.9		

AICc Rank = #/Total, P_x = percent of behavior among detections (m = milling, b = backtracking), V_{mag} = velocity magnitude, d = depth, C = conveyance, Fr = Froude number, T = temperature, TU = turbidity.
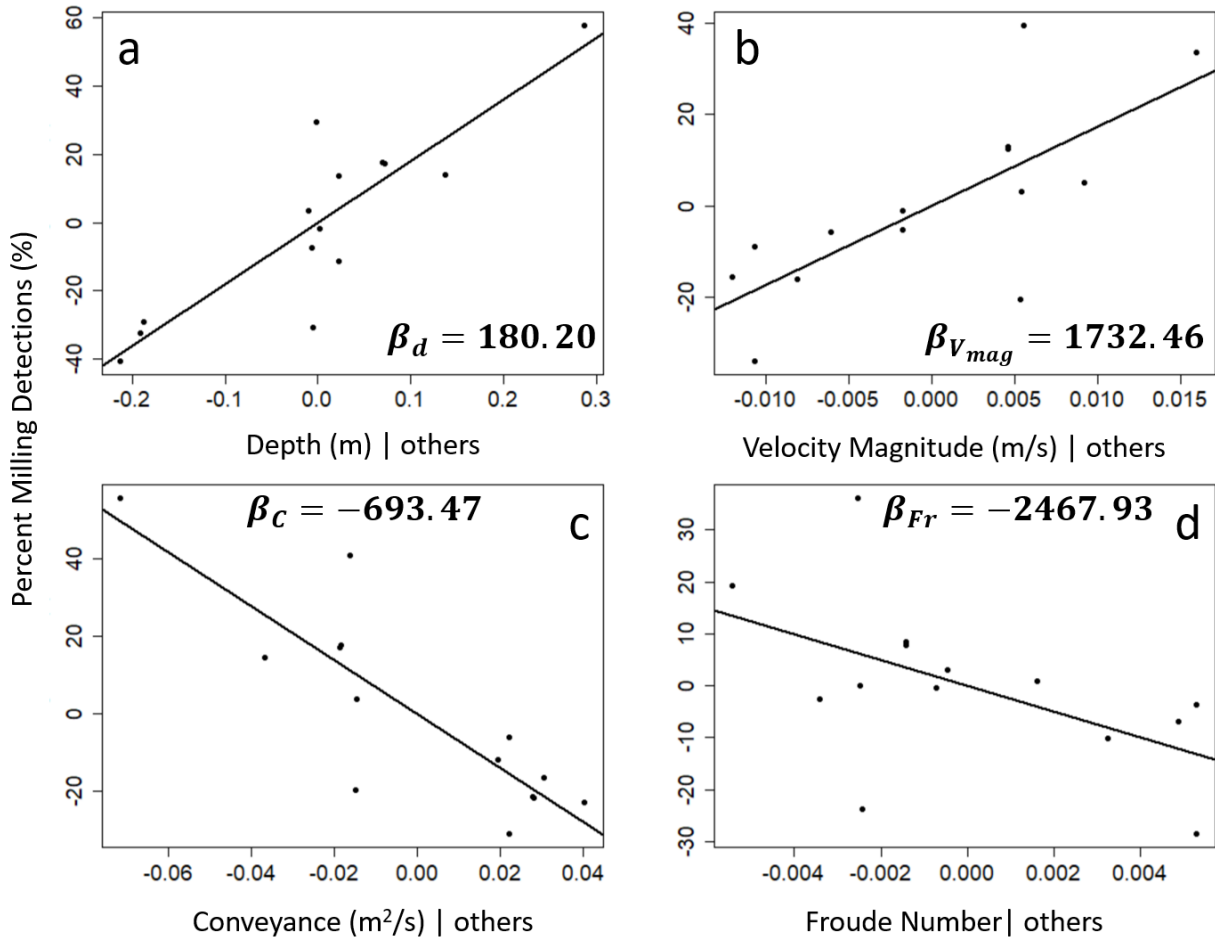
Figure 1.11. Added variable plots describing the relationship between each indicated predictive model parameter (given the magnitude of all others) with percent milling behavior as the response variable. Panels a through d are regression coefficients for depth, velocity magnitude, conveyance, and Froude number, respectively. Parameters belong to the highest AICc-ranked regression model for predicting percent milling behavior. Trendlines are fit to the points in each plot. The degree to which each trendline departs from horizontal (which would mean the parameter was equal to zero) indicates its relative predictive strength in the model.

Finally, we fail to reject hypotheses H_{4a}, H_{4d}, H_{4e}, and H_{4g} as velocity magnitude, Froude number, temperature, and four combinations of predictors yielded statistically significant models for predicting percent backtracking behavior (Table 1.8 Table 1.9). Temperature as a single predictor was found to be the best performing model and had a p value < 0.01, adjusted r^2 of 0.49, and w of 0.38. However, the combination of conveyance and temperature had a relatively low ΔAICc of 3.66, a p value of 0.02, and an r^2 value = 0.48. The two highest ranked models in this list (temperature and temperature/turbidity) dominated the weight of evidence, so the model with conveyance and temperature only received a *w* value of 0.06. We are highlighting this model because of our interest in hydraulic variables as drivers of migratory

habitat selection and behavior. An AVP for the conveyance/temperature model is shown in Figure 1.12. Figure 1. 13 includes a graphical simulation of how percent backtracking behavior decreases with increasing conveyance, with significant differences in value ranges as a function of temperature.
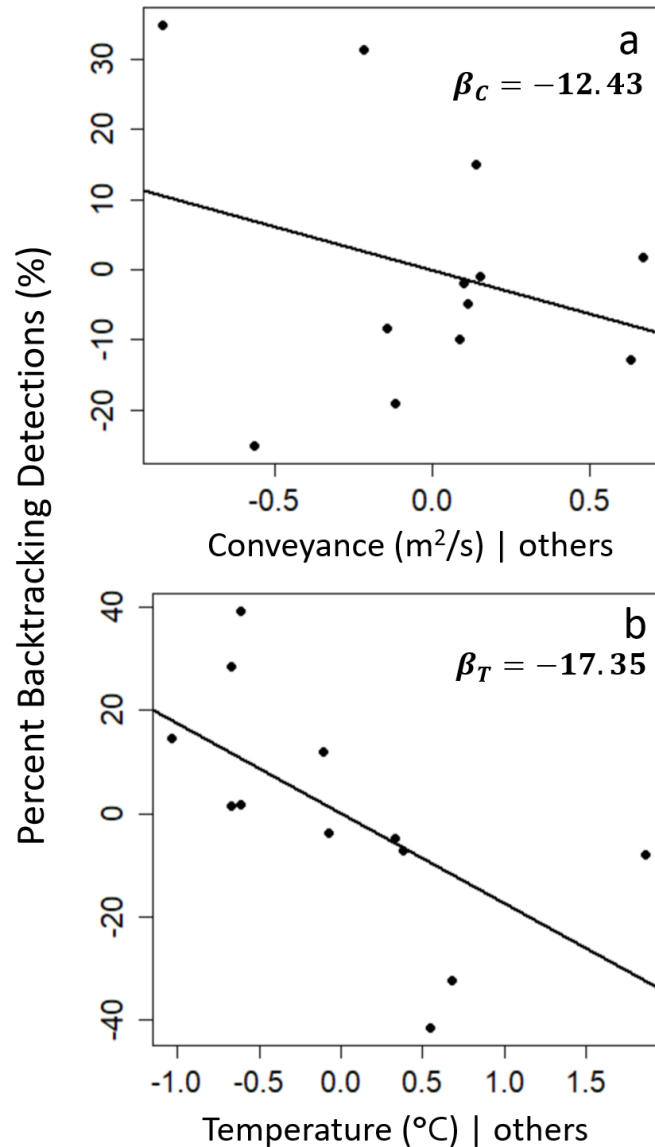
Figure 1.12. Added variable plots describing the relationship between each indicated predictive model parameter (given the magnitude of all others) with percent backtracking behavior as the response variable. Panels a and b are regression coefficients for conveyance and temperature, respectively. Parameters belong to the third highest AICc-ranked regression model for predicting percent backtracking behavior. Trendlines are fit to the points in each plot. The degree to which each trendline departs from horizontal (which would mean the parameter was equal to zero) indicates its relative predictive strength in the model.
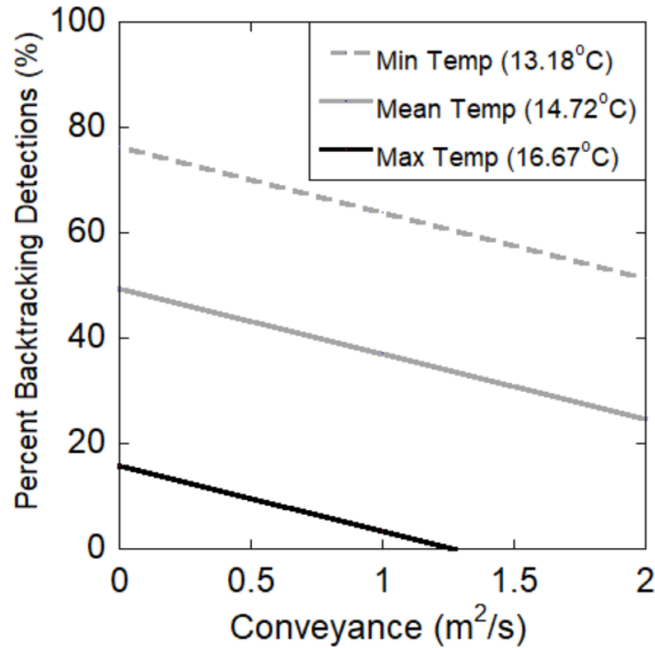
Figure 1. 13. Percent backtracking behavior is predicted using the third highest AICc-ranked model which is fit using a linear regression and includes conveyance and temperature as predictors. The plot includes continuous predictions of percent backtracking as a function of conveyance using the maximum, minimum, and mean values for temperature from our observed data.

2.5 Discussion

2.5.1 Habitat selection

The large difference in adult Chinook salmon detections between September and October sampling periods corresponds with the considerable difference in combined discharge and associated hydraulic changes at the confluence between September and October (237 m^3/s and 85 m^3/s, respectively). This result is consistent with the general understanding of the important role that mainstem river discharge magnitude and timing play in upstream migration of Chinook salmon, particularly in the California Central Valley (Hasler et al., 2014). However, this study investigated the role of microhabitat variables driven by discharge and acting as migratory navigation cues. Simply pointing to discharge magnitude as a navigation cue does not mechanistically link migratory behavioral responses. The comparison of depth and velocity magnitude conditions selected vs. those available throughout the study area at the time of observation showed

statistically significant differences in mean values, indicating that non-random microhabitat selection did occur.

It is particularly interesting that even though fish were attracted to higher discharge, they were attracted to lower velocity. One interpretation is that the fish may have been observed in holding locations, essentially pausing on their journey for any one of several reasons, including some awareness of the confluence itself. Another interpretation is that the direct hydraulic variable driving migratory behavior is conveyance, as our regression analysis suggests. This variable includes both depth and velocity components, meaning that neither can be analyzed independently of the other in this context. For example, our results suggest that greater swim depths are preferred, as long as there is adequate velocity present as well for rheotactic orientation.

Results indicate that localized conveyance is likely the missing intermediate variable translating channel-wide discharge into local hydraulics that fish experience and thus is an important driver of habitat selection, which can help explain some of the patterns of detection seen in Table 1.2. Overall, the Feather zone experienced the most detections. From a hydraulics perspective, this can be attributed to the greatest combined values of depth and velocity to yield high conveyance throughout that zone. Furthermore, the deep sites experienced the most overall detections and even though they did not all experience high velocities (Figure 1.4), localized cross-sectional area resulted in higher conveyance values. Conveyance was included in our best performing regression model for predicting detection rate and was ranked second-best as a singular predictive variable. This finding provides compelling evidence that conveyance plays a critical role in instantaneous micro-scale habitat selection during adult upstream migration in Chinook salmon. However, it does not completely dictate microhabitat selection among individuals.

Temperature and turbidity were also included as predictors and as mentioned in our study design, these micro-scale attributes cannot be disentangled from acting as indicators of natal source water and homing fidelity in our observations. Therefore, it is likely that homing occurs in conjunction with responses to

hydraulic flow features. In some cases, hydraulics may significantly influence navigational cues in migration as previously observed in this particular system (YARMT 2013).

Upstream migration by adult salmon involves constant compromise between bioenergetic cost of movement and fidelity to navigational cues, one of which is rheotaxis. Olfactory cues aside, an individual may choose the least energetically costly path through a channel network (deep, slow-moving areas), but they may lack a velocity field with sufficient magnitude and direction necessary to facilitate sufficient rheotactic orientation (Coombs et al., 2020). Likewise, choosing to occupy shallow, fast-moving areas is energetically costly and may result in exposure to turbulent flow structures of the same size as an individual fish shed by flow interacting with local features, such as large substrate particles, deposited wood, bedforms, and man-made structures (Harvey and Clifford, 2009). The avoidance of turbulent eddies of the same size as an individual fish has been documented in fishway studies (Silva et al., 2012) and such eddies may be more common in fast, shallow areas. Avoidance of turbulence may be due to energetic constraint rather than interference with rheotaxis, as turbulence has been shown to negatively affect fish swim speed and increase energetic cost (Enders et al., 2003; Lupandin, 2005).

The results of hand-held temperature and turbidity surveys (Figure 1.6) illustrate overall thermal and optical conditions of the two rivers during each DIDSON deployment period. In both periods, the LYR tended to be clearer than the LFR and the difference persisted throughout the study area with minimal mixing occurring before the downstream boundary (lateral differences at the downstream-most sampling stations in September and October of approximately 1.5 NTU and 1 NTU, respectively). It is unlikely that the range of turbidity values observed throughout this study were great enough to affect migratory behavior alone (Bjornn and Reiser, 1991). Although we found turbidity to be a significant predictor of habitat selection, there are likely other covariates at play that act as more important micro-scale navigational cues. Surface temperature differences between the two rivers changed dramatically between sampling periods. In September, the LFR was cooler and a dramatic lateral difference in temperature at the confluence junction can be seen before the LFR begins to thermally influence the east side of the channel toward the downstream

boundary. This differential in temperature may have played a role in the differences in reach-scale habitat selection during this period (Table 1.2), deterring Feather-origin fish from entering the LYR (consistent with the findings of thermal influence on migratory routing in this system by the YARMT). In the October period, the thermal condition switched; the LYR was cooler than the LFR and minimal mixing appeared to occur within the study area. The increase of temperature in the LFR is likely a result of the decrease in discharge combined with warm water input upstream of the study area at the Thermalito Afterbay outlet. Rates of detection changed very little among the three zones in the October period (Table 1.2), indicating that a thermal barrier at the confluence may potentially deter Feather-origin fish from entering the LYR.

2.5.2   Swimming behavior

Comparisons of swimming behavior type by sampling period, zone, and site type all show most detections to be exhibiting directed movement with 135 detections overall (Table 1.2). Milling and backtracking behavior occurred to a much lesser extent with 39 and 54 detections, respectively. It should be noted that these behaviors were not tracked through space beyond the DIDSON's field of view, so they cannot be used to characterize longitudinal movements within the study area. However, they do provide some indication of relative movement among detections. Because most individuals selected the LFR, we expected the majority of directed movement to occur in that zone. Our regression analysis did not provide an adequate model for predicting directed movement, suggesting that although salmon appear to have preferences for migratory microhabitats, upstream movement may occur in a wide variety of hydraulic, thermal, and optical conditions.

However, we did identify predictors for milling and backtracking behavior. This is more useful from a management perspective because it can be assumed that the majority of fish will be progressing upstream, but it may be possible to strategically minimize conditions that deter upstream movement via top-down controls on localized hydraulics such as discharge magnitude and ratio at a confluence. Our analysis suggests that milling occurs in response to localized hydraulics whereas backtracking may occur partially

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in response to hydraulics but is also influenced by temperature and turbidity where the presence or absence of olfactory homing cues may be at play. Although both our microhabitat selection and behavioral results show conveyance as the best hydraulic predictor variable for migratory habitat selection and movement, Moir et al. (2002) suggests that Froude number may be a better indicator for assessing salmonid habitat suitability for multiple body lengths due to its flexibility and scale-independent nature as a dimensionless value. In the absence of a clear biological mechanism for behavioral response to either cue, it may be useful to analyze both variables, depending on the applied research or management context.

2.5.3 Scientific and management implications

We see patterns in preference for specific fine-scale hydraulic conditions along the migratory pathway and indications that hydraulics are a partial driver of migratory swimming behavior. Discharge magnitude has traditionally been used as a proxy for the timing of migration initiation and upstream movement (Hasler et al., 2014; Quinn, 2018; Rand et al., 2006) and recent work shows that there may also be complex social interactions that drive upstream movement as well (Berdahl et al., 2017, 2016). However, fine details of upstream movement cannot be inferred from these large-scale phenomena. In many regions, flows are regulated, and flow schedules are carefully crafted annually to accommodate competing social, economic, and environmental demands. How flows translate into local hydraulics cannot be inferred but necessitates an assessment of the sub-reach-scale topographic regime, especially at the complex, vital locations that river confluences present to migratory fish. Understanding fine-scale patterns of migratory movement of adult salmon at confluences may be essential to their long-term conservation and survival by providing tools to minimize high rates of straying in imperiled populations occurring in managed river networks.

One reason to be optimistic about the future of river management for salmon is that we have witnessed major technological advancements in recent decades that allow for wholesale characterization and assessment of riverine habitats. LiDAR and multibeam sonar are examples of survey technology that allow for gathering highly detailed topographies as well as information on sediment composition and vegetation

cover. Computational fluid dynamics modeling has advanced significantly with access to ever-growing computing power, allowing for detailed and accurate simulations of open-channel hydraulics in a variety of aquatic settings. The field of ecohydraulics has already adopted these technologies to assess habitat availability and function for specific life-cycle stages of anadromous salmonids (Kammel et al., 2016; Moniz et al., 2019; Wheaton et al., 2018). There is little existing literature on coupling hydraulic and thermal attributes at a microhabitat scale and more work is needed before these mechanisms can be modeled concurrently (Ouellet et al., 2020).

2.6   Acknowledgements

2.7   References

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3   *Chapter 2: Hydraulic microhabitats at a regulated river confluence influence Chinook salmon migratory routing during drought*

3.1   Abstract

Upstream adult migration of Pacific salmon (*Oncorhynchus spp.*) from estuary to spawning grounds is understudied but is critical to population sustainability, especially during increasingly extreme droughts which may degrade habitat elements essential for migratory cuing. In regulated systems, river network confluences pose significant navigational challenges due to complex operational flow release criteria. Differing discharge magnitudes and ratios between tributaries may cause divergent confluence hydraulics and hydraulic microhabitat selectivity, influencing migratory routing. This study asks: (1) Do magnitudes of discharge in each confluence tributary (and resulting combined discharge) influence availability of preferred hydraulic microhabitats in one river versus the other? (2) Does the ratio of discharge magnitude influence availability of preferred hydraulic microhabitats in one river versus the other? We used data collected from California Central Valley fall-run Chinook salmon (*O. tshawytscha*) at the confluence of the Feather and Yuba Rivers as a model system for answering these questions. We combined observations of migratory behavior from dual-frequency identification sonars; observed microscale hydraulics corresponding to behaviors; spatially explicit, meter-resolution hydrodynamic modeling; and machine learning to generate a hydraulic microhabitat selectivity index and to simulate upstream migratory pathways for nine pertinent discharge scenarios and four discharge ratios among those. Statistically significant ($p < 0.01$) differences in preferred hydraulic habitat encountered at the confluence were found among both discharge scenarios and ratios. Discharge magnitude and ratio act as controls on distribution of preferred hydraulic microhabitats, and under certain conditions relevant to drought operations in this system, they could potentially impact migratory routing and propensity of straying.

3.2 Introduction

3.2.1 Background

3.2.1.1 *Climate change and drought*

Climate change poses significant threats to aquatic ecosystems due to extensively modified natural flow and thermal regimes to which organisms have adapted in recent millennia. In particular, increased duration and magnitude of drought conditions has changed the ecology of many landscapes across the world (Trenberth, 2011). As noted by Cook et al. (2018), drought signals manifest as a complex, interconnected web of environmental variation and linking climatic forcing to droughts can be a complicated task where landscape attributes of specific geographic regions must be accounted for (e.g., topography, snowpack, groundwater residence time and aquifer capacity, vegetation, biological communities, human land uses, and human demands on surface and subsurface water resources). Pacific salmon species occupy latitudes ranging from Central California (37°N) to coastal streams in northern Alaska, and Russia (70°N), all of which are subject to some degree of drought-related impacts in the 21st century according to widely-accepted statistical projections (Caretta et al., 2022; Dai et al., 2018; Xu et al., 2019).

Today, many Pacific salmon populations also inhabit catchments that have experienced varying degrees of fragmentation and hydrologic alteration due to water storage and conveyance infrastructure with the added complication that water resources are managed for a variety of human uses (Acreman et al., 2009; Magilligan and Nislow, 2005). Management criteria for reservoir operations typically include provisions for drought events that attempt to sustain systems and processes that depend on certain minimum flows, including fish species which may also receive additional regulatory protection under the U.S. federal Endangered Species Act, Canadian Species At Risk Act, the Japanese River Act of 1964, or other state or local conservation laws (Di Baldassarre et al., 2017; Good et al., 2007; Irvine et al., 2005; Suzuki, 2006). Minimum baseflows and drought operation criteria are often established for a regulated river on an individual river basis based on its historical hydrograph and anticipated seasonal needs for water diversion.

In cases where a drought-prone system must be managed for multiple species and populations with individual legal protections, a regulatory action may be taken by government officials to establish highly specific flow criteria that attempts to balance multi-species needs within a single catchment such as the Operational Criteria and Planning (OCAP) Biological Opinion for the California Central Valley produced by the National Marine Fisheries Service under Section 7 of the federal Endangered Species Act (NMFS 2009).

3.2.1.2   *Emergence of eflows and ecohydraulic methods*

Development of species- and even life stage-specific environmental flow (i.e., eflow) criteria can be highly contentious, and many regulatory actions to secure allocations of stored water for such prescribed flows have been met with stakeholder resistance and legal action (Fisher et al., 1991; Horne et al., 2017; Lackey, 2017; Tharme, 2003). Despite such external pressures in a growing number of countries, fishery managers must generate environmental flow schedules using the best available science to achieve habitat conditions most beneficial for the target species or life stage in question. Targets for habitat quality and function must then fit into a broader constellation of conservation goals such as enhancing population productivity or abundance metrics, conserving population structure, or addressing bottlenecks for mortality at vulnerable lifecycle stages.

In the case of prescribed flows for salmon habitat, weighted usable area (the output of the instream flow model PHABSIM) is a metric that has been commonly used in recent decades as a key objective input to generate flow schedules and instream flow criteria to achieve goals for habitat functionality based on channel hydraulics (Holm et al., 2001; Shirvell, 1989). Soon after its inception (Bovee, 1982, 1978), it was criticized by Mathur et al. (1985) as having built-in assumptions about specific physical habitat parameters being valid predictors of either fish habitat preference or optimal habitat value related to management goals. As discussed by Railsback (2016), PHABSIM in its original form is becoming obsolete in lieu of more sophisticated spatially explicit habitat modelling techniques. However, Stalnaker et al. (2017) contend that

it can still be an informative tool as part of a broader eflow assessment approach (as it has been in the instream flow incremental methodology framework). The debate continues.

Accessibility to two-dimensional (2D) hydrodynamic modeling software and recent advancements in the field of ecohydraulics have enhanced the potential for developing salmon habitat models that aid in drought planning and development of environmental flow criteria by making predictions about a variety of important individual ecological functions. Nahorniak et al. (2018) presented an automated approach for running large batches of 2D hydrodynamic models using modern computing techniques (including cloud computing resources) to efficiently generate precise and accurate 2D models to support salmon habitat restoration via channel modification and newly scalable restoration programs. Several ecohydraulic tools and frameworks then build on top of 2D modeling. For example, Benjankar et al. (2018) developed an integrated ecohydraulic modeling framework combining models of catchment hydrology, existing salmonid habitat models, and an analysis of channel hydraulics to assess whether strategic dam operations might be able to mitigate climate change impacts to riverine fishes in the South Fork Boise River (Idaho, USA). Schwindt et al. (2019) developed River Architect, an ecohydraulics-based modeling framework that includes fish stranding risk analysis, cottonwood seedling recruitment potential prediction, microhabitat mapping and seasonal abundance quantification, lifespan prediction for several river restoration techniques, and river project financial cost estimation.

3.2.1.3 *Importance of confluences*

Confluences (where a tributary channel meets a mainstem channel, forming a junction) represent complex hydraulic and geomorphic features within fluvial channel networks. Significant improvements have been made in understanding the physical and biological implications of these features since the mid-20th century (Gualtieri et al., 2017; Miller, 1958; Richards, 1980). As key features of migratory habitat for riverine fishes, the physical processes at play ultimately drive habitat functionality in space and time. For example, discharge ratio, upstream bed slopes, and channel junction angle are important drivers of bed morphology in the immediate up and downstream areas of confluences (Best, 1988, 1986; Boyer et al., 2006; Penna et

al., 2018). Bed morphology at confluences then directly affects mixing processes with implications for fish migration cuing (Constantinescu et al., 2016; Gaudet and Roy, 1995). A recent review by Yuan et al. (2022) highlights that confluences also represent longitudinal hotspots for ecological change in a river network with adjoining rivers potentially diverging in thermal regime, suspended sediment load, bed load, nutrient concentrations, water chemistry, and organic matter content.

Major rivers are managed for competing interests under complex legal statutes that often have layered local, state, and federal regulatory oversight (Bernazzani et al., 2012; Hillman, 2009; Lorenz et al., 2001; Moore et al., 2001; Zhang et al., 2018). As a result, a confluence of two major rivers may experience very different discharges from each river during low flow periods. A Chinook salmon (*Oncorhynchus tshawytscha*) escapement study indicated that discharge magnitude and ratio between two major rivers can have a strong influence on migratory routing and can lead to instances of high straying rates (YARMT 2013). In such cases, it is important to recognize that while discharge magnitude has been used to analyze reach- and catchment-scale patterns of adult salmon migration (Dahl et al., 2004; Hasler et al., 2014; Jager and Rose, 2003), it cannot be used on its own to explain the abiotic-biotic mechanism linking complex migratory responses to confluence physico-chemical conditions.

3.2.1.4   Prediction of upstream migration

Compared to other salmon lifecycle stages, little information exists on hydraulic habitat preference for migrating adults, though it is likely an important factor in regions where olfactory imprinting is interrupted or incomplete. Several habitat suitability curves (HSCs) for migrating adult salmon have been generated over the years with varying survey methods and inconsistent results. Radio telemetry surveys were done on the Kenai River in Alaska for late summer-run Chinook salmon (Burger et al. 1983). Snorkel surveys for spring-run Chinook salmon were used in the Wind River, a tributary to the Columbia River in Washington State (Wampler 1986) and for fall-run Chinook salmon in the Stanislaus River, California (Aceituno 1990). The properties of these HSCs are detailed in Table 2.1. These studies indicate that non-random hydraulic microhabitat selection does occur in migrating adult salmon, and it stands to reason that micro-scale

hydraulic conditions at a confluence may partially influence migratory navigational choices. However, the added habitat complexity at a confluence along with differences in peak velocity and depth among existing HSCs for migrating adult Chinook salmon preclude their use in our study.

Table 2.1. Summary of habitat suitability criteria found in previous assessments for migrating adult Chinook salmon. Curve type refers to the method of reporting habitat suitability. "% utilization" refers to numbers of fish detections corresponding to binned microhabitat conditions for depth or velocity. "Preference" is computed using % utilization and corrects for the amount of each habitat bin class available in the survey area.

HSC Source	Burger et al. (1982)	Wampler (1986)	Aceituno (1990)
Location	Kenai River, AK	Wind River, WA	Stanislaus River, CA
Chinook Salmon Phenotype	Summer-run	Spring-run	Fall-run
Water Temperature Range During Sampling (°C)	4.4 - 13.9	10.0 - 17.8	not reported
Survey Method	Radio Telemetry	Snorkel	Snorkel
Peak Velocity (m/s)	0.8	1.1	0.4
Velocity Range Sampled (m/s)	0 - 1.7	0 - 1.7	0 - 1.5
Peak Depth (m)	2.3	4.5	0.6 - 1.1
Depth Range Sampled (m)	0 - 3.9	0.3 - 4.6	0 - 1.5
Curve type (% Utilization vs. Preference)	% Utilization	Preference	Preference

3.2.1.5   Study System

Migratory habitat for Chinook salmon in the California Central Valley is now largely confined to low-lying rivers, most of which experience regulated flow regimes to accommodate agricultural, municipal, and industrial water use throughout the year (Brown and Ford, 2002; Marchetti and Moyle, 2001). The upstream migratory corridor for spawning adult Chinook salmon typically includes the San Francisco Bay-Delta estuary, mainstem Sacramento or San Joaquin River, and one large tributary (Santos et al., 2014). Excessive channelization has occurred in many areas within the migratory corridor, as flood control infrastructure has been constructed and prevailing land use practices have inhibited natural flood regimes in larger Central Valley rivers (Mount, 1995). This has led to simplification of migratory habitat and losses of riparian canopy cover and instream wood (Gorman and Karr, 1978; Simon and Rinaldi, 2006). Additional stresses imposed on adult salmon migrating upstream in this region include recreational fishing, poaching,

hydroacoustic impacts from in-water construction, and elevated water temperatures (Campbell and Moyle, 1992; Stadler and Woodbury, 2009; Strange, 2010).

Central Valley rivers are highly managed through controlled releases of water from reservoirs on most major tributaries in the Sacramento and San Joaquin basins. Rivers typically experience steady and consistent hydrologic regimes that are highly altered relative to more episodic historical conditions (Brown and Bauer, 2009). Although the system functions in an altered state compared to historical conditions, efforts have been underway in recent decades to integrate environmental flow management into release schedules (Jager and Rose, 2003; Moyle et al., 1998).

In 2009, the National Marine Fisheries Service released its "Jeopardy" Biological Opinion under the federal Endangered Species Act on the "Operations, Criteria, and Plan" for the federal Central Valley Project and State Water Project (composing the majority of Central Valley surface water management and supply infrastructure, see NMFS 2009). The analysis found that a business-as-usual approach to managing surface water would lead to the extirpation of federally listed Sacramento River winter-run Chinook and the Central Valley spring-run Chinook salmon. As a result, state and federal water operators are now required to include "pulse attraction flows" in their operating schedules (i.e., elevated flows from spawning locations or hatchery facilities timed to deliver source water to initiate spawning migration in ocean-going adults). Historically, rain and snowmelt-driven flow pulses triggered spawning events naturally during the annual hydrologic cycle. It is uncertain what quantitative aspects of flow, considering magnitude, duration, timing, frequency, and rate of change, are required to constitute an ecologically effective "pulse" for adult salmon migration, especially in light of the multiple other factors impacting salmon behavior today compared to pre-European colonization and subsequent industrialization (Hasler et al., 2014). Despite efforts to manage the system to accommodate the salmonid lifecycle, enhanced regional drought caused by climatic change is now further complicating river management in California (He et al., 2021).

3.2.2 Study purpose and scientific questions

This study investigated the influence of micro-scale hydraulic conditions at a regulated river confluence on routing pathways of Chinook salmon migrating to spawning grounds or a natal hatchery facility. Baldes and Vincent (1969) define microhabitat scale as "the physical conditions immediately surrounding an animal at a given time and place". Herein, we focus on the effects of hydrologic conditions that may be encountered by California Central Valley fall-run Chinook salmon during a drought year where minimum base flows are maintained in large, regulated rivers that provide water for a variety of agricultural, municipal, and industrial stakeholders (Herbold et al., 2018). This study addressed two questions: (1) Do magnitudes of discharge in each river at a confluence (and resulting combined discharge) influence availability of preferred hydraulic microhabitats in one river versus the other? (2) Does the ratio of discharge magnitudes influence availability of preferred hydraulic microhabitats in one river versus the other? The experimental design concept is discussed further in section 2.2 and graphically depicted in Figure 2.1.
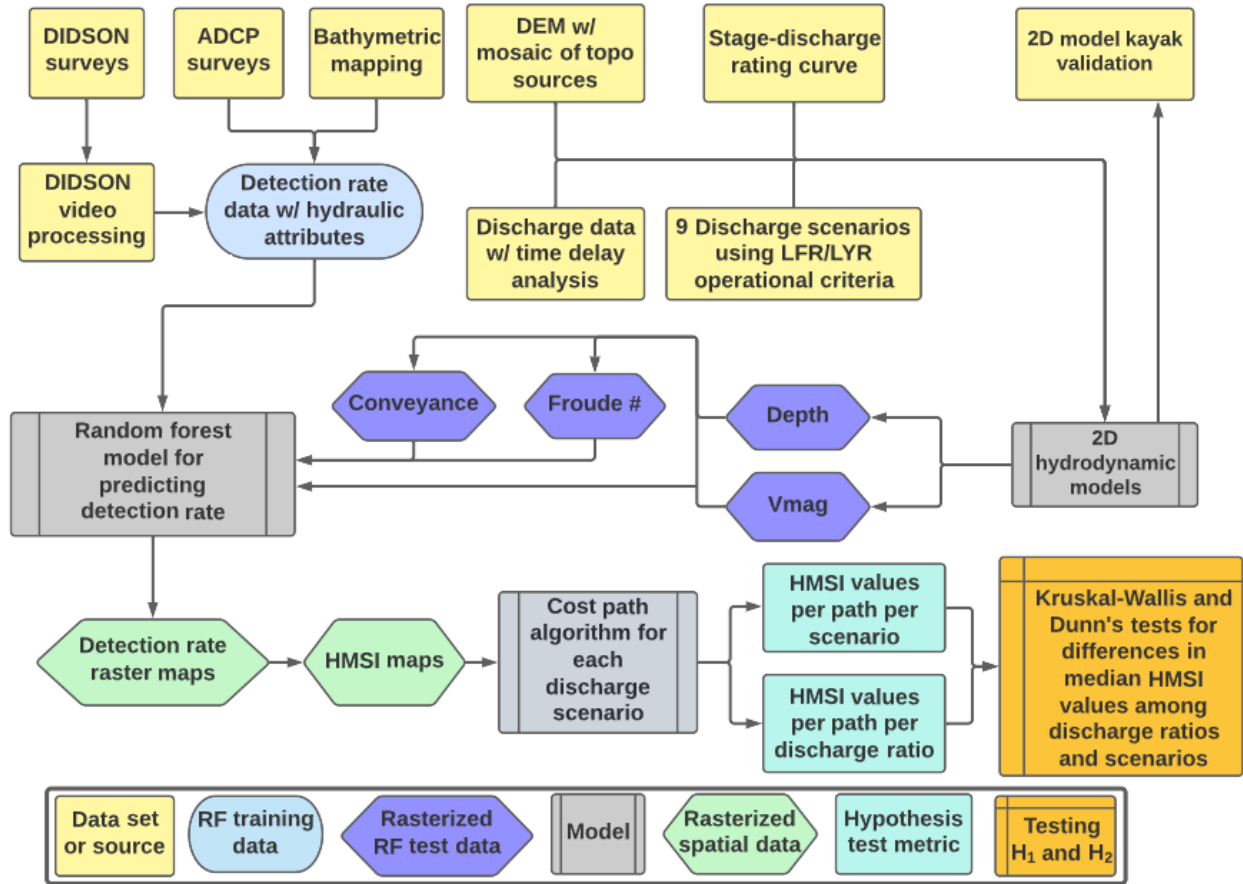
Figure 2.1. Conceptual flow chart describing our study design and methods.

3.2.3 Study area

This study occurs at the immediate confluence of the lower Feather River (LFR) and lower Yuba River (LYR), located in northeastern California in the northeastern portion of the California Central Valley (Figure 2.2). Specifically, the study area as well as the modeling domain includes approximately 1.42 km of the LFR and 0.85 km of the LYR upstream of the confluence and 1.13 km of the LFR downstream of the confluence (Figure 2.3). Environmental flows in these rivers are managed under different regulatory frameworks and operated somewhat independently of each other (though CA Central Valley water operations are coordinated by multiple interagency technical groups under the State Water Project and federal Central Valley Project, overseen by the U.S. Bureau of Reclamation and the CA Department of Water Resources, see Luis and Pasternack 2022).
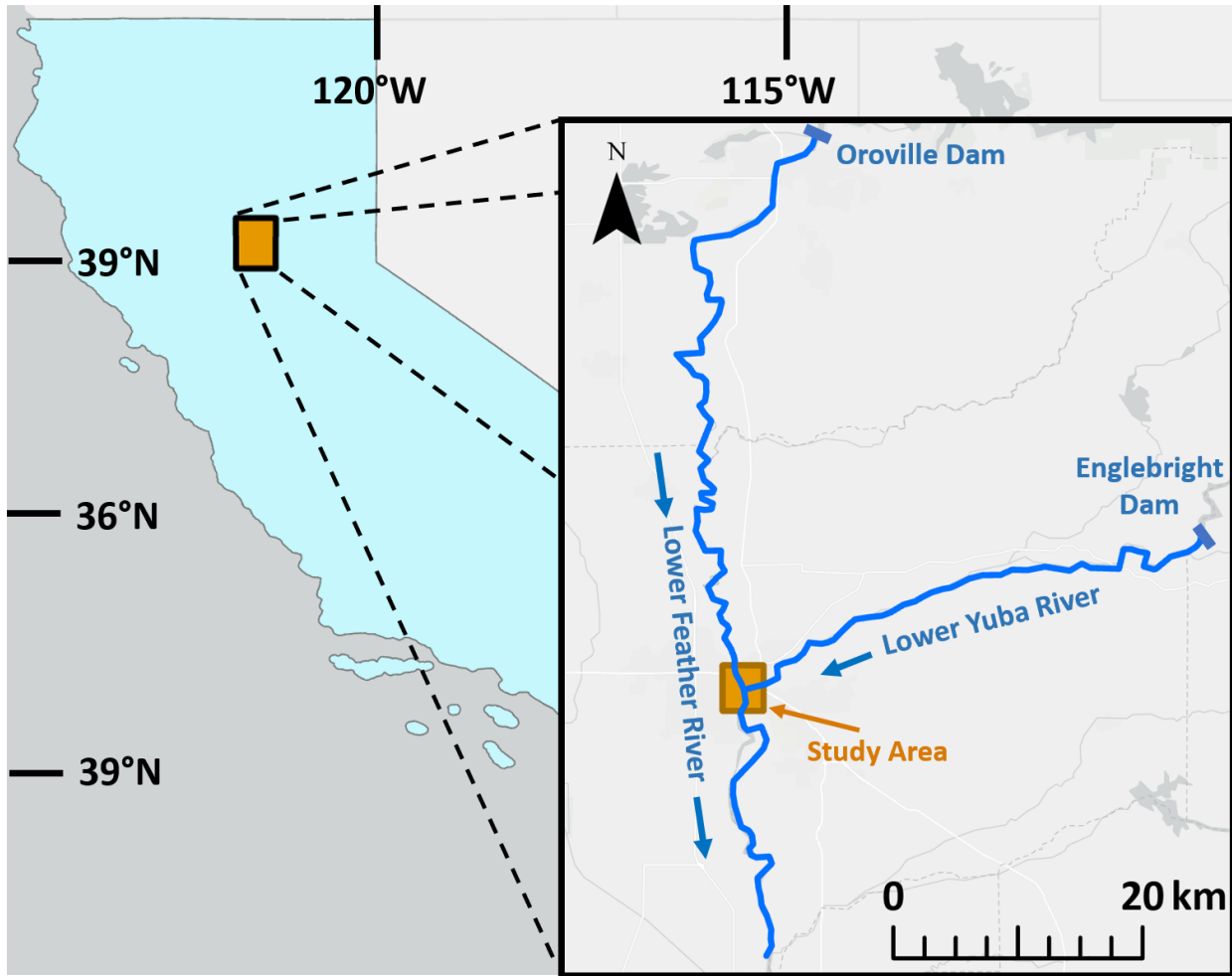
Figure 2.2. Location of the study area. The state of California is shaded in blue in the main panel. The inset identifies the lower Feather River, lower Yuba River, and the dams that create total fish passage barriers upstream of the study area. Blue arrows indicate flow direction. Base map image sources: ESRI, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS user community.

Figure 2.3. Map of the study area including the extent of the model domain, start and end points for the cost path analysis, kayak validation survey transects, and water surface elevation survey locations.

At the confluence of the LFR and LYR, the Feather River drainage area is 10,885 km^2. The LFR begins at the base of Oroville Dam, extending 117 km to its confluence with the Sacramento River. The CA Department of Water Resources filed a request with the Federal Energy Regulatory Commission to renew

the dam's operational license in 2005. This resulted in a request for a biological consultation under the federal Endangered Species Act with the National Marine Fisheries Service, which issued a Biological Opinion for the dam relicensing in 2016 (NMFS 2016). Following a spillway collapse in 2017 that resulted in mobilization and downstream aggradation of approximately 1 million tons of debris from Lake Oroville, license renewal is still pending (Nalin and Kotulla 2018, FERC 2022). The 2016 Biological Opinion set forth operational criteria that would minimize take of Endangered Species Act-listed species, including minimum baseflow criteria. Because this study focuses on the Central Valley fall-run Chinook phenotype, we selected LFR baseflow criteria for October through February where the bulk of migratory activity for this population occurs. During this period, in years where the LFR receives >55% of unimpaired runoff from the Feather catchment, the minimum baseflow for the river is 48.13m^3/s. In years where the LFR receives <55% of unimpaired runoff, the minimum baseflow is 33.97m^3/s.

The Yuba drainage area is 3480 km^2. The LYR begins at the base of Englebright Dam, extending 37.1 km to its confluence with the LFR. In 2008, the California State Water Resources Control Board approved a comprehensive interagency program that would protect and enhance approximately 39 km of aquatic and riparian habitat along the LYR. The program is called the Lower Yuba River Accord and is managed by the Yuba Accord River Management Team (YARMT 2013). Minimum baseflow criteria set forth for Yuba Water Agency operations to support native fish habitat is based on upstream reservoir storage volume in Englebright Lake. For the purposes of our study, we focus on criteria during October where minimum baseflows range from 14.16m^3/s in a very wet "schedule 1" year (annual reservoir storage of 7.08 x 10^8 m^3) to 9.91m^3/s in a critically dry "schedule 6" year (annual reservoir storage of 2.86 x 10^8 m^3). After findings by YARMT indicated rates of non-natal adult Chinook salmon straying into the LYR were likely influenced by flow conditions (72% of population escapement variation in the LYR were attributed to discharge magnitude and temperature), the National Marine Fisheries Service's California Central Valley salmonid recovery plan included a recovery action to "evaluate whether salmonid straying between the Feather and Yuba rivers can be minimized through flow management" (YARMT 2013, NMFS 2014).

3.2.4   Experimental design

Chapter 1 characterized microhabitat preference and micro-scale migratory swimming behavior responses to the following hydraulic variables: depth, velocity, conveyance, and Froude number. Chapter 2 utilizes a combination of 2D hydrodynamic models, a random forest machine learning algorithm, and a nearest neighbor cost path movement algorithm to simulate migratory movements past a confluence in response to these four hydraulic variables under a suite of drought-focused discharge scenarios (Figure 2.1). The nine discharge scenarios are shown in Table 2.2, including individual discharge magnitudes and citing the regulatory context from which they are derived. Scenarios 1-4 explore minimum baseflow conditions in the LFR and LYR under both wet and dry water year types. These first four scenarios result in three different ratios of discharge magnitude, shown in Table 2.2. Scenarios five and six use a 1:1 discharge ratio, using both wet and dry minimum baseflow criteria for the LFR (minimum LYR baseflows cannot legally occur in the LFR). Scenarios 7-9 use the same three discharge ratios found in scenarios 1-4, but instead use the dry-type LFR baseflow as the lower value (33.97 m^3/s).

Table 2.2. Discharge magnitudes and ratios for the nine modeled discharge scenarios used in this study. Regulatory context is cited for LFR and LYR baseflow criteria.

			LFR	
			<55% unimpaired runoff (NMFS 2016)	>55% unimpaired runoff (NMFS 2016)
			33.98 m^3/s	48.14 m^3/s
LYR	Schedule 6 (YARMT 2013)	9.91 m^3/s	Scenario 1 (3.4 : 1)	Scenario 2 (4.9 : 1)
	Schedule 1 (YARMT 2013)	14.16 m^3/s	Scenario 3 (2.4 : 1)	Scenario 4 (3.4 : 1)
	1:1 Ratio	33.98 m^3/s	Scenario 5 (1 : 1)	
		48.14 m^3/s		Scenario 6 (1 : 1)
	Inverse Ratios	81.55 m^3/s	Scenario 7 (1 : 2.4)	
		115.53 m^3/s	Scenario 8 (1 : 3.4)	
		166.50 m^3/s	Scenario 9 (1 : 4.9)	

2D hydrodynamic models were run for these nine scenarios and output raster maps for depth and velocity magnitude were produced; raster maps for conveyance and Froude number were subsequently derived from these. Using cell values in the four hydraulic raster maps for each scenario, a random forest model was used to generate spatially explicit predictions of detection rate; trained using the detection data from our previous study. We then scaled range of all detection rate values predicted among modeled scenarios to create a hydraulic microhabitat selectivity index (HMSI), scaled from zero to one. A cost path analysis was then performed to generate optimal upstream paths (seeking out the highest HMSI values along each path) from 10 laterally distributed starting positions across the downstream flow boundary, proceeding through the study area. This resulted in 10 cost paths for each of the nine scenarios.

Our study was designed to test two hypotheses. H_1: the magnitudes of discharge in each river at the confluence (and resulting combined discharge) influence median HMSI values encountered among the ten optimal migratory pathways per discharge scenario. H_2: the ratio of discharge magnitudes influences median HMSI values encountered among the ten optimal migratory pathways per discharge scenario. Null hypotheses state that there is no difference in median HMSI values encountered in cost paths among discharge scenarios or discharge ratios, respectively. The term "optimal" refers to the pathway derived by the cost path algorithm, seeking out the highest HMSI value in a nearest neighbor cell search. A Kruskal-Wallis test by ranks was used to test for statistically significant differences in median HMSI values among (1) nine discharge scenarios, and (2) ratios of discharge magnitude. Dunn's test for multiple comparisons was used to test for significant pairwise differences among the nine discharge scenarios and ratios of discharge magnitude to determine which scenario and ratio had the greatest effect among all examined. Not only were we interested in migratory routing at the confluence but also the relative strength of influence of hydraulic microhabitats, indicated by the HMSI variable.

3.2.5   Habitat selection data

In 2019, surveys of migratory habitat selection for adult fall-run Chinook salmon were conducted in the study area using dual-frequency identification sonars (DIDSON, see Chapter 1). The DIDSON is a multibeam imaging sonar that can be used to render acoustic returns in a video format, allowing for underwater observation of fish behavior (Belcher et al., 2002, 2001; Moursund et al., 2003). The 2019 surveys occurred during two, 4-day periods in September and October, capturing two different discharge ratios between the LFR and LYR (8.66 and 4.02, respectively), resulting in different spatial distributions of depths and velocities throughout the study area. These sampling periods were selected based on their correspondence with the California Central Valley fall-run Chinook salmon spawning migration as well as known operational criteria at upstream dams. In 2019, the Feather River Hatchery accounted for 43.6% of hatchery-origin Chinook collected in the Sacramento and San Joaquin basins during the fall-run migration window. The hatchery is located ~ 61.9 RKM upstream of the LFR-LYR confluence. That year, 27,103 Chinook salmon returned to the hatchery with 51,967 in-river returns, totaling 79,070 fish (CDFW 2022). Naturally spawning populations of spring- and fall-run Chinook persist in the LYR with no hatchery production in that river. In 2019, the LYR experienced 3,446 in-river returns (CDFW 2022).

Sampling occurred among 12 DIDSON deployment sites, capturing a representative range of depth and velocity conditions occurring throughout the site, both above and below the confluence. A multiple regression analysis investigated potential predictive variables with detection rate (# individuals/m^3/s) as a response variable. Four hydraulic variables are included as attributes of detection rate (depth, velocity magnitude, conveyance, and Froude number). Depths for each DIDSON deployment were derived from the 2019 bathy-topographic surveys described below. Velocity magnitudes were computed from acoustic doppler current profiler surveys conducted in conjunction with the DIDSON surveys. Conveyance is defined as follows:

$$\underline{C} = \underline{u} * \underline{d} \tag{1}$$

where u is mean velocity magnitude in m/s and d is mean depth in m. C results in units of m²/s and can be interpreted as the discharge per unit width of the wetted channel. It represents the flow that an individual fish experiences at a given point in the wetted channel and has been used in similar applications for assessing habitat suitability (Kammel et al., 2016; Moniz et al., 2019). Froude number is dimensionless and describes the ratio of inertial forces to gravitational forces in flow. It has also been used in other investigations into salmonid habitat suitability (Ayllón et al., 2009; Lamouroux and Souchon, 2002; Persinger et al., 2011):

$$\underline{Fr} = \frac{\underline{u}}{\sqrt{g*\underline{d}}} \tag{2}$$

where u is the mean velocity magnitude at each site in m/s, g is the gravitational acceleration constant in m/s², and d is the mean depth at each site in m.

In an Akaike information criteria analysis corrected for small sample sizes (AICc), conveyance (m²/s) was found to be the most important predictor among hydraulic variables tested (Cavanaugh and Neath, 2019; Portet, 2020). The best scoring model under AICc was a combination of conveyance, temperature, and turbidity as predictors with $p < 0.001$ (F test for significance) and a combined r^2 of 0.42. This study utilizes detection rate data and corresponding hydraulic predictors found in Chapter 1 to address the new scientific questions posed here.

3.2.6   Topo-bathymetric surveying and DEM construction

A digital elevation model (DEM) was created for the study area using several sources of topo-bathymetric point data (Figure A.A.7. Sources of elevation point data used to construct the final digital elevation model used in this study.). In 2019, bathymetric surveys were conducted using a boat mounted Hydrolite single beam echosounder (minimum depth of 0.3 m; depth accuracy of 1 cm; sampling frequency of 200 Hz; Seafloor Systems, Inc.) in sync with a Trimble R8 real-time kinematic GPS (horizontal and vertical accuracies of ~ 1 and 2 cm, respectively) receiving ground-based corrections on the fly at 1 Hz. Cross-

sectional transects were mapped approximately one channel width apart. At the locations of DIDSON data collection, multiple cross-sections were performed with very close longitudinal spacing to ensure the most detail where there was the most data. In addition, 8-12 longitudinal transects were surveyed down the length of the study area, because the primary topographic variability on the riverbed was longitudinal, not cross-sectional. Taken together, longitudinal and lateral surveys produced good coverage relative to the morphological structure present (see Figure A.A.7 in Appendix A). The large island at the center of the confluence contained some complex topography, and in January 2020, bare-earth topography was collected there using a Trimble R8 RTK GPS. To map riverbanks and islands just beyond the wetted area and water surface elevations needed in this study, a very small clip of pre-existing near-infrared and green LiDAR data was used, accounting for 8.7% of largest wetted area among hydraulic model outputs. It had been collected in 2017 by Yuba Water Agency and processed by our group to obtain a 0.9144 m (i.e., 3-ft) raster (Silva and Pasternack, 2018). Processed LiDAR points within the clip were incorporated into the DEM. Counting all points in the largest wetted area domain, the overall DEM point density was $4.55/3$ m^2.

All topo-bathymetric point data were processed to generate a DEM using ESRI ArcGIS software and the four iterative stages described by French and Clifford (2000): interpolation, visualization, editing, and augmentation. Erroneous bathy-topographic data points were identified and manually removed. Augmented points were also added manually to conserve known contours in the DEM and avoid any artifacts in the DEM that might occur from surface interpolation. A triangulated irregular network was generated from the final set of bed elevation points, and this was converted to a 3-m resolution raster based on overall point density and computational efficiency in the subsequent hydrodynamic modeling step. A smoothing algorithm using nearest neighbor cell averaging was applied to areas in the final DEM expected to be wetted in our discharge scenarios (bed elevations < 13.4 m) to further minimize surface interpolation artifacts.

3.2.7 2D hydrodynamic models and model validation

The 2D hydrodynamic model TUFLOW HPC$^{©}$ (Build 2018-03-AE; BMT Commercial Australia Pty Ltd) was used to simulate flow through the study area under the nine discharge scenarios shown in Table 2.2. TUFLOW HPC generates time- and depth-averaged gridded solutions of open channel hydraulics by solving the 2D shallow water fluid dynamics equations (mass and momentum consideration) that include fixed initial conditions such as discharge and water surface elevation, as well as fixed parameters of the model domain such as eddy viscosity coefficients and roughness coefficients (n). A gridded Cartesian computational mesh also provides better computational efficiency compared to an unstructured mesh, and is well-suited for this application due to the relatively simple channel geometry in our study area (Kim et al., 2014; Liu, 2014). Data outputs of the model include raster maps of depth, water surface elevation (WSE), velocity magnitude, and bed sheer stress. All output rasters were created at a 3-m^2 cell resolution.

The Smagorinsky formulation for eddy viscosity was used to account for momentum diffusion via turbulence in the model's momentum equations (BMT Commercial Australia Pty Ltd, 2018). This equation requires parameters for both a constant coefficient and an initial Smagorinsky coefficient that is then updated on a cell-by-cell basis; we used 0.4 and 0.5, respectively. TUFLOW HPC also requires several geospatial data layers as inputs to define boundary conditions for the model. The first is a topographic layer in which we used the final DEM raster described above. The second is a polygon shapefile that defines the Manning's n coefficient(s) being used for roughness. Because our study area is dominated by sand-sized substrate with gentle bedforms and intermittent bank vegetation, we used a uniform Manning's n value of 0.03 in all model runs in this study (Arcement and Schneider, 1989; Limerinos, 1970). Finally, cross-sectional polygons defining the upstream flow boundary (or boundaries in our case) were included with a corresponding discharge magnitude, as well as the downstream boundary with corresponding cross-sectional WSE. Figure A.A.8 in Appendix A shows the second order polynomial stage-discharge rating curve that was generated for our study area. WSEs were measured using a Trimble R8 RTK GPS near the downstream boundary of the study area under various discharge conditions from 2017 to 2019 to develop

this curve. The curve was then used to interpolate WSEs that correspond to our modeled discharge scenarios. These WSE survey locations are shown in Figure 2.3. Discharge data was collected from the California Department of Water Resources' Data Exchange Center (CDWR 2022).

This study used the 2D model water velocity validation method of Barker et al. (2018). This approach is a variation of large-scale particle image velocimetry (e.g., Dramais et al. 2011). While this approach yields less accurate individual point velocity values than point-scale velocity instruments (e.g., acoustic doppler, electromagnetic, and propellor velocimeters), Barker et al. (2018) found it significantly outperformed model validation with those traditional tools for four reasons: (i) ability to observe velocity in locations that cannot be waded (i.e., too fast and/or too deep) and locations where a boat cannot hold position; (ii) better representation of the full range of velocities present, (iii) ability to collect velocity direction data, and (iv) collection of so much more data that model performance metrics have far higher accuracy and statistical significance.

On a windless day, a kayaker kept their boat moving exactly at the speed and direction of the water around it using floating debris as a visual aid. A Trimble R8 RTK GPS tracked kayak position at 1 Hz. Distance travelled per second was computed as a surface velocity and this value was assigned to the midpoint position of each measurement. Based on visual site reconnaissance, it was possible to map what appeared to be the full range of velocity for enough area to test model performance thoroughly (Figure 2.3). In addition to obtaining observed surface velocities, the method of Barker et al. (2018) was used to find a depth-average velocity constant of 0.63 and apply this to the observed data to obtain field-estimated depth-average velocities. Both the observed surface values and the estimated depth-averaged values were compared to depth-average model velocities at the same coordinates for the same steady flow regime that occurred during the day of the kayak survey (Figure 2.4).

Model performance test metrics included coefficient of determination, bias (i.e., y-intercept distance from the origin), and mean signed and unsigned percent error (-4.11% and 28.27%, respectively; see Table A.B.1 in Appendix B for additional performance metrics). The coefficient of determination between observed

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surface and modeled depth-averaged velocities was 0.76, which is above the typical level of model performance in the published literature. Further analysis required finding and applying depth averaging correction factor of 0.63 to surface velocities observed by kayak to compare to depth-averaged velocities predicted by the model.
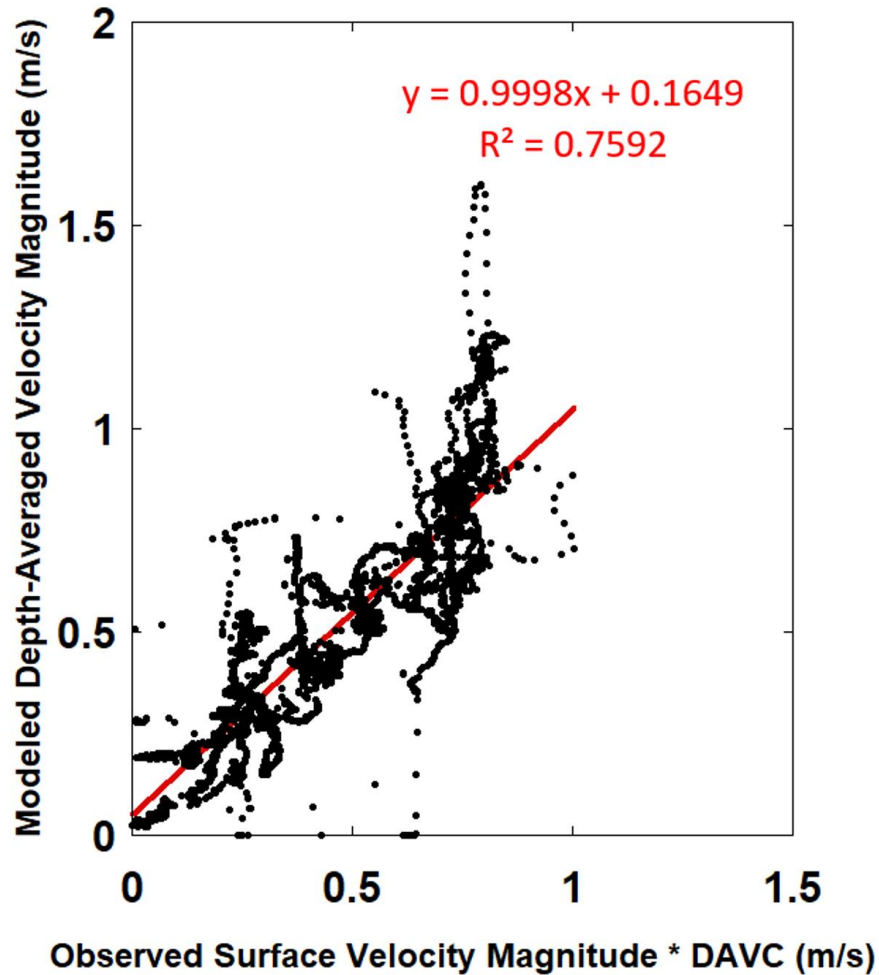
Figure 2.4. Results of the kayak velocity validation survey. This plot compares the observed surface velocities multiplied by the depth-averaged velocity constant (DAVC) to the modeled depth-averaged velocity magnitude values from the TUFLOW model outputs to assess model accuracy and performance.

3.2.8   Random forest model

We utilized a random forest model to produce spatially explicitly estimates of detection rate throughout the wetted portion of the study area. A random forest model is a commonly used non-parametric machine

learning algorithm that uses a classification and regression tree technique combined with a bootstrapping component to make robust predictions on a test data set using a training data set. Randomly selected values for a predictor variable (a fixed value for continuous data or a single class for categorical data) form nodes along a decision tree to make a prediction of a response variable value. Homogeneity is maximized within nodes and heterogeneity is maximized between nodes (Breiman, 2001; Cutler et al., 2007).

In a random forest process, a user defined number of trees are grown using random samples of the training data, with predictor values forming nodes along each tree. These trees are used to make predictions for out-of-bag (OOB) data (not included in the bootstrapped data set in each iteration). This feature of the random forest process eliminates the need for an additional cross-validation step to evaluate model performance (Cutler et al., 2007; Segal, 2004). Errors and accuracies of modeled predictions are averaged across the forest using these repeated OOB predictions. As a result, additional cross-validation to evaluate model performance is not necessary as this is a built-in feature of the random forest process (Cutler et al., 2007; Segal, 2004). The bootstrapping component is also useful in that it avoids issues of model overfitting, which can be a concern in other statistical modeling approaches (Williams, 2011).

The R package *randomForest* (Breiman, 2001; Liaw and Wiener, 2002; R Core Team, 2022) was used to produce spatially-explicit predictions of detection rate. Modeling was performed with this package for each of the nine discharge scenarios using the four hydraulic variables from the 2019 DIDSON sampling campaign (depth, velocity magnitude, conveyance, and Froude number) to train the model. We utilized an approach for model calibration similar to van Poorten et al. (2013). Parameters for node size (*nodesize*) and number of variables tested per node (*mtry*) were systematically tuned in preliminary trials to achieve the lowest value for residual mean squared error and holding the number of trees (*ntree*) at 250. To ensure stable predictions and stability of mean error values across the forest, the final model was run with 1000 trees. Final model parameters were: *nodesize* = 4, *mtry* = 1, *ntree* = 1000. Spatially explicit predictions of detection rate within the model domain were made using spatially explicit values for the four hydraulic

variables, derived from the 2D hydraulic model outputs for depth and velocity magnitude for each of the nine discharge scenarios.

3.2.9   Cost path analysis

The cost path algorithm in ESRI's ArcGIS Pro was used to simulate upstream migratory movement of adult Chinook salmon through the model domain. We created a hydraulic microhabitat selectivity index (HMSI) to describe degree of preference for a given cell in the domain. The HMSI is scaled from zero to one, using the highest (equal to 1) and lowest (equal to 0) predicted values of detection rate among the nine discharge scenarios via the random forest's predictive output maps. Spatially explicit detection rates were converted to HMSI values and HMSI maps were generated by creating triangulated irregular networks from TUFLOW grid points and converting those to $3m^2$ rasters. Because HMSI maps are derived from TUFLOW outputs, HMSI maps span the wetted area for each discharge scenario.

The cost path algorithm uses an iterative nearest neighbor search process given a user-specified starting location to progress through a raster by identifying the "lowest cost" adjacent cell repeatedly until the path reaches a user-defined end point. In this study, the expected path is defined as following the maximum HMSI value available. Because the ArcGIS tool seeks minimum values, we created a "lowest cost" variable by simply computing 1-HMSI.

In this study of upstream migration, the starting point is at the downstream end of the confluence domain. To avoid bias resulting from specifying a single starting point, we generated 10 starting positions spaced evenly, extending laterally across the downstream boundary of the model domain (Figure 2.3). Meanwhile, at the upstream end of the study area, a fair cost basis was needed to compare the two rivers even though they were mapped to different upstream limits. A fair cost basis requires having equivalent channel lengths in each river upstream of the confluence. To obtain equal upstream channel lengths, a center point at the confluence was approximated and used to generate equidistant upstream endpoints in LFR and LYR. Final distances for upstream and downstream of the confluence were 1080.2 and 1005.7 m, respectively.

Cost path parameters were set to produce single paths. Each of the nine discharge scenarios resulted in 10 paths, starting from each of the ten starting points (which all converged to one path after varying distances from their starting positions). The 30 final cost paths were each stationed in 10-m intervals and the HMSI values at each point was added to the attribute table of the station point file for analysis. Given that paths had different lengths, number of points per path among all paths varied between 698 and 742 points.

3.2.10   Data analysis

HMSI values along the 10 cost paths in each discharge scenario were analyzed to answer the two scientific questions (section 3.2.2) and stated hypotheses (section 3.2.4). To investigate whether discharge magnitude in each river is driving the availability of high value hydraulic microhabitats in one river versus the other, Kruskal-Wallis (KW) rank sum tests were used to test for differences in median HMSI values encountered in the 10 cost paths in each discharge scenario at 95% confidence (Kruskal and Wallis, 1952; Ostertagová et al., 2014). KW tests were also used to test median differences in HMSI values encountered in all cost paths associated with the four discharge ratios examined in this study (each of which included cost paths from two different discharge scenarios, or three different scenarios in the case of the 3.4:1 ratio, see Table 2.2). A Kolmogerov-Smirnov (KS) test for goodness of fit revealed that our data do not meet normality requirements for ANOVA, so the non-parametric KW test was used (Massey, 1951). KW and KS tests were performed in R using the base library (R Core Team, 2022).

A statistically significant KW test only indicates that one median value among samples is different from the others. In order to identify which discharge scenario and discharge magnitude ratio resulted in the greatest difference in median HMSI value from one or more of the others, Dunn's test for multiple comparisons using ranked sums was used to compute pairwise comparisons among all possible paired combinations of discharge scenarios and ratios of discharge magnitude (Dunn, 1964). Dunn's test allows for examination of differenced in ranked median HMSI values among discharge scenarios and ratios to determine which is most different (i.e., results in the highest value habitat along simulated migratory

pathways. Because the Dunn's test includes all possible pairwise comparisons among the nine discharge scenarios, there were 36 comparisons in all. The R package *rstatix* was used to perform the Dunn's tests and because the test involves multiple pairwise comparisons, adjusted p values were computed using the Bonferroni method (Dunn, 1961; Kassambara, 2022).

3.3 Results

3.3.1 Random forest model performance

With 17.43% variance explained (and mean sum of squared residuals equal to 0.0024), our random forest model contains some significant uncertainty arising from the ecological function under investigation and the focus on a small subset of contributing factors. Specifically, most habitat studies seek to predict usage of stationary ecological functions, such as holding, hiding from predators, and spawning. This study is characterizing fish migration, which is not only influenced by hydraulics around the fish, but also by other physico-chemical cues biological behaviors, such as predator-prey interactions. Further, among physical cues, this study only addressed hydraulic cues. The variable importance plot in Figure 2.5 shows that conveyance was the most important variable in the random forest process while depth was the least important. These results are still meaningful and indicate predictive capability of the model because conveyance, velocity magnitude, and Froude number all have a velocity component, and ranked higher than depth in predictive power. For any given habitat cell in the model domain, the velocity magnitude value relative to the depth value provides key information for predicting HMSI.
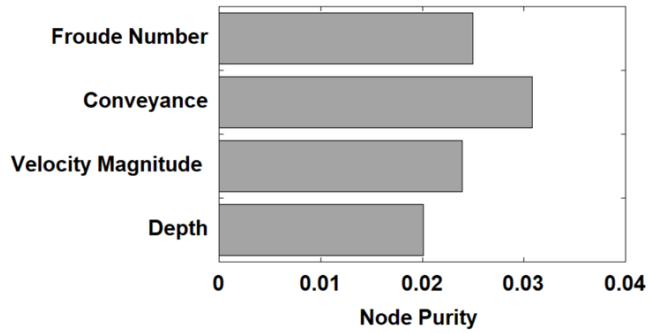
Figure 2.5. Variable importance plot produced by the random forest model ranking the relative strength of each hydraulic predictor in predicting Chinook salmon detection rate.

3.3.2   Cost path results

Migratory routing at the LFR/LYR confluence, driven by hydraulic selectivity, resulted in different rivers being chosen upstream of the confluence among the nine discharge scenarios (Figure 2.6). Remarkably, river selection was completely independent of where across the river a fish starts the journey through the study area. In scenarios 1-6, all migratory paths quickly converge. In scenarios 7-9, path convergence still occurs well before the confluence, but after a longer travel distance. This is due to the greater availability of high value habitat distributed laterally, downstream of the confluence near the starting positions. The LFR is chosen in scenarios 1-5 and the LYR is chosen in scenarios 6-9. The plot of HMSI values encountered along each cost path in Figure 2.7 shows that HMSI values upstream of the confluence tend to be higher in scenarios 6-9 than in scenarios 1-5. This is a direct result of the spatial distribution of HMSI values throughout the model domain under each condition, but further testing was needed to determine the relative effects of discharge versus discharge ratio.
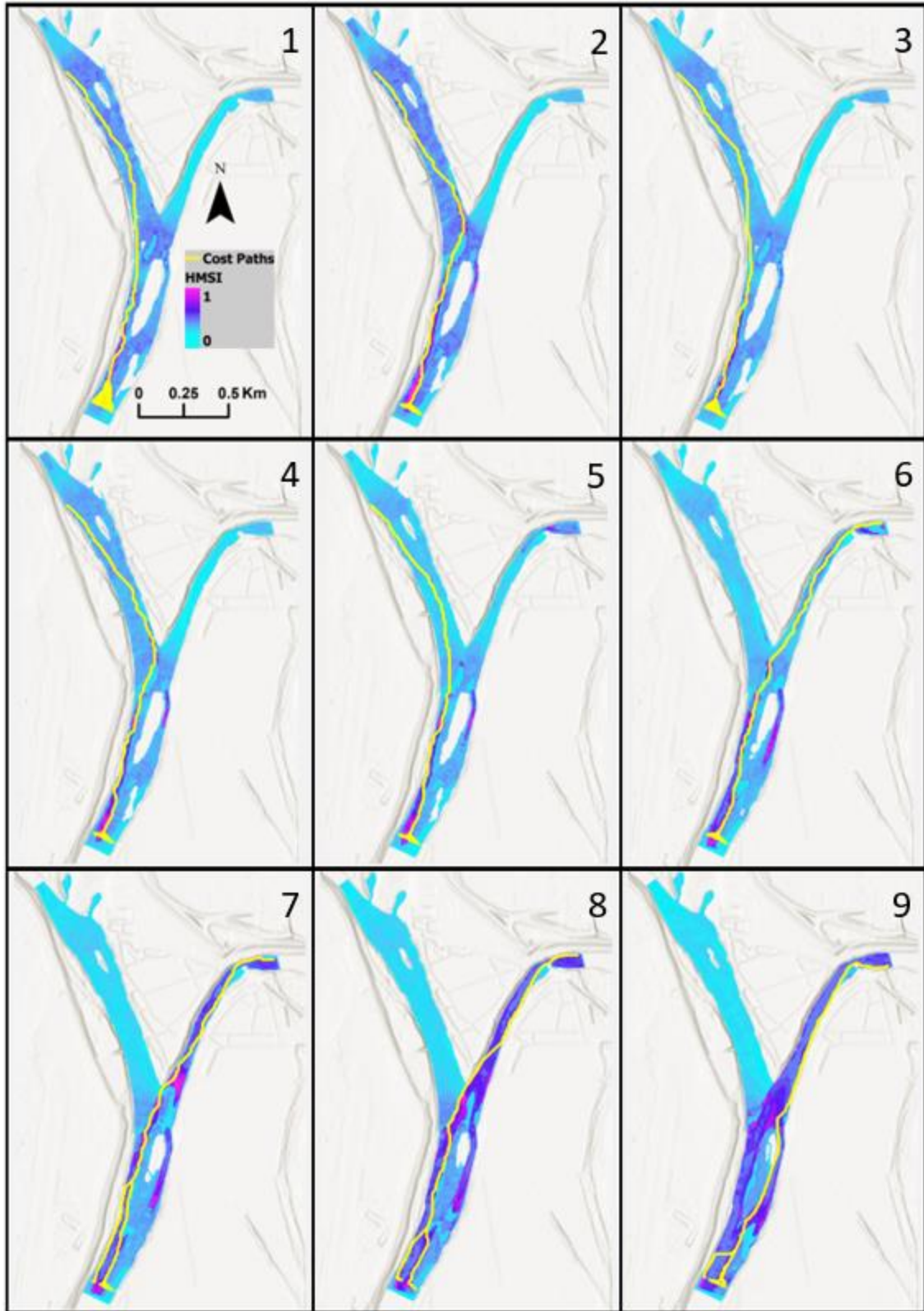
Figure 2.6. HMSI raster maps and cost paths simulated for each of the 9 discharge scenarios. Raster layers have a 3m cell resolution. Scenarios are numbered in the upper right corner of each panel.
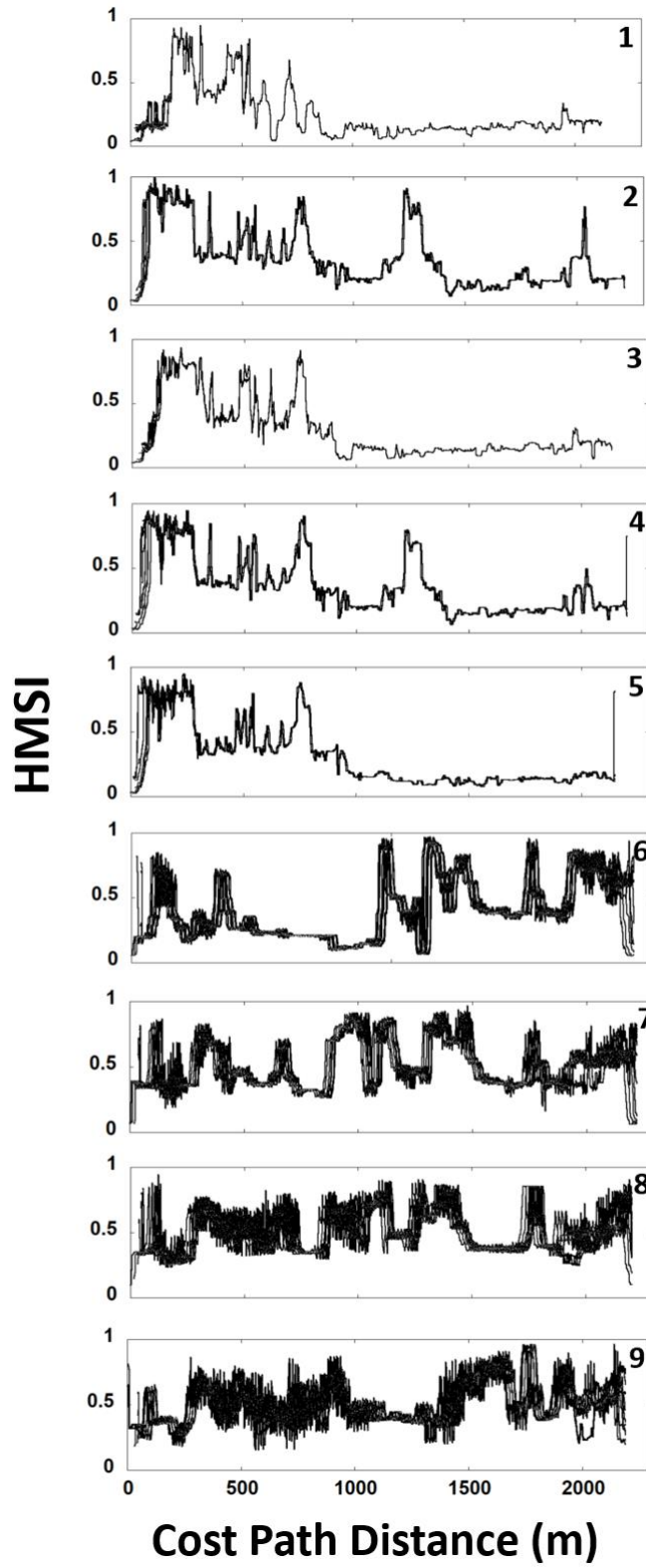
Figure 2.7. HMSI values encountered along each cost path in each scenario. Scenarios are numbered in the upper right corner of each panel.

3.3.3   Question 1: discharge effect

The KW test for differences in median HMSI values encountered in cost paths per discharge scenario was statistically significant at 95% confidence (p <0.01), indicating at least one of the nine discharge scenarios resulted in greater value habitat overall compared to the others (Table 2.3 and Figure 2.8). Of the 36 pairwise tests, 31 (86%) had differences in ranked sums that were statistically significant. Table 2.4 includes paired differences in order of the sizes of difference between ranked sums. The greatest difference in median HMSI values was between scenario 1 and scenario 9. Following this first pair of discharge scenarios are comparisons between scenario 1 and Scenarios 7 and 8; the second and third highest combined discharges that we examined.

Table 2.3. Results of Kruskal-Wallis rank sum tests for differences in median HMSI values encountered among the nine discharge scenarios and four discharge ratios that occurred among the nine scenarios.

	DF	X^2_{KW}	p value
Scenarios	8	15834.0	< 0.001
Ratios	3	1648.7	< 0.001

Table 2.4. Results of Dunn's test for multiple comparisons. The pairwise comparisons of discharge scenarios are ordered by the absolute value of the difference in ranked sums between HMSI values along all cost paths per scenario, in each of the two scenarios analyzed. Adjusted p values are shown using the Bonferroni method.

Scenario a	Scenario b	N_a	N_b	rank a	rank b	|diff|	z	p	p_{adj}
1	9	7017	7216	19161.38	44164.65	25003.27	79.72	**< 0.01**	**< 0.01**
1	8	7017	7244	19161.38	43803.82	24642.44	78.64	**< 0.01**	**< 0.01**
1	7	7017	7320	19161.38	43694.13	24532.75	78.49	**< 0.01**	**< 0.01**
3	9	7027	7216	22516.59	44164.65	21648.06	69.04	**< 0.01**	**< 0.01**
3	8	7027	7244	22516.59	43803.82	21287.23	67.96	**< 0.01**	**< 0.01**
5	9	7084	7216	22916.16	44164.65	21248.49	67.91	**< 0.01**	**< 0.01**
3	7	7027	7320	22516.59	43694.13	21177.54	67.78	**< 0.01**	**< 0.01**
5	8	7084	7244	22916.16	43803.82	20887.66	66.82	**< 0.01**	**< 0.01**
5	7	7084	7320	22916.16	43694.13	20777.97	66.64	**< 0.01**	**< 0.01**
1	6	7017	7339	19161.38	34378.43	15217.06	48.72	**< 0.01**	**< 0.01**
4	9	7275	7216	29735.39	44164.65	14429.26	46.42	**< 0.01**	**< 0.01**
4	8	7275	7244	29735.39	43803.82	14068.43	45.31	**< 0.01**	**< 0.01**
4	7	7275	7320	29735.39	43694.13	13958.74	45.07	**< 0.01**	**< 0.01**
2	9	7283	7216	30259.86	44164.65	13904.79	44.75	**< 0.01**	**< 0.01**
2	8	7283	7244	30259.86	43803.82	13543.95	43.63	**< 0.01**	**< 0.01**
2	7	7283	7320	30259.86	43694.13	13434.27	43.39	**< 0.01**	**< 0.01**
3	6	7027	7339	22516.59	34378.43	11861.85	37.99	**< 0.01**	**< 0.01**
5	6	7084	7339	22916.16	34378.43	11462.27	36.79	**< 0.01**	**< 0.01**
1	2	7017	7283	19161.38	30259.86	11098.48	35.47	**< 0.01**	**< 0.01**
1	4	7017	7275	19161.38	29735.39	10574.01	33.78	**< 0.01**	**< 0.01**
6	9	7339	7216	34378.43	44164.65	9786.22	31.55	**< 0.01**	**< 0.01**
6	8	7339	7244	34378.43	43803.82	9425.38	30.42	**< 0.01**	**< 0.01**
6	7	7339	7320	34378.43	43694.13	9315.70	30.15	**< 0.01**	**< 0.01**
2	3	7283	7027	30259.86	22516.59	7743.28	-24.75	**< 0.01**	**< 0.01**
2	5	7283	7084	30259.86	22916.16	7343.70	-23.52	**< 0.01**	**< 0.01**
3	4	7027	7275	22516.59	29735.39	7218.80	23.07	**< 0.01**	**< 0.01**
4	5	7275	7084	29735.39	22916.16	6819.23	-21.84	**< 0.01**	**< 0.01**
4	6	7275	7339	29735.39	34378.43	4643.04	15.00	**< 0.01**	**< 0.01**
2	6	7283	7339	30259.86	34378.43	4118.57	13.31	**< 0.01**	**< 0.01**
1	5	7017	7084	19161.38	22916.16	3754.78	11.92	**< 0.01**	**< 0.01**
1	3	7017	7027	19161.38	22516.59	3355.21	10.63	**< 0.01**	**< 0.01**
2	4	7283	7275	30259.86	29735.39	524.47	-1.69	0.09	1.00
7	9	7320	7216	43694.13	44164.65	470.52	1.52	0.13	1.00
3	5	7027	7084	22516.59	22916.16	399.57	1.27	0.20	1.00
8	9	7244	7216	43803.82	44164.65	360.84	1.16	0.25	1.00
7	8	7320	7244	43694.13	43803.82	109.68	0.35	0.72	1.00

N_a and N_b are the number of HMSI values along the cost path in each scenario, ranks *a* and *b* are the ranked sums per Dunn (1964), \|*diff*\| is the absolute value of difference in ranked sum between scenarios, *z* is the z statistic for testing significance at 95% confidence. p_{adj} is the adjusted *p* value using the Bonferroni method. Bolded p values are statistically significant.

Figure 2.8. Box and whisker plot indicating the median, quartiles, minima and maxima, and outliers (hollow circles) for HMSI values encountered along all cost paths in each scenario.

3.3.4   Question 2: discharge ratio effect

As with the KW test for Question 1 regarding differences among discharge scenarios, the KW test for differences in median HMSI values encountered in cost paths per discharge ratio was statistically significant at 95% confidence (p <0.01), indicating at least one of the four discharge ratios resulted in greater value habitat overall (Table 2.3 and Figure 2.9). The results of the Dunn's test shown in Table 2.5 (ordered in the table by the size of difference between ranked sums for each ratio) showed the highest difference in median HMSI values encountered between discharge ratios of 1:1 and 4.9:1. The relationship between HMSI and discharge ratio appears to be more complicated than between HMSI and discharge magnitude, as the second greatest paired difference between ratios was 3.4:1 and 4.9:1. This is likely due to the 3.4:1 ratio appearing in three different discharge scenarios (as opposed to two, like the other three ratios examined), and so a greater sample of HMSI values represented by the 3.4:1 ratio. We did not find a directly proportional

relationship between ratio and HMSI, indicating confluence discharges and combined discharge magnitude are more important predictors of habitat value within the confluence.

Table 2.5. Results of Dunn's test for multiple comparisons. The pairwise comparisons of discharge scenarios are ordered by the absolute value of the difference in ranked sums between HMSI values along all cost paths per scenario, in each of the two scenarios analyzed. Adjusted p values are shown using the Bonferroni method.

Ratio a	Ratio b	N_a	N_b	rank a	rank b	|diff|	z	p	p_{adj}
1:1	4.9:1	14423	14499	28748.62	37180.13	8431.507	38.32363	**<0.001**	**<0.001**
3.4:1	4.9:1	21536	14499	31022.25	37180.13	6157.879	30.64074	**<0.001**	**<0.001**
1:1	2.4:1	14423	14347	28748.62	33321.61	4572.984	20.73084	**<0.001**	**<0.001**
2.4:1	4.9:1	14347	14499	33321.61	37180.13	3858.523	17.51486	**<0.001**	**<0.001**
2.4:1	3.4:1	14347	21536	33321.61	31022.25	2299.36	-11.4052	**<0.001**	**<0.001**
1:1	3.4:1	14423	21536	28748.62	31022.25	2273.628	11.29548	**<0.001**	**<0.001**

N_a and N_b are the number of HMSI values along the cost path corresponding to each discharge ratio, ranks a and b are the ranked sums per Dunn (1964), \|diff\| is the absolute value of difference in ranked sum between discharge ratios, z is the z statistic for testing significance at 95% confidence. p_{adj} is the adjusted p value using the Bonferroni method. Bolded p values are statistically significant.
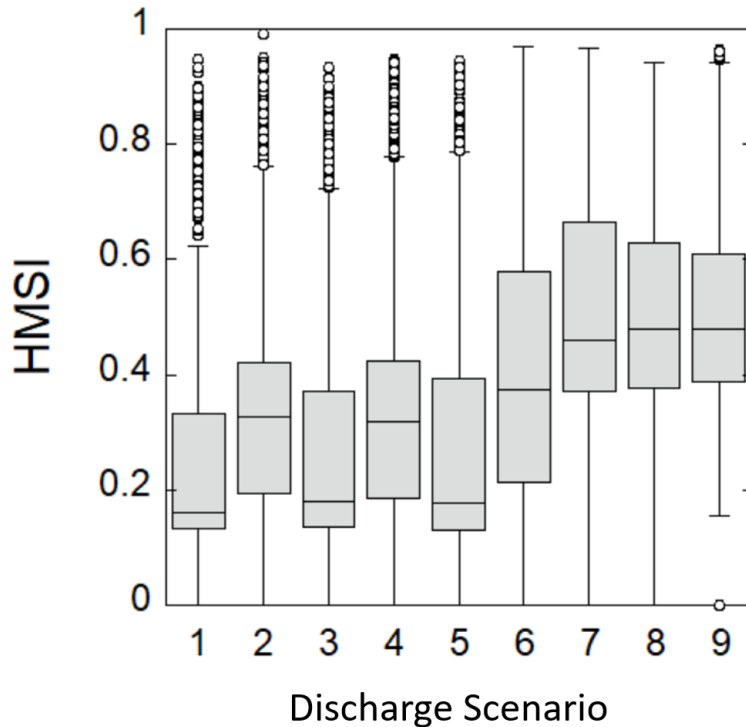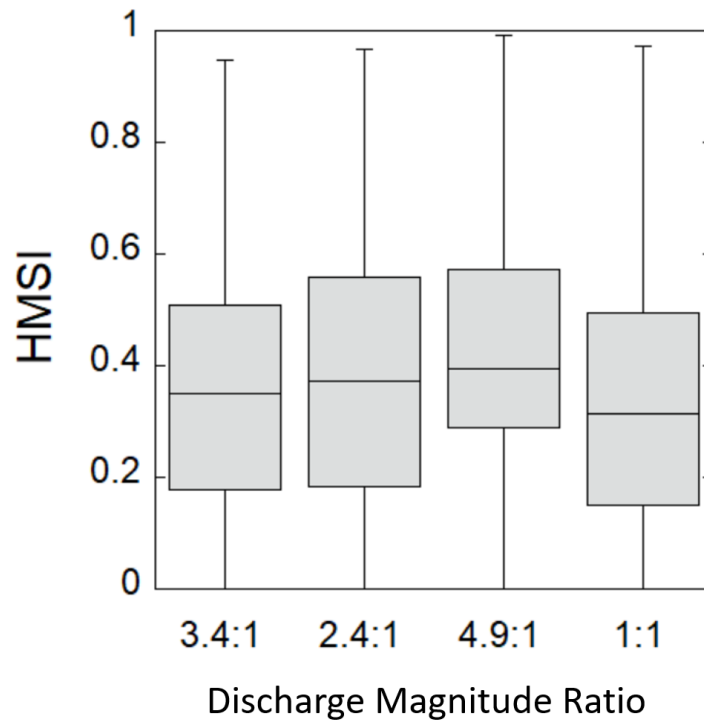

Figure 2.9. Box and whisker plot indicating the median, quartiles, minima and maxima for HMSI values encountered along all cost paths corresponding to the four discharge ratios that occurred among the nine discharge scenarios.

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3.4 Discussion

3.4.1 Migratory routing in the LFR and LYR

Our results suggest migratory routing at the LFR/LYR confluence is partially driven by micro-scale hydraulic cues, as hydraulic selectivity is driven by discharge conditions. The simulations presented here are intended to compliment the findings of Chapter 1 which showed hydraulic variables to be important factors in migratory microhabitat selection and rheotactic swimming behavior. Based on DIDSON surveys conducted in 2019, it appears conveyance is the strongest hydraulic component of microhabitat selectivity.

Discharge magnitude was found to be an important driver of the amount and distribution of high-value hydraulic habitat. Results of the present study support previous patterns of adult Chinook escapement in this system, as the LYR has experienced elevated rates of strays in conditions where LYR discharge magnitude greatly outweighs that of LFR (YARMT 2013). The conveyance variable has a velocity component, and thus is strongly driven by discharge magnitude as can be seen in scenarios 6-9 which had relatively high HMSI values compared to scenarios 1-5.

Discharge ratio was also found to be a statistically significant driver of hydraulic habitat distribution, though we expected to find a clearer relationship between discharge ratio and availability of high-value habitat at the confluence. Our investigation into this effect suggests discharge ratio may be an important predictor of migratory routing within a certain range of discharge magnitude values. At a confluence, depending on the size of discharge ratios, a backwater effect may also occur in the river with a lower discharge, lowering velocities in that river upstream of the confluence and yielding lower HMSI values that might be attractive to migrating salmon.

An example of discharge ratio influencing migratory routing can be seen in Table 2.4 where scenarios 7-9 are highly influential, having the three greatest combined discharge magnitudes among our simulations when compared to scenario 1. The differences in ranked HMSI sums among scenarios 7-9 were markedly different, with the comparison between scenarios 9 and 1 having almost twice the difference compared to

the comparison between scenarios 7 and 1. This can be seen graphically in Figure 2.7 where scenario 9 has higher overall HMSI values along the cost paths when compared to scenario 7. Therefore, in the context of potential drought conditions at the LFR/LYR confluence, a situation with a high combined discharge occurring simultaneously with a high discharge ratio has the potential to greatly determine migratory routing via hydraulic habitat selectivity. Again, this is the situation that was observed in 2010 in this system that resulted in an acute pulse of LFR-origin fall-run Chinook salmon straying into LYR.

3.4.2   Information gaps and future modeling applications

Even though adult salmon migration has been studied for decades in many different systems and species, researchers, managers, and policy makers still lack a cohesive, holistic quantitative model of the navigational cues for homing and upstream travel. To date, research has shown that this process is extremely complex, involving many different sensory inputs as well as endocrine responses in an individual fish. Our hope is that this modeling study provides some compelling evidence that micro-scale hydraulic cues also play an important role. These results may support future research and modeling efforts to unify olfactory responses, density-dependent behavior, micro-scale hydraulic selectivity, innate exploratory behavior, and responses to other habitat characteristics such as temperature, turbidity, pathogens, substrate, and channel complexity. A good starting point would be a study that tracks both hydraulic habitat selectivity and fidelity to olfactory cues so that degree of influence of micro-scale habitat characteristics could be disentangled from olfactory homing mechanisms for a given species, population, and location. It is well understood that olfaction is a primary driver of homing and is likely the dominant driver of an individual's navigational choices (Cooper et al., 1976; Dittman et al., 1996; Hasler and Scholz, 1983; Ueda, 2011) However, there have also been multiple cases in which olfaction was shown to be compromised, such as hatchery-origin fish released away from their natal facility and denied the sequence of olfactory imprinting associated with outmigration (Huber et al., 2015; Jonsson et al., 2003; Keefer and Caudill, 2014; Murdoch et al., 2009; Sturrock et al., 2019). Exposure to waterborne pesticide compounds that are toxic to olfactory organs is another reason in which olfactory physiology may be compromised in adult salmon (Tierney et al., 2010,

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2008). In these cases, hydraulic navigation cues may play a critical role in navigation in lieu of olfactory cues. The degree to which this occurs may also vary among species and migratory phenotypes. Bett and Hinch (2016) proposed a hierarchical navigation hypothesis based on existing empirical evidence that habitat selection in upstream migration occurs using a hierarchy of navigational cues with imprinted odors being the primary cue, conspecific odors being a secondary cue, and non-olfactory environmental factors as tertiary cues. Our intent was to provide some novel insight into how such non-olfactory cues may be incorporated in upstream navigation.

3.4.3   Implications for environmental flow management strategies

Our findings highlight a broad need for future research and development of modeling tools that account for environmental navigational cues on homing and migration in adult salmon. With the exception of pulse attraction flows, research supporting flow regulation and watershed management strategies for salmon habitat functionality focuses on spawning, incubation, and juvenile rearing and outmigration (Harnish et al., 2014; Matella and Merenlender, 2015; Schaller et al., 2014; Zeug et al., 2014). Supporting these life stages is important for maintaining and improving population productivity and abundance for broader ecosystem support as well as fishery management. However, population attributes such as genetic structure, migration phenology, and spatial structure are conserved through successful adult migration and homing to natal streams (Narum et al., 2008; Powell and Campbell, 2020; Vähä et al., 2007). In some cases, maintaining these attributes may be critically important for conservation efforts. For imperiled populations that experience high rates of straying, it may be prudent for water managers to consider developing and incorporating operational criteria into flow schedules that support successful homing by avoiding hydraulic conditions at key points along the migratory route that may encourage straying.

3.5   Acknowledgements

3.6   References

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4   Chapter 3: Abiotic variables are often neglected in studies of homing and straying in anadromous salmonids

4.1   Abstract

Despite decades of research on homing and straying in anadromous salmonid fishes, there remains a broad lack of investigation into abiotic drivers of homing and straying behavior. This article accomplishes two goals: (1) it develops a conceptual framework supported by existing literature for why abiotic factors that drive homing and straying behavior in salmonids are important and should be considered in mechanistic frameworks, and (2) it conducts a meta-analysis using a targeted literature search in Web of Science via Boolean criteria based on this framework to test whether analyses of abiotic variables and testing of abiotic factors identified in our framework are (a) increasing though time in the published literature, and (b) disproportionately included among homing and straying-related study designs, study locations, and/or study species. After filtering search results to exclude duplicates and irrelevant articles, only 70 out of 169 articles included at least one abiotic variable. An augmented Dickey-Fuller time series analysis revealed that instances of abiotic variable inclusion and testing of abiotic factors in published studies per year have experienced slight increasing trends since 1990 (0.37 and 0.22 per year, respectively). Among study types, species, and locations, there were no differences in the number of abiotic variables included or tested. Biotelemetry studies had the greatest percentage of ≥1 abiotic variable included with 21 out of 32 papers (65.6%). The U.S. West Coast and British Columbia dominated study locations with 62 papers, 21 of which included ≥1 abiotic variable (33.9%). Atlantic salmon were used in the greatest number of papers at 38, followed closely by Chinook salmon at 34. Of the papers using these species, 19 (50.0%) and 13 (38.2%) included ≥1 abiotic variable, respectively. Taken together, results suggest a systematic lack of inclusion bias against abiotic components in the homing and straying literature. Homing and straying are critical facets of the salmonid lifecycle, and researchers currently lack a comprehensive conceptual model for how the abiotic environment drives migratory patterns of diverse salmon species. Future homing and straying research should be conducted in the context of both biotic and abiotic drivers.

4.2   Introduction

Homing in anadromous salmonids, defined as the return from ocean spawning grounds to freshwater spawning habitat of natal origin, is a highly complex phenomenon intertwining biotic and abiotic dynamics (Dittman and Quinn, 1996). Decades of research on this topic have shown that a myriad of biotic and abiotic processes play out at each stage of the salmonid lifecycle to achieve upstream migration from coastal and estuarine habitats to riverine spawning grounds (Craigie, 1926; Hasler and Scholz, 1983; Hasler and Wisby, 1951; Quinn, 1993; Quinn and Fresh, 1984; Westley et al., 2013). Straying is a facet of upstream adult migration that has received attention for various research and management interests. Straying refers to an individual's upstream migration terminating at a location other than that of their natal origin. Keefer and Caudill (2014, referred to hereafter as "K&C") provided an excellent review of homing and straying mechanisms with a focus on the biological causes and consequences of straying in salmon populations. K&C outlined seven biological causal mechanisms for straying: (1) incomplete juvenile imprinting; (2) interrupted juvenile imprinting; (3) adult sensory failure; (4) adult memory failure; (5) density dependent reproductive behaviors; (6) genetic and life history effects; and (7) attraction to non-natal sites. These are hereafter referred to as "biological HS mechanisms".

Although these biological HS mechanisms have been studied extensively for several decades, we conjecture that the literature has underrepresented abiotic factors linked to homing and straying behavior. The term "abiotic variable" is used throughout this article. It describes a measurable quantity that represents either a single physical environmental parameter (e.g., water depth or water velocity) or an environmental indicator (e.g., water temperature indices or passage barrier classifications) that occurs in the environment that comprises anadromous salmonid habitats at all life stages. This term excludes artificial habitat attributes related to hatchery rearing facilities or controlled laboratory conditions. It also excludes attributes of environmental conditions that do not have an explicitly defined link to a habitat feature such as dates, times, and locations.

The first objective of this study was to provide new theoretical developments that extend the K&C framework by developing a comprehensive list of abiotic homing/straying factors (hereafter referred to as "abiotic HS factors", defined and listed in Table 3.1a and Table 3.1b). These abiotic HS factors have direct links to the biological HS mechanisms identified by K&C. Our intent is not to criticize K&C's review, but rather to support their findings and conclusions with an expanded analysis of abiotic HS factors that link anadromous salmonid species to the habitat features that they experience at each life stage. Certain causes of straying identified by K&C coincide with specific life stages and Table 3.1a and Table 3.1b are structured accordingly. Incomplete and interrupted juvenile imprinting are combined into one category and adult memory failure is excluded from this analysis, as it does not have an abiotic component. Figure 3.1 includes a flow chart describing the methods and analytical steps taken in this review.

The second objective of this review was to conduct a meta-analysis to test hypotheses related to three specific questions about the existing literature in light of the broader conceptualization of abiotic-biotic linkages. The meta-analysis was designed to address the following three questions: (1) Are instances of inclusion of abiotic variables and tests of abiotic HS factors increasing over time? (2) Are abiotic variables incorporated into study designs disproportionately among study method types, study regions, and/or study species? (3) Are abiotic HS factors linking abiotic variables to K&C's biological HS mechanisms being tested disproportionately among study method types, study regions, and/or study species? Figure 3.2 includes two example analyses from our literature sample, identifying instances where abiotic variables were analyzed to test abiotic HS factors that link back to biological HS mechanisms identified by K&C.
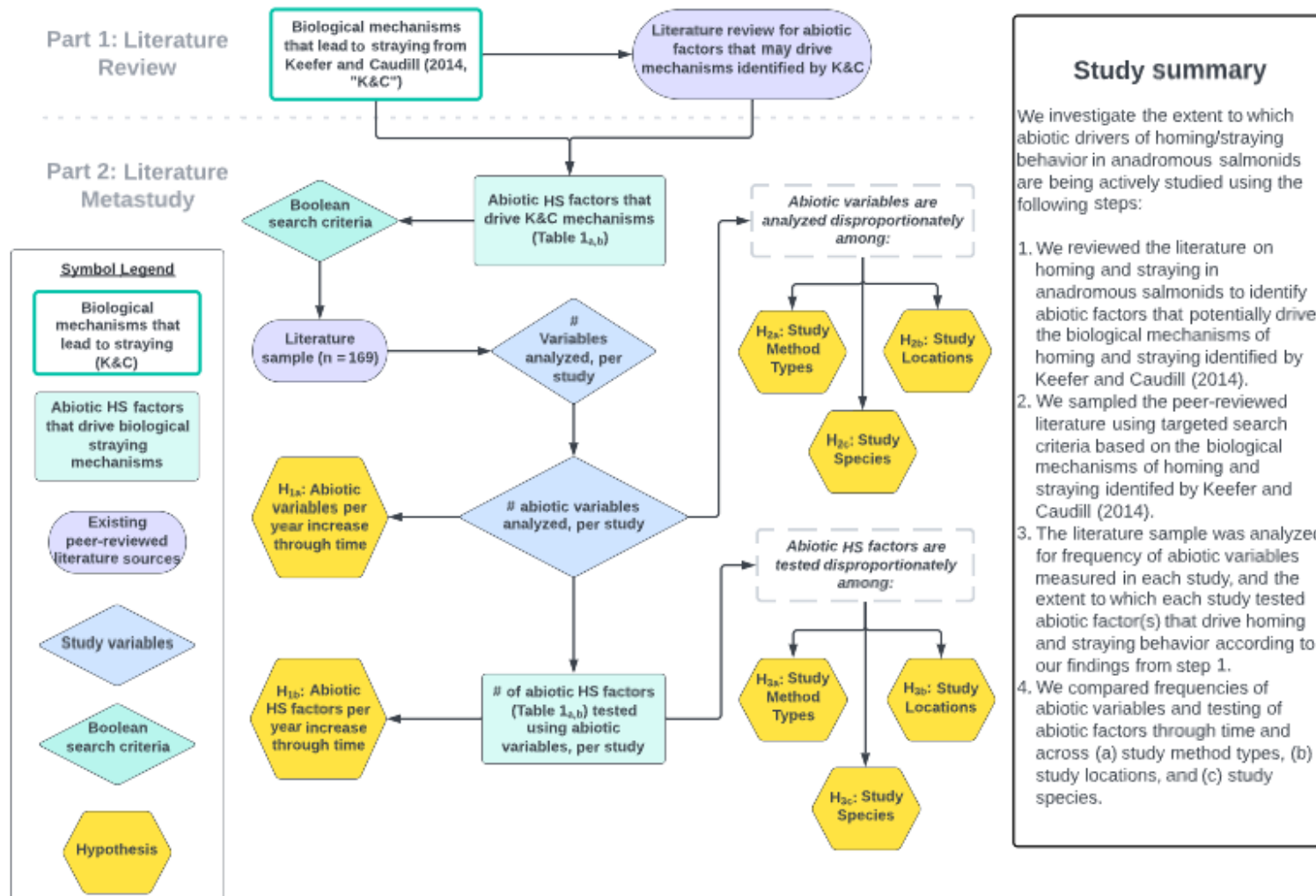
Figure 3.1. Conceptual flow chart and summary of the literature review and metastudy conducted.
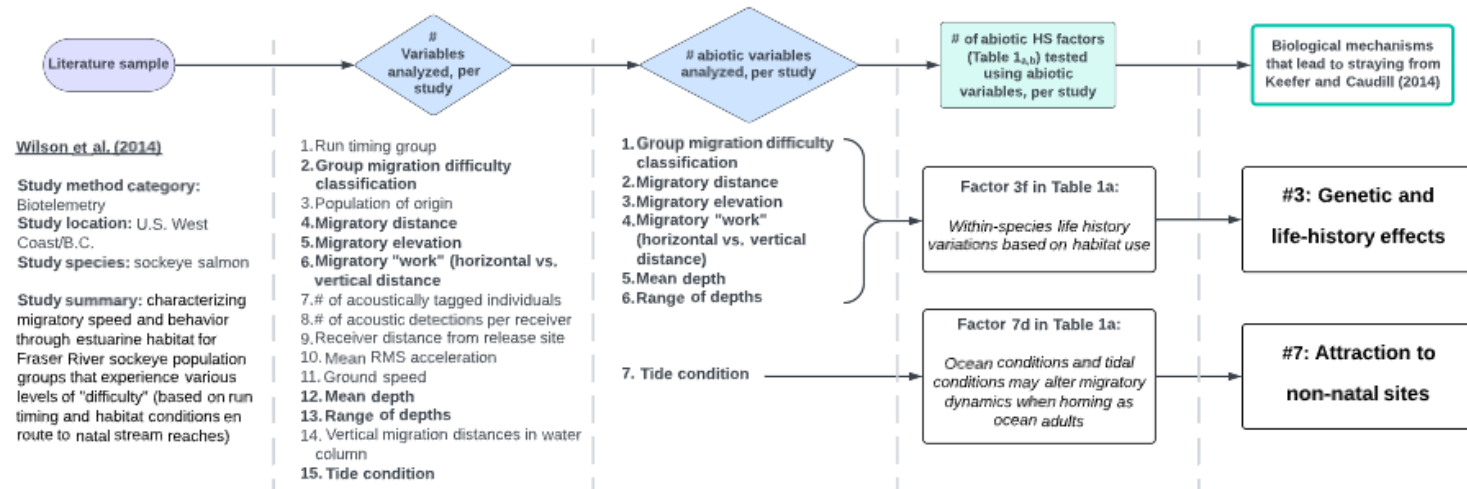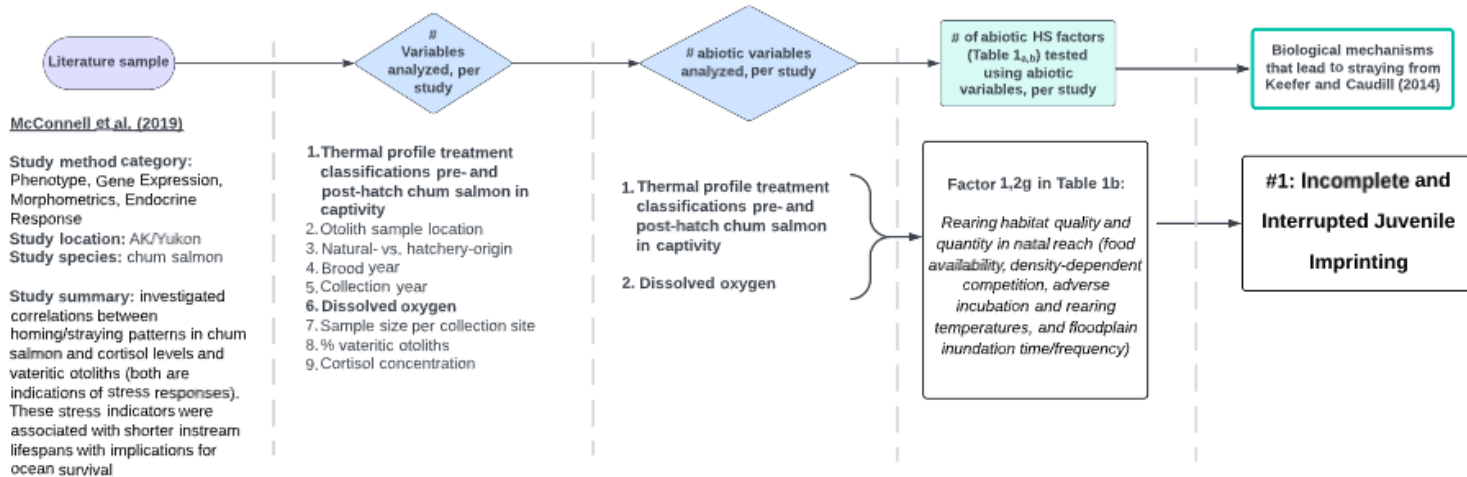
Figure 3.2. Examples of our analysis of sampled literature to identify abiotic variables and abiotic HS factors that drive the biological HS mechanisms identified by Keefer and Caudill (2014). Colors and symbols are consistent with items shown in Figure 3.1.

4.2.1　Definitions of Criteria and Terms

The scope of this review is limited to anadromous salmonid species. Freshwater resident salmonids are excluded as well as other fish species that exhibit diadromous life history strategies (Meyers, 1949). Table 3.1a and Table 3.1b include categories related to study scale and life stage, which allowed for more explicit identification of relevant environmental drivers. "Local-scale" HS factors are those that may occur at the scale of a single river segment or any smaller area. "Large-scale" HS factors are those that may occur across one or more subcatchments (where a study catchment has been identified, but only specific river reaches, segments, or areas within it are analyzed), across a whole catchment, across multiple catchments, or in estuarine, coastal, and oceanic habitats. The "juvenile" category refers to any life stage ranging from egg to smolt at entry to brackish water. "Adult" ranges from sub-adult following entry to the marine environment to the spawner stage.

4.2.2　Incomplete or Interrupted Juvenile Imprinting

Early studies on olfactory imprinting in juvenile salmon revealed that the parr-smolt transformation is a critical point in the lifecycle in which a cascade of endocrine activity within individuals coincides with neurological mapping of odor cues (Dittman et al., 1996; Hasler and Scholz, 1983; Morin and Døving, 1992). Recently, both Havey et al. (2017) and Armstrong et al. (2021) found that this phenomenon occurs much earlier, demonstrating olfactory imprinting in sockeye and Atlantic alevin, respectively. It is unclear how the timing of imprinting may occur across species, populations, or whether phenotypic plasticity may occur within a given population. However, existing evidence does suggest that olfactory imprinting may be impaired, interrupted, or prevented entirely by several abiotic HS factors.

Juvenile freshwater residence time refers to the time spent rearing in freshwater habitats prior to smoltification and entry into the estuary. Residence time can vary depending on species and migratory phenotype, density and competitive interaction among individuals, and location of natal habitat within a catchment (Roni et al., 2012; Scheuerell et al., 2009; Unwin, 1986). However, this period may be cut short

in the event of flood flow pulses that force passive downstream transport through highly confined and channelized river habitats that experience high velocities (Pavlov et al., 2008). Density effects due to limited suitable rearing habitat at low flow periods may also initiate premature downstream movement as discussed by Walters et al. (2013) and Einum et al. (2006), though more research is needed in order to characterize density-dependent juvenile movement across species and life history types (Grossman and Simon, 2020).

Increased production of thyroid hormones has been linked to olfactory imprinting and the endocrine controls in this process are well understood at this point (Dittman et al., 1994; Hasler and Scholz, 1983; Lema and Nevitt, 2004; Ueda et al., 2016). Because salmon are poikilothermic, thyroid activity is strongly mediated by temperature and can be inhibited under elevated temperature conditions (Grau et al., 1982; Nisembaum et al., 2020). In dry years where stream temperatures are elevated in spawning and rearing habitats, olfactory imprinting may be interrupted or inhibited due to physiological limitations. This may impact multiple age classes in a single population during a prolonged drought period. Because we now have evidence that imprinting occurs at the alevin stage, species-specific incubation temperature thresholds should also be put into the context of olfactory imprinting potential such as those identified by (Murray and McPhail, 1988). Physiological impediments to olfactory imprinting may also result from sublethal exposure to pesticide compounds such as atrazine in Atlantic salmon (Moore et al., 2007) and carbamates in coho salmon (Jarrard et al., 2004) which have been shown to inhibit critical electrophysiological olfactory processes at the parr/smolt stage. Pesticides have been shown to harm endocrine processes in alevin, though more work is needed to characterize contaminant effects to olfactory imprinting at this life stage (Du Gas et al., 2017; Giroux et al., 2019).

4.2.3   Genetic and Life History Effects

A critical facet of anadromous salmonid life histories is exploratory dispersal of behaviorally polymorphic juveniles and adults within a population (Hamann and Kennedy, 2012; Peterson et al., 2016; Quinn, 1993). This innate behavior is responsible for their persistence over the past 144 million years in the face of a

major ice age, violent geological activity, fluctuations in sea level, and changing patterns of habitat formation and destruction through stochastic processes (Waples and Hendry, 2008). With an innate baseline rate of straying, genetic diversity within a metapopulation can be conserved over time in fragmented populations in a phenomenon known as the portfolio effect (Figge, 2004). Waples et al. (2009) identified four key characteristics of disturbance regimes that may drive salmon dispersal and resultant population structure: (1) frequency, (2) magnitude, (3) duration, and (4) predictability; and that anthropogenic alterations to these characteristics might lead to loss of population resilience over time due to reduced facilitation of dispersal and fragmentation (i.e., a simplification of the genetic "portfolio").

Climate-driven hydrologic regimes, both floods and droughts, work together with topography, sediment regime, and other factors to yield habitat disturbance patterns expressed as flood frequency, timing, duration, and magnitude (Poff et al., 2006). Natural flow regimes drive the availability and amount of riverine habitats that support salmon based on: (1) floodplain inundation for juvenile foraging (Benke et al., 2000; Junk et al., 1989; Scott et al., 2019); (2) erosion and sediment transport dynamics (i.e. geomorphic effective discharges) that dictate grain size distributions and functional habitat units (Basso et al., 2015; Doyle et al., 2005; Yarnell et al., 2006); (3) vegetation in main channel or seasonally inundated floodplains for habitat complexity (Beland et al., 2004; Jeffres et al., 2008; Tabacchi et al., 1998); (4) nutrient availability and downstream transport for productivity (Doretto et al., 2020; Mallin et al., 1993; Vannote et al., 1980); and (5) stream hydrographs, temperature regimes, surface-hyporheic interaction, and dissolved oxygen supply in spawning reaches that are suitable for egg incubation and egg-to-fry survival (Beechie et al., 2006; Malcolm et al., 2004; Soulsby et al., 2009).

Hydrologic disturbance regimes can also be dramatically altered by the construction of dams and regulation of flows (Magilligan and Nislow, 2005). This can also lead to profound changes to temperature regimes throughout a watershed, altering the dynamics of thermal disturbances that historically occurred (Lessard and Hayes, 2003; McCullough, 1999; Willis et al., 2021). For example, in a dam-free catchment prior to human development, small-scale thermal disturbances may have driven intra-basin dispersal and population

structuring such as the loss of riparian shading due to a wildfire. Having constructed dams and regulated flows and temperatures in that same catchment today, thermal disturbances may be more frequent, more widespread, and with greater magnitude. In response, populations may become more genetically homogenized when occupying habitat in a permanently disturbed condition.

4.2.4   Adult Sensory Failure

The landscapes that many salmon populations traverse during their spawning migration often pose threats to olfactory physiology and other sensory systems that are critical for successful homing (Tierney et al., 2010). Non-point source contamination by agricultural pesticides (many of which are toxic to salmonid olfactory processes, (see Tierney et al., 2008) can occur at a broad scale in a catchment with the primary driver of aquatic concentrations being stormwater runoff, though sediment and groundwater have also been shown to be an important means of storage and transport of certain pesticide compounds (McKnight et al., 2015; Parker et al., 2007; Weston et al., 2004). Once contaminants are waterborne, fate is dependent on various physical, chemical, and microbial processes acting on each individual compound (Holvoet et al., 2007). At a catchment scale, it is likely that intensity of application per unit area rather than the total area of application has more of an effect on aquatic toxicity levels (Hunt et al., 2006).

Point-source contamination may also occur due to poor construction management practices or wastewater effluent (McNeill, 1996; Santhi et al., 2001). Management techniques involving construction of detention ponds and wetlands may result in reductions of waterborne contaminants (Fulton et al., 1999; Haberl et al., 2003; Harrell and Ranjithan, 2003). In a study on efficacy of non-point source agricultural pollution removal in constructed wetlands, Díaz et al. (2012) found that continuous flow through wetlands were more effective than flood pulse wetlands, suggesting that different engineering approaches for water quality management may have varying reach-scale benefits to salmon olfaction (Vymazal and Březinová, 2015).

The susceptibility of migrating adult salmon to pathogen infection is largely driven by host-pathogen-environment interactions as recently demonstrated by Teffer et al. (2022). Temperature has been shown to

be a critical driver of pathogen abundance via increased rates of replication and may increase infection rates in cases where high temperatures cause thermal stress to salmon (Benda et al., 2015; Bettge et al., 2009; Ewing et al., 1986). Therefore, community composition of pathogenic organisms present in migratory habitat may be less important than the thermal regime that ultimately drives infection rates. Pathogenic agents take the form of bacteria, viruses, ectoparasites, microsporidia, myxozoa, and other taxa; and pathogenic loads in individuals have shown to vary in time and space and by sex (Bass et al., 2017; Bradford et al., 2010; Miller et al., 2014). These antagonistic ecologies are known to affect rates of upstream migration, pre-spawn mortality, renal and respiratory function, and cause lesions on various organ tissues (Kocan et al., 2004; Teffer et al., 2018); but the direct physiological impacts to organs specifically involved in olfaction (olfactory rosette, olfactory bulb, or greater telencephalon) are not well understood (Abe et al., 2020; Kudo et al., 2009). Given the physiological demands of olfactory navigation and the severe impacts to physiological function from various infection types, it is likely that pathogens directly affect olfaction though further research is needed to characterize this effect.

Increased attention has been given in recent decades to effects of anthropogenic noise pollution on fishes (Popper and Hastings, 2009; Slabbekoorn et al., 2010). Lethal and sub-lethal injuries to fish tissue occur in the form of swim bladder barotrauma, a common source of this is impact pile driving during in-water construction projects (Casper et al., 2012; Halvorsen et al., 2012), as well as acute injuries to epithelial receptor and neuromast cells that are critical for detecting sound and water velocity which are important sensory inputs to navigation in current (Chambers et al., 2014; Hastings et al., 1996; McCauley et al., 2003; Smith and Monroe, 2016). In addition to acute injury, underwater noise impacts fish behavior with "startling" and avoidance behaviors observed in response to sound stimuli (Hawkins and Popper, 2018; Nedwell et al., 2006). Thresholds of sound pressure levels eliciting behavioral responses have been identified for some species though much of this work has taken place in pelagic settings. Neither acute injury nor behavioral effects resulting from anthropogenic sound have been investigated in the context of migrating adult salmon. However, there is abundant evidence to suggest noise pollution interferes with the

sensory mechanisms and environmental cues involved in homing, and managers do currently have access to baseline thresholds for developing regulatory requirements. For example, Popper et al. (2014) developed a set of fish-specific guidelines and best management practices for noise-generating activities including underwater explosions, pile driving, seismic air guns, low- and mid-frequency naval sonars, and commercial shipping.

4.2.5 Density-dependent Reproductive Behaviors

Density-dependent behavioral effects in migrating and spawning adult salmon are known to occur simply as a function of fish-density per unit of habitat area, and variability through time is often thought of in terms of run size. Behaviors in response to density include collective navigation, altered run timing, and localized straying due to spawning habitat saturation (Berdahl et al., 2017, 2016; Mortensen et al., 2002; Quinn and Fresh, 1984). However, it is also important to consider multi-scale habitat features that may result in limitation of migratory and spawning habitat, or otherwise result in greater densities.

Perhaps the most widely publicized and studied cause of salmonid habitat limitation is construction of dams and other infrastructure that create impassible barriers, restricting access to various habitat types upstream of them. In a global assessment of 40,000 existing dams, Barbarossa et al. (2020) found the highest rates of aquatic habitat fragmentation occurring in the United States, Europe, South Africa, India, and China. Zarfl et al. (2015) estimated that at least 3,700 new hydropower projects (though most occur in tropical areas without endemic salmon populations) were planned or under construction which would reduce Earth's free-flowing rivers further by 21%. In addition to isolating upstream habitat and reducing the historical range of a salmon population, dam construction also leads to several geomorphic effects downstream which further reduce and degrade available habitat. The alteration of natural flood and sediment supply regimes by flow regulation at a dam (especially the magnitudes of peak flows) results in channel simplification with losses of multi-thread channels, channel avulsion, floodplain activation, and sediment recruitment and transport dynamics (Ligon et al., 1995; Pitlick and Wilcock, 2001). Loss of geomorphic processes results in a

corresponding loss of sediment particles that are of the size required for successful redd construction, limiting the amount of viable spawning habitat available overall (Kondolf and Wolman, 1993; Kondolf, 2000).

Flood duration and frequency may also play important roles in initiating upstream migration and driving density. Flood flows (even just high-flow "pulses") are known to initiate upstream movement from estuarine to mainstem habitats by creating low salinity "freshets" near river mouths, allowing ocean going adults to follow a negative salinity gradient (Huntsman, 1948; Quinn, 2018). In regulated river systems, pulse attraction flows are often utilized to mimic a natural flood event and provide a cue for migration and these efforts have been met with mixed success (Hasler et al., 2014; Peterson et al., 2017; Thorstad and Heggberget, 1998). However, when pulses are too short or too few, many adults return simultaneously during a brief optimal period, leading to high densities upstream. Putative relationships between flood frequency/duration and density effects in adult salmon have not yet been explicitly tested. Although flow pulses are actively used as a fish-migration management tool, further research is needed to identify relationships between pulse flows and salmon movement, and they are likely to be species- and system-specific.

Thermal barriers may partially or totally restrict spawning habitat in cases where thermal refugia are not available and warm water temperatures signify non-viable spawning grounds. This possibility is discussed in more detail in the following section on attraction to non-natal sites. In such cases, spawner densities may increase in tributaries with viable spawning and incubation temperatures as strays compete with spawners of local origin. One final consideration of density-dependent behavior driven by habitat conditions is actually a lack of density-mediated fidelity to natal spawning grounds in small populations (the inverse of the "collective navigation" hypothesis presented by Berdahl et al. 2016). If collective migratory movement of spawners is facilitated by high densities, small populations may be more easily deterred by adverse habitat conditions in natal habitat. For low-density spawning runs, stray rates within or among catchments may be more sensitive to key habitat variables such as discharge and temperature. Further research is needed

across species and geographic regions to characterize multi-scale migratory responses of low-density spawning runs to adverse habitats encountered along their migration route.

4.2.6   Attraction to Non-natal Sites

The previous abiotic HS factors discussed include more intricate biological and ecological linkages between habitat features and homing/straying behavior. However, in some cases, salmon may simply find the physical characteristics of non-natal habitats more attractive relative to their reach of natal origin. This may occur as a product of natural phenomena or anthropogenic disturbance. The seasonal variation in likelihood of disturbance in salmon habitats means that run timing also may affect spawning site fidelity and rates of straying (Hendry and Day, 2005). As previously discussed regarding genetic effects, salmon exhibit exploratory behavior when homing and there is evidence that catchment size, tributary proximity, and distances between natal spawning habitat to the estuary may influence migratory routing and encourage exploration of non-natal tributaries over time (Olsen et al., 2010; Peterson et al., 2016). Total catchment area plays a role but so too does drainage pattern which is a function of topography driven by regional orogeny, epeirogeny, underlying lithology, climate and precipitation patterns, and vegetation cover (Dietrich et al., 2003; Howard et al., 1994; Istanbulluoglu and Bras, 2005; Massong and Montgomery, 2000; Sklar and Dietrich, 2001; Tomkin and Braun, 1999; Zernitz, 1932). The removal of total passage barriers typically opens access to more optimal spawning habitat (because this is often the goal of such projects), which may be more attractive than existing natal spawning grounds (Hogg et al., 2015; Lin and Robinson, 2019; Pess et al., 2014). In cases where partial passage barriers exist, individuals with natal spawning grounds upstream of a barrier who do not pass successfully are forced to seek out non-natal habitat (Gowans et al., 2003).

Stream discharge and temperature are critical environmental variables which mediate the quality and quantity of viable spawning habitat (Rand et al., 2006; Tetzlaff et al., 2005). In addition to the condition of surface flow entering upstream, hyporheic exchange at spawning sites provides inputs of cool water which

can be essential for successful egg incubation and post-hatch survival (Hanrahan, 2008; Tonina and Buffington, 2009). Warm temperatures can lead to a host of water quality issues including low dissolved oxygen in spawning gravels (Sear et al., 2014; Tonina and Buffington, 2009) and in the water column affecting spawning adults (Dahlberg et al., 1968; Priede et al., 1988; Sergeant et al., 2017), as well as increased parasite abundance (Benda et al., 2015; Bettge et al., 2009; Ewing et al., 1986). As such, migrating adult salmon have been shown to exhibit altered behavior in response to poor hydrologic and thermal conditions. Salinger and Anderson (2006) found adult Chinook to slow and delay upstream migration above an optimal temperature of 16.3°C in the Columbia River. Goniea et al. (2006) observed a similar delay in migration timing of adult Chinook salmon in the same system along with increased temporary use of cooler tributaries. Conversely, Keefer et al. (2008) found upstream migration rates for Snake River sockeye to increase in response to low flows and elevated temperatures, with only one individual permanently straying into a cooler tributary out of 31 radio-tagged fish.

These contrasting behaviors likely point to different strategies for coping with low flows and elevated temperatures and strategies likely vary among species and systems. On one hand, it may be beneficial to delay migration and wait for cooler temperatures and higher flows to signify conditions that are adequate and stable for successful spawning. This same behavior would also allow more time for pioneering and possibly permanent straying. On the other hand, it may be beneficial to migrate rapidly in hopes of maximizing pre-spawn survival and minimizing exposure to elevated temperatures prior to reaching spawning grounds. Drought magnitude and frequency are expected to increase in the 21st century due to anthropogenic climate change which may permanently alter migratory dynamics for certain species (Prudhomme et al., 2014).

The marine phase of the salmon lifecycle is notoriously difficult and expensive to study and as such, there are many information gaps as far as ocean habitats influencing homeward migration across species (Pearcy and McKinnell, 2007; Quinn, 2018). Temperature appears to influence ocean habitat use and has been studied in a variety of ecological contexts. Global-scale oceanographic phenomena such as the Pacific

Decadal Oscillation and North Atlantic Oscillation have been shown to affect population structuring in Atlantic salmon (Horreo et al., 2011) and dispersal patterns in Chinook salmon (Westley et al., 2015) stemming from migratory behavioral responses to thermal conditions in natal catchments. Behavioral thermoregulation during the marine phase has also been documented in Atlantic and chum salmon and appears to be an important facet of behavioral responses to sea surface temperatures with respect to somatic condition and foraging dynamics (Hanson et al., 2013; Kitagawa et al., 2016; Kitahashi et al., 2000; Lacroix, 2013; Tanaka et al., 2000).

In addition to thermal impacts to homing and migratory behavior, other physical habitat attributes may also play a role. Drenner et al. (2015) demonstrated that wind-driven currents can facilitate estuary entry in Fraser River sockeye salmon. This may be due to enhanced delivery of olfactory cues to coastal habitats, energy-saving movement in shoreward currents, or a combination of the two. In response to proposed marine renewable energy (MRE) infrastructure, Godfrey et al. (2015) investigated off-shore migratory behavior of Scottish Atlantic salmon and found that local MRE design alternatives would likely impact foraging and vertical migration. Copping et al. (2021) recently provided a comprehensive review of potential impacts of MRE infrastructure to fish including collision risk, underwater noise, electromagnetic fields (i.e. geomagnetic interference, see Lohmann et al., 2008 and Putman et al., 2013), aggregation behavior, and habitat displacement. It is unclear to what extent these may occur in the case of salmon and if existing MRE infrastructure is already having impacts to marine dispersal and migration.

Avoidance of poor water quality may drive migratory behavior in coastal habitats, particularly with respect to hypoxic zones. Ocean hypoxia often results from a eutrophication event via nutrient enrichment combined with increased temperatures which can occur seasonally or episodically depending on the timing and frequency of oceanographic and terrestrial nutrient inputs (Breitburg, 2002; Levin and Breitburg, 2015). Avoidance of hypoxic zones in favor of oxygen refugia in coastal and estuarine habitats has been observed in several fish species (Craig, 2012; Ludsin et al., 2009), however little is known about salmonid-specific responses to low oxygen conditions. Nearshore coastal hypoxia is known to occur in important marine

salmon habitats such as the eastern Pacific coast, Gulf of Alaska, Gulf of Maine, northern European coastlines, and areas in northern Japan (Fennel and Testa, 2019; Grantham et al., 2004; Levin et al., 2009; Rabalais et al., 2010), and further research is necessary to characterize migratory behavioral responses of salmonid species to hypoxic conditions.

An international collaborative effort is underway to survey multiple Pacific salmon species and their open ocean habitats to (1) characterize genetic population structure, (2) identify endocrine controls on growth and maturity during the ocean phase, (3) sample eDNA to identify other species utilizing pelagic habitats, (4) gauge the presence and risk of microplastic contaminants in ocean habitats (NMFS 2022). The results of this effort will aid in understanding biological and ecological aspects of the marine phase (especially pertaining to population structure and dispersal) and how habitat may drive patterns of homing and straying.

Table 3.1a. Abiotic homing and straying (HS) factors are listed with their corresponding biological HS mechanisms identified by Keefer and Caudill ("K&C", 2014), as well as the mechanistic links between abiotic HS factors and biological HS mechanisms. Biological HS mechanisms from K&C that were not habitat-related were omitted. This table includes those that occur at large spatial scales. Separate abiotic HS factors are listed that correspond to either juvenile or adult lifecycle phases. Abiotic HS factors are indicated by a number and a letter, the number indicates the biological HS mechanism that each is associated with.

Biological HS Mechanisms (from *Keefer and Caudill 2014*)	Large-scale (single catchment, partial catchment, multi-catchment)				
	Juveniles			Adults	
		Abiotic HS Factor (cause)	Link to K&C's Biological HS Mechanism (effect)	Abiotic HS Factor (cause)	Link to K&C's Biological HS Mechanism (effect)
1,2) Incomplete and Interrupted Juvenile Imprinting	**a**	Hydrologic regime during juvenile outmigration	Flood flow pulses may reduce juvenile residence time by passive transport		
	b	Flood frequency	Flashy floods may interrupt floodplain access, limiting residence time		
	c	Landscape scale geomorphic setting (constrained, incised channels), artificially simplified channels lacking complexity, rearing saturation effects	Modified channels throughout migratory corridor may reduce rearing habitat and increase vulnerability to predation		
	d	Landscape with high levels of toxic runoff (ag valley)	Impairment of olfactory imprinting		

3) Genetic and life-history effects	a	Interannual variation in flood flow magnitude (floods that may reduce juvenile residence time by passive downstream transport)	Straying as a genetic adaptation (portfolio effect)	e	Hydrologic regime during adult escapement (Inconsistent or inadequate flow pulses (for delivery of olfactory cues to coastal habitat) among adjacent watersheds may inhibit migratory cues)	Straying as a genetic adaptation (portfolio effect)
	b	Flood duration and frequency (flashy floods may interrupt floodplain access, reducing residence time)		f	Within-species life history variations based on habitat use (i.e. "river-type" vs. "lake-type" in sockeye)	
	c	Landscape scale geomorphic setting: underlying lithology prone to erosion that may result in sedimentation that degrades rearing habitat.		g	Landscape scale geomorphic setting: underlying lithology prone to erosion that may result in sedimentation that degrades spawning habitat, also drainage pattern and elevation gradient affect population structure.	
	d	Water temperature fluctuations due to climatic influence like interannual variability in rain or snowpack/melt		h	Water temperature fluctuations due to climatic influence like interannual variability in rain or snowpack/melt	
4) Adult sensory failure				a	Landscape with high levels of toxic runoff (ag valley)	Impairment of odor detection or other sensory mechanisms for navigation
				b	Presence of pathogens that may affect homing ability (epizootic or	

				conditions promoting proliferation of marine-borne pathogens/parasites)
6) Density-dependent reproductive behaviors		a	Landscape scale geomorphic setting: limited spawning grounds, limited by suitable substrate or thermal barriers	Watershed scale straying occurs due to spawner saturation
		b	Flood duration and frequency	Limited flood flows may attract the majority of a spawning cohort during a single event, resulting in spawner saturation
		c	Adverse hydrologic conditions (low flows, high temps), or poor sedimentary conditions for spawning may deter small populations	Adverse conditions across a watershed may cause small populations to stray (seeking secondary habitat criteria without density dependent behavioral cues)
7) Attraction to non-natal sites		a	Watershed size	High rates of straying may occur in shorter, more dynamic coastal watersheds as opposed to larger inland systems

		(more efficient to explore), anthropomorphic disturbance may deter them
b	Adverse hydrologic conditions (low flows, high temps)	Adverse conditions across a watershed may cause small populations to stray, seeking secondary habitat criteria.
c	Poor water quality (high temp, low DO)	May lead to straying if initial freshwater conditions are not indicative of viable spawning habitat upstream.
d	Adverse oceanographic conditions	Ocean conditions may alter migratory dynamics when homing as ocean adults (or returning to sea for iteroparous species)

Table 3.1b. Abiotic homing and straying (HS) factors are listed with their corresponding biological HS mechanisms identified by Keefer and Caudill ("K&C", 2014), as well as the mechanistic links between abiotic HS factors and biological HS mechanisms. Biological HS mechanisms from K&C that were not habitat-related were omitted. This table includes those that occur at small spatial scales. Separate abiotic HS factors are listed that correspond to either juvenile or adult lifecycle phases. Abiotic HS factors are indicated by a number and a letter, the number indicates the biological HS mechanism that each is associated with. Lettering in this table is continuous from Table 1a for each biological HS mechanism.

Biological HS Mechanisms (from *Keefer and Caudill 2014*)	Local scale (reach scale or finer)				
	Juveniles			Adults	
		Abiotic HS Factor (cause)	Link to K&C's Biological HS Mechanism (effect)	Abiotic HS Factor (cause)	Link to K&C's Biological HS Mechanism (effect)
1,2) Incomplete and Interrupted Juvenile Imprinting	e	Habitat complexity in natal rearing areas	The availability of predator refugia can impact both residence time and stress, affecting imprinting		
	f	Point source pollution in natal rearing habitats OR introduction of non-natal water via mechanical release	Inhibits olfactory imprinting		
	g	Rearing habitat quality and quantity in natal reach (food availability, density-dependent competition, adverse incubation and rearing temperatures, and floodplain inundation time/frequency)	The quality of available rearing habitat may influence juvenile residence time and imprinting physiology		

3) Genetic and life-history effects	**i**	Interannual variability in the quality and quantity of natal rearing habitat	Straying as a genetic adaptation (portfolio effect)	**l**	Localized disturbances result in interannual variability in the viability of natal spawning reaches (prone to fires, landslides, etc.)	Straying as a genetic adaptation (portfolio effect)
	j	Local scale geomorphic setting: local area of interest prone to sedimentation which may degrade rearing habitat		**m**	Local scale geomorphic setting: geomorphic habitat unit types and resultant features	
	k	Interannual variability in localized controls to water temperature in natal rearing habitat (i.e., hyporheic flow or riparian shading)		**n**	Interannual variability in localized controls to water temperature in natal rearing habitat (i.e., hyporheic flow, tributary inflow, or riparian shading)	
4) Adult sensory failure				**c**	Point source contamination of compounds toxic to olfactory processes OR introduction of non-natal water via mechanical release	Impairment of odor detection, vision, lateral line function, or acute injury to swim bladder -

	d	Noise generating activity or light pollution that may affect migratory behavior (pile driving, construction, industrial processes)	all used for navigation
6) Density-dependent reproductive behaviors	**d**	Local scale geomorphic setting: confined spawning grounds, limited by suitable substrate due to channel simplification and/or lack of natural "channel evolution" processes.	Local scale straying occurs due to spawner saturation
	e	Localized disturbances result in interannual variability in the viability of natal spawning reaches (prone to fires, landslides, etc.)	
	f	Localized degradation to spawning habitat (high temps, low flows, sedimentation, low DO, etc.) may deter small populations	Localized adverse conditions may cause small populations to alter migratory timing/movement or even stray (seeking secondary habitat criteria without density-dependent behavioral cues)
7) Attraction to non-natal sites	**e**	Drainage pattern and spatial arrangement of adjacent spawning tributaries, or passage issues (partial barriers)	Spatial proximity to adjacent spawning tributaries is thought to be a factor in straying

| | f | Large discrepancies in flow and temperature at river confluences during the migration of small populations | Physical migratory cues may dominate in low-density spawning cohorts |
| | | | Spawners that are olfactorily impaired may rely on secondary cues like flow and temperature |

4.3   Meta-analysis

The goal of the literature metastudy was to evaluate the extent to which abiotic variables are included in study designs of homing and straying and whether abiotic HS factors that drive homing and straying patterns are actually being tested. After a systematic literature search, each of 169 final publications in the dataset was examined for study type, region where the study occurred, spatial extent (scale) at which the study occurred, species investigated, and all variables measured and analyzed. Abiotic variables and corresponding studies were identified as well as the abiotic HS factors that were directly tested.

4.3.1   Systematic Literature Search

The five causes of straying identified by K&C that have links to abiotic HS factors were used to generate Boolean search criteria to sample existing literature. The Web of Science™ ("WoS", Clarivate) database was queried using targeted Boolean search criteria specific to each of the biological HS mechanisms identified by K&C but containing search terms specific to the potential abiotic HS factors that we identified. These search strings, including terms and Boolean operators, are listed in Table 3.2Table 3.3. Five searches were conducted according to the five biological HS mechanisms investigated.

The five WoS searches yielded 332 articles, but that included 75 duplicate items that were eliminated. 55 of the remaining articles pertained to species other than anadromous salmonids and were also eliminated (including freshwater resident salmonids and other diadromous species). Of the 202 remaining, 33 articles focused on anadromous salmonids but were found to not be relevant to the topic of homing and straying and were eliminated. Existing reviews, syntheses, and guidance documents were also excluded from the metastudy. A final set of 169 articles was investigated in the metastudy, the full list as well as their attributes is included in Table A.C.1 in Appendix C.

Table 3.2. Biological homing and straying mechanisms identified by Keefer and Caudill (2014) and corresponding Boolean search criteria used in Web of Science search.

Straying Mechanism from K&C	Boolean Search String
Incomplete/Interrupted Juvenile Imprinting	TS = (Salmon AND imprinting AND (juvenile OR smolt OR smoltification OR parr OR fry) AND (natal OR rearing OR hatchery OR stress OR hormones OR "residence time" OR "water quality" OR odor))
Adult Sensory Failure	TS = (Salmon AND adult AND (homing OR straying) AND (olfaction OR toxicity OR pesticide OR runoff OR "sensory impairment" OR sedimentation OR "gill fouling" OR hydroacoustic OR noise OR pile driving OR turbidity OR geomagnetic OR rheotaxis OR pathogens))
Density Dependent Reproductive Behaviors	TS = (Salmon AND adult AND (homing OR straying) AND (abundance OR saturation OR competition OR density OR "spawning habitat" OR "carcass survey" OR counts OR telemetry OR discharge OR "flow pulse" OR hydrograph))
Genetic and Life History Effects	TS = (Salmon AND (homing OR straying) AND (portfolio effect OR landscape OR stochasticity OR stability OR phenology OR "migration timing" OR microsatellites OR "single nucleotide polymorphism" OR "genetic marker"))
Attraction to Non-Natal Sites	TS = (Salmon AND adult AND (homing OR straying) AND (proximity OR watershed OR basin OR temperature OR "dissolved oxygen" OR "water quality" OR discharge OR hydraulics OR turbidity OR sedimentation OR "spawning gravel" OR substrate OR "hyporheic flow"))

4.3.2   Analytical Methods

An augmented Dickey-Fuller (ADF) test in the R package *tseries* was used to test whether instances of inclusion of abiotic variables in study designs and tests of abiotic HS factors per year have increased over time (Dickey and Fuller, 1979; Said and Dickey, 1984; Trapletti, 2022). The ADF test uses an autoregressive model and is designed to test for the presence of a "unit root" in a time series (null hypothesis), or whether the time series exhibits "stationarity". The presence of a unit root in the model would result in either a positive or negative directional trend through time. A stationary process is stochastic and may oscillate, but its unit root is equal to zero. It does not trend in any direction and its unconditional probability distribution does not change in time. In an ADF test, the autoregressive model takes the following form:

$$\Delta y_t = \alpha + \beta t + \gamma y_{t-1} + \delta_1 \Delta y_{t-1} + \cdots + \delta_{p-1} \Delta y_{t-p+1} + \varepsilon_t \qquad (1)$$

where y is a variable at time t, α and β are regression constants, γ is the coefficient representing the unit root, δ is a unit root coefficient given the change operator Δ, and p is the lag order used in the autoregression model. The R package *tseries* defaults to a lag order integer value p based on the following:

$$p = (N_t - 1)^{1/3} \qquad (2)$$

where N_t is the number of time steps analyzed in the time series.

The ADF test produces a t statistic "DF_τ" based on the following ratio of the γ coefficient to its standard error:

$$DF_\tau = \frac{\hat{\gamma}}{SE(\hat{\gamma})} \qquad (3)$$

A 95% confidence level was used to test for statistical significance (ADF test is statistically significant if $DF_\tau < DF_{\tau\,crit}$).

A one-way ANOVA test (see Ross and Willson, 2017) at a 95% confidence level was used to test for differences among mean values of (i) number of abiotic variables included per study, and again among mean values of (ii) number of abiotic HS factors tested per study among categories of the following: study method type, study location, and study design (see stated hypotheses 2a-c and 3a-c in Table 3.3). These hypotheses were tested using the whole set of papers as well as the subset that contained at least one abiotic variable.

Table 3.3. Hypotheses tested in this review.

		Hypothesis
H1	a	The number of abiotic variables included in the literature have increased consistently over time
	b	The number of abiotic HS factors tested in the literature have increased consistently over time
H2	a	Abiotic variables are included disproportionately among study types.
	b	Abiotic variables are included disproportionately among study regions.
	c	Abiotic variables are included disproportionately among study species.
H3	a	Abiotic HS factors are tested disproportionately among study types
	b	Abiotic HS factors are tested disproportionately among study regions
	c	Abiotic HS factors are tested disproportionately among study species

4.4 Results

Of the 169 papers analyzed, only 70 (41%) included at least one abiotic variable in their study design; 42 included two or more abiotic variables (25%) and 21 included three or more (12%, see Figure 3.3). The most common study method type (Table 3.4) was population genetics/dynamics (42 papers) and 12 of those included at least one abiotic variable (28.6%). Biotelemetry studies had the greatest percentage of ≥1 abiotic variable included with 21 out of 32 papers (65.6%). The U.S. West Coast and British Columbia dominated study locations (Table 3.5) with 62 papers, 21 of which included ≥1 abiotic variable (33.9%). Atlantic salmon were used in the greatest number of papers at 38 (Table 3.6), followed closely by Chinook salmon at 34. Of the papers using these species, 19 (50.0%) and 13 (38.2%) included ≥1 abiotic variable, respectively. Table 3.7 includes a list of all species included in our sample of the literature as well as their taxonomic classification. Table A.C.2 in Appendix C includes a summary of frequencies of abiotic variable type among classes of study method type, study location, and study species.
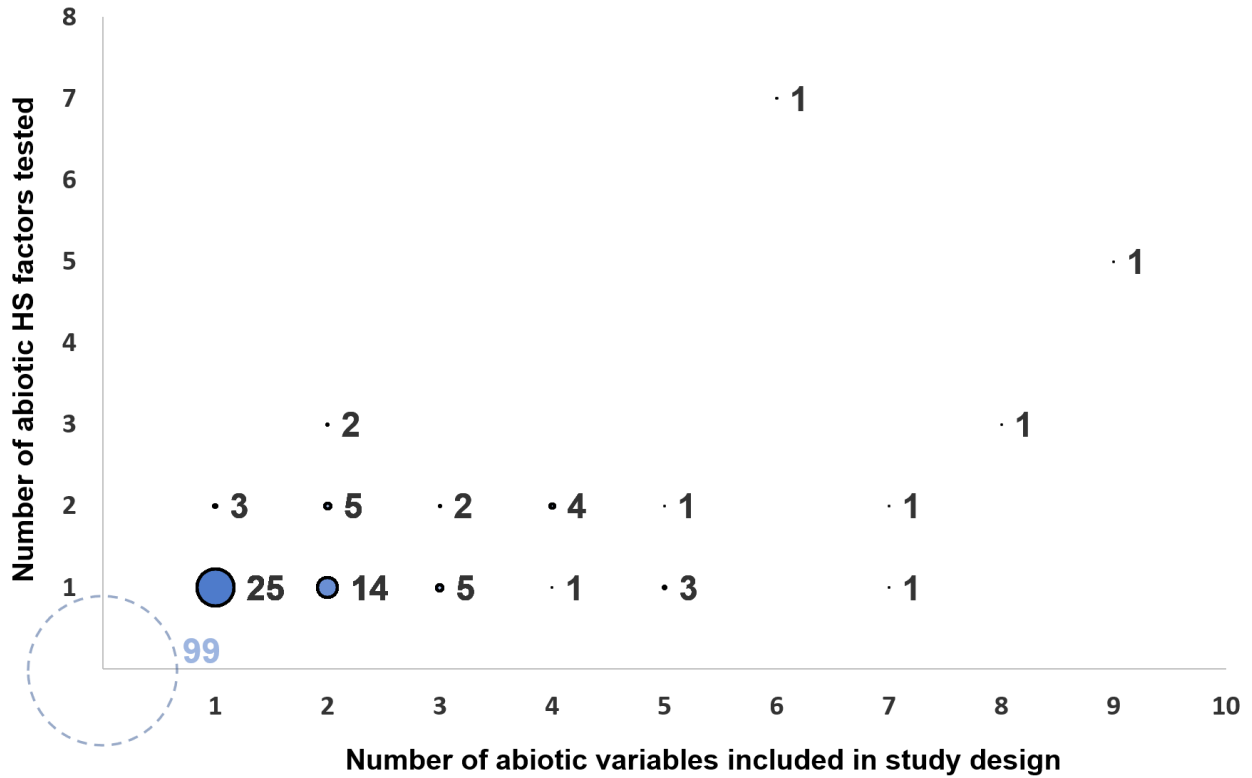
Figure 3.3. Number of abiotic variables included in each source vs. how many abiotic homing/straying (HS) factors were tested in each of those sources. Point sizes and adjacent number indicate how many sources correspond to each combination of abiotic variables and abiotic homing and straying factors. The point at (0,0) indicates that 99 sources contained zero abiotic variables and tested zero abiotic homing and straying factors.

Table 3.4. Summary of abiotic variables included, and abiotic homing and straying factors tested among study method types.

Study Type	Total number and percentage of studies included in review	Number and percentage of studies measuring ≥ 1 environmental habitat variable	Mean number of abiotic variables included	Mean number of abiotic HS factors directly tested
Population Genetics/Dynamics	42 (24.9%)	12 (28.6%)	2.7	1.8
Mark-recapture	36 (21.3%)	14 (38.9%)	2.1	1.7
Biotelemetry	32 (18.9%)	21 (65.6%)	2.8	1.4
Lab-based/Closed system	27 (16.0%)	12 (44.4%)	1.9	1.2
Phenotype, Gene Expression, Morphometrics, Endocrine Response	12 (7.1%)	5 (41.7%)	1.0	1.0
Modeling (population, lifecycle, habitat)	11 (6.5%)	4 (36.4%)	3.5	1.3
Microchemistry to track movement	6 (3.6%)	1 (16.7%)	2.0	1.0
Stationary counts (weir, redd, etc.) or catch data	3 (1.8%)	1 (33.3%)	4.0	2.0
All Studies	169	70 (41.4 %)	2.4	1.5

Table 3.5. Summary of abiotic variables included, and abiotic homing and straying factors tested among study locations.

Study Location	Total number of studies included in location	Number of studies measuring ≥ 1 environmental habitat variable	Mean number of abiotic variables included	Mean number of abiotic HS factors directly tested
U.S. West Coast and B.C.	62	21 (33.9%)	3.0	1.7
Europe	36	18 (50.0%)	2.8	1.6
Lab or Model	31	12 (38.7%)	2.0	1.2
AK and Yukon	22	9 (40.9%)	1.8	1.3
Japan	8	4 (50.0%)	2.5	1.0
North American Atlantic Coast	7	4 (57.1%)	3.0	1.8
South America	2	1 (50.0%)	1.0	1.0
New Zealand	1	1 (100.0%)	1.0	1.0
All Studies	169	70 (41.4%)	2.4	1.5

Table 3.6. Summary of abiotic variables included, and abiotic homing and straying factors tested among study species.

Study Species	Total number of studies including species	Number of studies measuring ≥ 1 environmental habitat variable	Mean number of abiotic variables included	Mean number of abiotic HS factors directly tested
Atlantic	38	19 (50.0%)	2.5	1.7
Chinook	34	13 (38.2%)	2.5	1.8
Sockeye	22	11 (50.0%)	2.4	1.2
Coho	15	4 (26.7%)	3.0	1.0
Chum	14	8 (57.1%)	3.0	1.3
Steelhead	12	4 (33.3%)	1.8	1.8
Multiple Oncorhynchus spp.	10	2 (20.0%)	1.5	1.5
Pink	7	2 (28.6%)	1.5	1.5
Brown Trout	5	3 (60.0%)	1.7	1.3
N/A, theoretical model	5	1 (20.0%)	2.0	1.0
Charr (Salvelinus spp.)	4	0 (0.0%)	0.0	0.0
Brook Trout	1	1 (100.0%)	2.0	1.0
Grayling	1	1 (100.0%)	3.0	1.0
Masu	1	1 (100.0%)	1.0	1.0
All Studies	169	70 (41.4%)	2.4	1.5

Table 3.7. Species included in the literature sample used in the metanalysis component of this study and their taxonomic classification.

Family	Subfamily	Tribe	Genus	Species	Common Name
Salmonidae	Salmoninae	Oncorhynchini	Oncorhynchus	O. *tshawytscha* (Walbaum, 1792)	Chinook salmon
				O. *nerka* (Walbaum, 1792)	sockeye salmon
				O. *kisutch* (Walbaum, 1792)	coho salmon
				O. *keta* (Walbaum, 1792)	chum salmon
				O. *gorbuscha* (Walbaum, 1792)	pink salmon
				O. *masou* (Brevoort, 1856)	masu salmon
				O. *mykiss* (Walbaum, 1792)	steelhead trout
		Salmonini	Salmo	S. *salar* (Linnaeus, 1758)	Atlantic salmon
				S. *trutta* (Linnaeus, 1758)	brown trout
			Salvelinus	S. *leucomaenis* (Pallas, 1814)	whitespotted char
				S. *alpinus* (Linnaeus, 1758)	arctic char
				S. *fontinalis* (Mitchill, 1814)	brook trout
	Thymallinae	*N/A*	Thymalus	T. *thymallus* (Linnaeus, 1758)	European grayling

Among the 169 papers analyzed, one was dated in 1968 and did not include any abiotic variables. The remainder of sample continues onward from 1990, so we began our time series analysis there (Figure 3.4). The ADF test for stationarity in the number of abiotic variables included in study designs through time and the number of abiotic HS factors tested through time resulted in non-significant p values of 0.42 and 0.38, respectively (Table 3.8). This indicates the presence of a unit root in each time series, resulting in positive directional (non-stationary) trends through time. At 95% confidence, the literature sample shows a positive directional increase through time for both, though the rates of increase are still low (increases of 0.37 abiotic variables included per year and 0.22 abiotic HS factors tested per year). The time series exhibits peaks and valleys, with the magnitude of the peaks increasing through time.
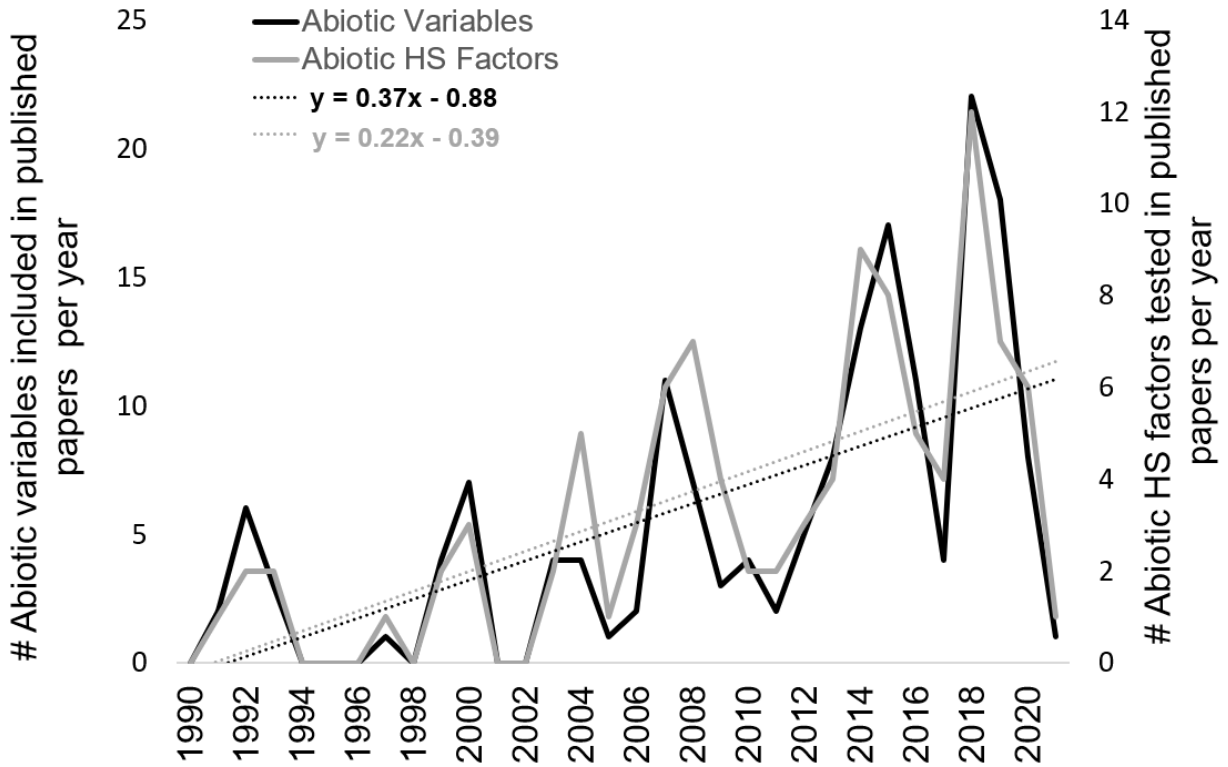
Figure 3.4. Time series plot of both the number of abiotic variables included in study designs, and the number of abiotic homing/straying factors tested in published papers per year. Trendlines for both show a linear increase through time since 1990.

Table 3.8. Results of the augmented Dickey-Fuller test for timeseries stationarity. Hypotheses test whether there is a "unit root" present (i.e. non-stationarity) at 95% confidence in (a) the number of variables included, or (b) the number of abiotic homing and straying factors tested per year through time among the studies in our literature sample. Non-significant results indicate that there is a unit root present which results in a positive linear trend in the time series.

		DFτ	*DFτ crit.*	*Lag Order*	*P-value*
H1	a	-2.40	-3.45	3	0.42
	b	-2.49	-3.45	3	0.38

ANOVA tests for differences in mean abiotic variables included and abiotic HS factors tested among study

method types, locations, and species did not yield any statistically significant differences at 95% confidence

($p > 0.05$ for both hypotheses, see Table 3.9 and Table 3.10). We failed to reject our null hypotheses. These

results suggest that both abiotic variables and abiotic HS factors are excluded uniformly in study designs

across the literature on homing and straying in anadromous salmonids.

Table 3.9. Results from the one-way ANOVA tests for differences in mean values of abiotic variables included (H2) and abiotic homing and straying factors tested (H3) among all papers analyzed. a, b, and c are study method type, study location, and study species, respectively.

		SS	*df*	*MS*	*F*	*P-value*	*F crit*
H2	a	32.99	7	4.71	1.75	0.10	2.07
	b	8.49	7	1.21	0.43	0.88	2.07
	c	31.28	13	2.41	0.86	0.60	1.78
H3	a	5.36	7	0.77	0.84	0.56	2.07
	b	3.34	7	0.48	0.52	0.82	2.07
	c	8.42	13	0.65	0.70	0.76	1.78

Table 3.10. Results from the one-way ANOVA tests for differences in mean values of abiotic variables included (H2) and abiotic homing and straying factors tested (H3) among only the papers that included at least one abiotic variable in their study design. a, b, and c are study method type, study location, and study species, respectively.

		SS	*df*	*MS*	*F*	*P-value*	*F crit*
H2	a	24.69	7	3.53	1.06	0.40	2.16
	b	13.43	7	1.92	0.96	0.47	2.18
	c	13.87	13	1.07	0.28	0.99	1.90
H3	a	5.48	7	0.78	0.81	0.58	2.16
	b	1.64	7	0.23	0.84	0.56	2.18
	c	3.56	13	0.27	0.27	0.99	1.96

4.5 Discussion

Our results illustrate a systemic bias of excluding abiotic variables in the literature on salmon homing and

straying. Only 41.4% of studies including at least one in their study design (25% with two or more and 12%

with three or more), largely independent of study method type, location, or species. The Boolean search

criteria that we generated were based on a thorough review of potential abiotic HS factors that coincide

with K&C's biological HS mechanisms of straying behavior. Admittedly, we did not conduct an exhaustive literature review including white and gray literature, government reports, fish monitoring databases, etc., but we designed the metastudy to sample existing peer-reviewed literature in a way that would represent all facets of research on homing and straying in anadromous salmonids. Furthermore, our impression is that inclusion of this additional non-peer-reviewed literature would not appreciably change the results of our analysis of peer-reviewed papers. Our findings point to a significant lack of focus in the peer-reviewed literature on biotic-abiotic interactions that play important roles in driving patterns of homing and straying. In many cases, published analyses and results could be better contextualized and synthesized with the addition of an abiotic component that characterizes migratory responses to habitat conditions. Our time series analysis shows a trend of improvement of this issue, though it still appears to be pervasive.

4.5.1 Study Method Types

4.5.1.1 Population genetics

Whether an individual adult salmon successfully homes to its natal stream or strays to a non-natal site has obvious implications from the perspective of that individual's reproductive success. However, patterns of homing and straying among many individuals may have profound population-level effects. It is this aspect of their life history that has allowed salmonids to persist over multiple landscape scale disturbance events throughout the last 24 million years (Waples et al., 2008, 2009; Waples and Hendry, 2008). From a management and conservation genetics standpoint, maintaining genetic population structure within a population or among subpopulations is often a high priority for the sake of resilience in the face of future disturbances (Folke et al., 2004; Schindler et al., 2010). Therefore, using genetic markers to characterize population structure is a common research approach to inform conservation programs and prioritize species recovery actions. However, it has been our experience that published research in this area tends to ignore many of the potential abiotic HS factors that may have led to present-day population structures. The results of our metastudy support this hypothesis, with only 28.6% of population genetics studies including one or more abiotic variables despite being the most frequent study method type among the papers that we

analyzed (42 out of 169). Conservation programs could be aided by addition of abiotic variables in study designs to help identify management actions that facilitate desired migratory routing and the conservation or improvement of future genetic structure and diversity.

4.5.1.2   Tracking migratory movement

Mark-recapture, biotelemetry, microchemistry, and stationary count methods accounted for a combined 46% of papers analyzed. Each of these methods are used to track or account for movement of individuals in order to understand the consequences of precise movements in various ecological contexts. As noted in our abiotic framework, drivers of straying may occur in early or late lifecycle stages, and therefore characterizing migratory movement in the context of homing and straying may require different methodological approaches depending on the life stage being analyzed. Mark-recapture studies, accounting for 21.3% of papers analyzed had 38.9% include one or more abiotic variable. Some key metrics that can be generated from this method are abundance, survival, migration and passage rates, and habitat utilization (Bottom et al., 2005; Letcher and Horton, 2008; Levy and Northcote, 1982; Schwarz and Dempson, 1994). Mark-recapture methods are well-suited for investigating the effects of abiotic HS factors on migratory routing and habitat selection, and responses to abiotic stressors that may influence rates of straying in accordance with our abiotic framework. We found that many mark-recapture studies that did not include an abiotic component, often included location information (i.e. tagging and recovery sites) without any accompanying abiotic data attributes. This can be useful for continuing specific projects in a given location by researchers with local and institutional knowledge of the project, but ultimately this hinders the advancement of the basic understanding of salmonid life history as well as applied research elsewhere. Biotelemetry studies accounted for 18.9% of all papers analyzed but had the highest instance of one or more abiotic variables included in study designs at 65.6%. Biotelemetry research applications are similar to mark-recapture in that they track movement, but they differ in that they are designed to directly measure continuous movement rather than infer movement indirectly based on two observed locations. Perhaps biotelemetry studies had a higher instance of abiotic study components because there is a natural inclination

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to characterize potential abiotic drivers of real-time movements because they can be measured concurrently and compared directly. Microchemical analysis is often used to track movements by comparing stable isotope ratios in various tissues with georeferenced isotopic signatures of habitats that have been occupied by an individual. 3.5% of papers analyzed used this method and only 16.7% (one paper) included an abiotic variable. Similar to the other studies tracking migratory movement, the microchemistry studies that did not measure any abiotic variables only included location information via habitat occupancy at various life stages without any abiotic data attributes to help explain patterns of movement among those locations. Finally, stationary counts made up 1.7% (3 papers), one of which measured an abiotic variable. Methods of this kind, such as redd surveys, can generate metrics similar to mark-recapture studies where movement between detections must be inferred.

4.5.1.3   Other methods

In addition to tracking fish movement and characterizing population-level consequences of movement, there are also complex physiological processes within individuals that influence patterns of migratory movements throughout the lifecycle, and ultimately drive patterns of homing and straying in adults. These processes can often be measured both in controlled lab conditions and in field samples. Lab-based studies accounted for 16.0%, of which 44.4% included abiotic variables. By isolating effects and controlling for confounding variables, laboratory-based methods can be extremely useful for quantifying effects of abiotic variables on behavioral and physiological responses. We found that many of the studies without abiotic analyses focused on characterizing olfactory physiology, isolating endocrine responses to odor cues and mapping sequences of neurological activity in the organs involved in olfaction. Lab-based studies will remain important in the future, as many conservation research programs continue to pivot their focus to climate change effects and models of physiological tolerances in salmonid species (Debes et al., 2021; Elliott and Elliott, 2010; Zhang et al., 2019). For this reason, we expect to see increased focus on biotic-abiotic linkages in this category. The broad category of phenotype expression, gene expression, morphometrics, and endocrine response accounted for 7.1% of papers analyzed with 41.7% including an

abiotic variable. Methods in this category are also well suited for investigating biotic-abiotic linkages as they can resolve mechanistic gaps between abiotic drivers and observed physiological processes that have direct or indirect consequences for homing and straying dynamics. One example is sampling levels of cortisol in juveniles which is an indicator of stress, and which has also been shown to affect olfactory imprinting at critical life stages (Carruth, 2002). Continued investigations into physiological responses to habitat conditions will benefit future research on homing and straying in salmonids as more biotic-abiotic linkages are disentangled and characterized. The final methodological category was modeling studies, accounting for 6.5%, with 36.4% including one or more abiotic variables. Publishing conceptual models of population dynamics, lifecycle processes, and habitat interactions in the context of homing and straying can be beneficial for establishing a quantitative framework for future empirical investigations.

4.5.2   Study Locations

4.5.2.1   The U.S. Pacific Coast and British Columbia

The US Pacific Coast and British Columbia was the dominant study region among our sampled literature, having both a wide variety of ecosystems and many of the anadromous salmonid species ranges represented within it. Rather than discuss every major watershed in this region, we compare and contrast British Columbia with California. The southernmost extent of the US Pacific coast includes the California Central Valley and coastal California watersheds, which have been highly degraded since the mid-19th century due to natural resource exploitation, construction of water management infrastructure, alteration of natural hydrologic regimes, and intensive agricultural and industrial land use (Mount, 1995; Yoshiyama et al., 2001, 1998). Being southernmost in latitude and having a relatively arid climate, California salmon-bearing streams will also be put under immense pressure as mean annual temperatures increase and precipitation decreases with anthropogenic climate change (Matella and Merenlender, 2015; Moyle et al., 2017; Trenberth, 2011). Elevated levels of straying in California Chinook salmon populations as a result of hatchery production practices has already been documented and continues to be an issue of concern (Huber et al., 2015; Sturrock et al., 2019).

The northernmost extent of the Pacific North American range includes the Fraser River catchment as well as other coastal catchments including the Skeena, Stikine, Nass, and Taku drainages. A status review of *Oncorhynchus spp.* in British Columbia by Slaney et al. (1996) found that out of 5487 stocks analyzed, 624 stocks were at high risk, 78 were at moderate risk, 230 were of special concern, and 142 had been extirpated in the 20th century. Since then, additional risk analyses have identified imperiled populations in the face of climate change, land use, passage barriers, and fishing pressure (Finn et al., 2021; Healey, 2011; Hinch et al., 2012). Although loss and degradation of existing habitat has not been as dire as in California, relatively high rates of straying have been found to occur such as 42.9% of coho in the Coldwater River catchment in the interior Fraser basin (Turcotte and Shrimpton, 2020). In a setting like British Columbia where straying may not have such severe consequences for conserving specific evolutionarily significant units via migratory phenotypes (i.e. winter-run Chinook in the California Central Valley, see Thompson et al., 2020), straying may be perceived by researchers and managers in a different light. For Chinook salmon in the upper Fraser River, Walter et al. (2009) demonstrated that gene flow via straying resulted in increased effective populations sizes among subpopulations and enhanced a diverse genetic structure, though they only alluded to potential abiotic drivers of straying patterns. Our analysis found that 33.9% of papers from the U.S. West Coast and British Columbia included one or more abiotic variables in their study designs. Given the diversity of species, habitats, and management goals in this region, future studies conducted in the context of homing and straying would have more utility with the inclusion of biotic-abiotic linkages to identify drivers of homing and straying patterns that may have important management implications.

4.5.2.2 *Alaska and Yukon*

Continuing north, Alaska and the Yukon Territory are home to a wide range of salmonid species as well, including the northernmost extent of the range of *Oncorhynchus spp.* and representing 13% of papers in our analysis. With less human development than areas to the south, Alaska and Yukon contain some of the most pristine salmon habitat in the world. Nevertheless, many of these populations have felt the effects of fishing pressure, mining, extraction of petroleum products, and urbanization in some areas (Alessa et al.,

2011; Mauger et al., 2017; Trammell et al., 2021). Similar to fishery management considerations in British Columbia, understanding patterns of gene flow via straying and genetic drift in small, isolated populations lacking interaction with strays can be useful in understanding contemporary genetic stock structure in wild populations (Garvin et al., 2013; Olsen et al., 2003). Unlike areas to the south, little is known about the consequences of hatchery strays in Alaska and the Yukon Territory. Grant (2012) noted that approximately 31% of Alaska's salmon are hatchery-produced and that over time, managers may expect to see some of the consequences of reproductive interaction between wild- and hatchery-origin populations that have been documented elsewhere. With a large proportion of wild salmon production and economically important ocean salmon fisheries that depend on wild production, future research on homing and straying in this area must investigate abiotic drivers of dispersal. Significant climate change impacts are predicted in far northern latitudes as well as continued mining and natural resource extraction in the 21st century (Cheung and Frölicher, 2020; Conley et al., 2013; Hinzman et al., 2005).

4.5.2.3   Europe

Europe was the second most represented region in our analysis at 21% of papers analyzed. Atlantic salmon is the dominant species in this region and dispersal among European nations in the North Atlantic is complex. With centuries of human land use in this region, habitat fragmentation has often limited dispersal and driven contemporary genetic stock structure (Nielsen et al., 1999; Seliger and Zeiringer, 2018). Northern Europe also leads the world in Atlantic salmon farming with Norway being the number one producer (Iversen et al., 2020). Approximately half of Norway's wild stocks have experienced genetic introgression with farmed escapees and the extent of genetic interactions with other populations in the North Atlantic remains unknown (Glover et al., 2017, 2012). Bolstad et al. (2017) documented significant alterations in life history traits of previously wild stocks that had experienced multiple generations of hybridization with farmed escapees, suggesting that wild Atlantic salmon populations in the North Atlantic are at risk of degraded genetic structure if current farming practices continue. Another challenge to these populations is susceptibility of recruitment and post-smolt survival to climate forcing indices such as the

Atlantic Multidecadal Oscillation and the North Atlantic Oscillation (Friedland et al., 2009; Horreo et al., 2019; Todd et al., 2008). Homing and straying dynamics among Atlantic salmon in Europe are complicated by the widespread exposure to artificially reared individuals and sea surface temperature anomalies that result in poor ocean rearing conditions that affect migration. Future studies of abiotic drivers affecting dispersal of both wild and farmed individuals will be critical in developing management plans that can mitigate the genetic homogenization that is taking place in this region and restore population resilience.

4.5.2.4 *Other regions*

Japan, the North American Atlantic Coast, South America, and New Zealand were represented in the fewest papers in our analysis at a combined 10.7%. Hokkaido Island in Japan produces a large number of hatchery-origin fish and ocean harvest rates have steadily increased for pink and chum salmon as a result (rates of masu salmon harvest are still in decline, see Morita et al., 2006). Efforts are underway in Japan to refine management strategies to mitigate straying of hatchery-origin salmon and maintain genetic integrity of wild populations, however knowledge of abiotic drivers of straying in Japanese populations is limited at this point (Kitada, 2020; Nagata et al., 2012). Atlantic salmon occur along the North American Atlantic Coast, ranging from the Connecticut River north to Newfoundland and Labrador in Northern Canada, with a distinct demographic divide between northern and southern populations around the Gulf of St. Lawrence (Rougemont and Bernatchez, 2018). Commercial exploitation of these populations in the 20th century was so intense that it led to indefinite closures of the ocean fishery in the U.S. and Canada (Dempson, 2001; Saunders, 1981). Currently, hatchery supplementation occurs and salmon-focused watershed restoration efforts in recent decades have had some success in restoring habitat functionality and connectivity (Holbrook et al., 2011; Izzo et al., 2016; Kocik et al., 2022). For northern populations in Newfoundland and Labrador, Bradbury et al. (2014) demonstrated that genetic structure is mostly determined by genetic drift within populations and little effective straying occurs. In the southern extent of this region, straying among populations may be more of a management concern due to habitat fragmentation and hatchery practices. Similar to observations in California hatcheries, Gorsky et al. (2009) demonstrated the

importance of hatchery release strategies for homing and straying rates of Atlantic salmon in the Penobscot River basin. New Zealand and areas of southern South America (Argentina and Chile) have had anadromous salmon species introduced to their waterways and farming occurs in these areas as well (Di Prinzio and Pascual, 2008; Fløysand et al., 2016; Quinn et al., 2001; Soto and Norambuena, 2004). Research on non-native salmon straying in these areas has focused more on characterizing contemporary population structure, genetic stability, rates of gene flow, and threats to endemic species than informing conservation goals or management intervention to conserve them (Ciancio et al., 2015, 2005; Correa and Gross, 2008; Kinnison et al., 2011, 2002; Unwin and Quinn, 1993).

4.5.3   Study Species

In their synthesis of published data on straying in anadromous salmonids, Keefer and Caudill (2014) included a breakdown of straying patterns by species so we will not duplicate that effort here. Rather, we discuss specific life history strategies by species or groups of species in the context of biotic-abiotic linkages that are meaningful for homing and straying dynamics. Although these are defining characteristics, some may apply across multiple species in certain cases.

4.5.3.1   River spawners with complex age structures

The majority of salmonid species that turned up in our search primarily spawn in freshwater rivers and have complex age structures in ocean stocks and in a given spawning cohort. Three out of the eight species in this category exhibit semelparity (Chinook, coho, and masu) with sexually mature individuals spawning only once in their lifecycle. Atlantic and Chinook salmon were the most dominant species with 38 and 34 papers, respectively. This is not surprising given the cultural significance as well as their importance from a natural resource perspective (Dyrset et al., 2022; Woo and Noakes, 2014). Notably however, 50% of Atlantic salmon papers included at least one abiotic variable while only 38% of Chinook papers did so. These findings are closely aligned with percentages of abiotic study variables present in European studies (also 50%) compared to the U.S. West Coast and British Columbia (33.9%). Coho and masu comprise the

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remaining semelparous species in this category and they appear to receive less research attention with 15 and 1 paper, respectively. Remaining iteroparous species were steelhead, brown trout, brook trout, and European grayling and were represented in 12, 5, 1, and 1 papers, respectively. Species that rely on riverine habitat for spawning and juvenile rearing are vulnerable to a wide array of potential hazards to olfactory imprinting and homing as we identified above in our abiotic framework (Table 3.1a and Table 3.1b). It is somewhat encouraging to see the high instance of abiotic components included among the Atlantic salmon literature. Much of the terrestrial range of this species has seen centuries of intensive land use practices that degraded and fragmented river networks critical to the persistence of wild stocks (Aas et al., 2011). With continued cooperation and investment among natural resource agencies, the research on abiotic influences on this species can serve as an example to others in this category (Lennox et al., 2021).

4.5.3.2   *Chum salmon and the estuarine environment*

Chum salmon utilize brackish estuarine habitats for juvenile rearing (as do pink salmon in some cases), and spawning occurs in lower river reaches that may be tidally and chemically influenced by estuarine water (Johnson et al., 1997; Quinn, 2018). As such, they face some challenges to abiotic HS factors that are characteristic of these environments. Appearing in 14 papers in our analysis (8 with one or more abiotic variables included), chum received relatively less attention than the freshwater spawning species despite the complexity of the habitats utilized by this species. Pesticide compounds, many of which are toxic to olfactory physiology, have been shown to accumulate in estuarine sediments via agricultural runoff (Arias et al., 2011; Cruzeiro et al., 2016; Kuivila and Foe, 1995). In a review on this topic, Cuevas et al. (2018) highlight the innovations that have come about in recent years for detecting concentrations of pesticide compounds in the estuarine environment that are relevant to the salmonid lifecycle and new understandings of physiological and trophic pathways for exposure. For chum salmon, exposure to elevated levels of estuarine pesticides may inhibit olfactory imprinting in early juvenile stages or at the critical parr-smolt transformation. Another stressor typical of estuarine habitats is the development of hypoxic zones via eutrophication (Breitburg, 2002; Breitburg et al., 2009; Howarth et al., 2011). Salmon exhibit elevated

levels of cortisol in response to hypoxic conditions, and rates of cortisol production are directly linked to the endocrine pathways that underlie olfactory imprinting (Björnsson et al., 2011; Carruth, 2002; Kvamme et al., 2013; Oldham et al., 2019). Kim et al. (2015) also demonstrated that for chum salmon, salinity has a direct link to olfactory imprinting and odor memory. This has potential management implications for estuaries that have salinity compliance requirements based on freshwater outflow.

4.5.3.3   *Sockeye salmon and lakes*

Sockeye were the third-most represented species in our analysis with 22 papers (11 including one or more abiotic variables). Despite reductions in annual recruitment, sockeye still account for a significant portion of commercial ocean harvest which has resulted in increased focus from fishery managers over the last two decades from a perspective of population productivity, abundance, and population structure (Peterman and Dorner, 2012; Ruggerone and Connors, 2015). Having adapted to complex aquatic environments, sockeye salmon utilize lakes for rearing and spawning. Phenotypic differentiation occurs within some populations with "stream type" individuals spawning in streams and "lake type" individuals utilizing littoral habitats to spawn (often alluvial fans at stream outlets, see Arostegui and Quinn, 2019 and Pavey et al., 2011). Changes in air temperatures and hydrologic regimes are expected to alter water temperatures, stratification patterns, timing of mixing events, and food web dynamics in temperate lakes within the range of this species (Hill et al., 2009; Shimoda et al., 2011). Thermal stress to early lifecycle stages may inhibit olfactory imprinting for some individuals. Over time, this may also cause selection pressure to favor the stream spawning phenotype, simplifying population structure, and altering homing and straying dynamics. Depending on land uses in their surrounding drainage area, lakes can also susceptible to pesticide accumulation which can inhibit olfactory processes at multiple life stages (Ackerman et al., 2008; Lukyanova et al., 2016; O'Toole et al., 2006).

4.5.3.4   *Pink salmon and their simplified age structure*

Pink salmon were represented in only seven papers in our analysis (with two including one or more abiotic variables), suggesting that they are relatively understudied. We expect this to change in the next several

decades as they become an increasingly more important commercial harvest species, and also in response to introductions in the Great Lakes and in Scandinavia which have been problematic for salmonid species in these regions (Sandlund et al., 2019; Urawa et al., 2016; Wen-Hwa and Lawrie, 1981). Pink salmon are unique among the salmonid species in that they have a predominantly simplified age structure (strict two year life-cycle), meaning that they have a lack of variation in age at maturity which results in highly predictable spawning cycles of two years with greater abundance in odd years for Pacific Ocean populations (Kaev, 2012; Radchenko et al., 2007). Phenotypic plasticity is a hallmark of salmonid species and has allowed them to persist through multiple global-scale disturbance events (Waples et al., 2009). However, the simplified age structure of pink salmon makes them vulnerable to acute disturbances that may impact a spawning cohort of rigid age class distribution in a given year. A disturbance event may result in high rates of straying such as sea surface temperature anomalies or alterations to thermal regimes in river networks, potentially resulting in decreased recruitment in a single age class. Deviations from the two-year cycle have been observed in introduced populations in the Great Lakes (Kennedy et al., 2005; Wagner and Stauffer, 1980). The extent to which this may occur in the endemic Pacific Ocean populations as a response to climate change is uncertain, as is the implications for homing and straying dynamics in the face of potential changes to competition and density effects in a more complex age structure.

4.5.3.5   *Char in a warming subarctic*

Our analysis turned up two species of char: the arctic char (3 papers), and whitespotted char (1 paper), comprising a small portion of our set. Char generally spawn in cool freshwater streams in subarctic latitudes. Populations at the southernmost extent of their range are susceptible to elevated stream temperatures (Mari et al., 2021). Arctic char are the northernmost freshwater fish that occur in the world and are an important species in commercial harvests. Zhu et al. (2017) recently noted that there is likely interannual variation in spawning cohort abundance, and differences in recruitment rates among populations, though more monitoring data is needed to characterize population dynamics across their range. This finding is consistent with the lack of information turned up in our search. Because juvenile char are known to be susceptible to

low survival rates in elevated stream temperatures, stress brought on by a warming subarctic climate may impact olfactory imprinting at critical early life stages which may ultimately affect homing and straying dynamics (Bolduc and Lamoureux, 2018; Nilsson et al., 2015; Schindler and Smol, 2006). In a transplant experiment in southern Hokkaido, Japan, Morita et al. (2000) documented phenotypic plasticity with respect to anadromous migrators vs. freshwater residents in a fragmented population. Individuals transported from above an impassable dam showed higher incidence of freshwater residency compared to those that had existed below the dam. The degree to which climate-driven selection pressure on rates of anadromy may occur in char species in the future is unknown.

4.5.4   Abiotic variables vs. abiotic HS factors

We found that the majority of studies in our analysis that included at least one abiotic variable in their study design tended to test only one or two of the abiotic HS factors that we identified in our framework (Figure 3.3). This result is not surprising, but it is concerning. Our collective professional experience has been that studies designed to comprehensively address environmental drivers of homing and straying behavior in salmonids are rare, which was the primary motivation for conducting this review and metastudy. Abiotic variables are often included in study designs without a direct mechanistic link to the causes of homing and straying as defined by K&C. Within our three study variables (study method type, location, and species), the two most prevalent classes each had the greatest mean number of abiotic HS factors tested (excluding the stationary counts study type), though our ANOVA test did not yield a statistically significant difference among classes for any variable. What little differences we found are likely a product of disproportionate funding and management priorities among salmon research programs. From both a basic and applied science perspective, future research on homing and straying could benefit from more comprehensive research approaches that are designed to test multiple abiotic HS factors to fill knowledge gaps more quickly and efficiently and work toward a universal model of homing and straying across salmonid species and regions. Our time series analysis indicates that there has been improvement over the last three decades, but

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more attention to this aspect of salmonid research is still greatly needed to advance conservation of declining populations and species.

4.6   Conclusion

In developing the abiotic framework to support the existing synthesis of K&C, we established biotic-abiotic linkages between the biological causes of straying and the abiotic drivers that may promote these causes. Our hope is that this framework can help guide future research on homing and straying patterns in salmonid species by identifying abiotic variables that are relevant to scientific questions that have yet to be investigated. We also hope that future investigations into abiotic HS factors can incorporate results into a holistic understanding of this behavioral phenomenon among salmon researchers. One of the key take aways from K&C is that results from existing literature on this topic are difficult to adopt into unifying conceptual models because studies are carried out a different spatial scales, time scales, and have other confounding attributes. This issue could be alleviated in the future by proactive incorporation of a holistic mechanistic framework into study designs during the planning and scoping phase.

Our metastudy of existing literature confirmed our hypothesis that abiotic drivers of homing and straying have been largely neglected in the existing literature. It included a targeted literature search based on key terms that represent the biotic-abiotic linkages we identified in our abiotic framework. It was not an exhaustive search of all material on this topic. However, with only 41% of the papers in our search having any sort of investigation into abiotic drivers of homing and straying, we conclude that this is a glaring bias. The environment in which salmonid species occur is changing quickly as a result of anthropogenic climate change, land use, water management infrastructure, fragmentation, and rates of commercial exploitation (Moyle et al., 2017). The ability to home is a critical facet of the salmonid lifecycle and a key factor in maintaining their biological and ecological integrity. Research on this topic must improve to more adequately conserve and manage salmonids at all scales.

4.7   Acknowledgements

4.8   References

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5 *Appendix A: Local hydraulics influence habitat selection and swimming behavior in adult California Central Valley fall-run Chinook salmon at a large river confluence*

This file is organized by sections that correspond to the main chapter. It includes additional background information to support the conceptual diagram presented in the chapter as well as additional details of the study methods. The details on hydraulic modeling included in this appendix also apply to the models run in Chapter 2.

5.1   Introduction

5.1.1   Landscape-scale Habitat Attributes

5.1.1.1   Hydro Facility Operations, Climate, Hydrology

Climate, hydrology, and hydro-facility operations control the joint flow regime occurring at a river confluence. Regional climate drives precipitation and thermal regimes. These in turn influence the amount and frequency of rainwater pulses a basin receives each year and the extent of snow-water equivalent that will provide meltwater flow pulses during spring and summer months (Rasouli et al., 2020; Singh et al., 2000). Landscape-scale hydrologic regimes act as top-down controls on flow magnitude, frequency, duration, timing, and rate of change, including and interannual variation of these attributes (Edwards et al., 2015). River discharge at a basin or reach scale has been used to partially explain the timing of population-level adult salmon migratory movements with implications for flow management in the context of accommodating or facilitating migration (Anderson and Beer, 2009; Dahl et al., 2004; Peterson et al., 2017). In basins with regulated rivers, many dam operation schedules are partially planned to control downstream discharges (Acreman et al., 2009; Bradford et al., 2011; Gendaszek et al., 2018; Saltveit et al., 2019), as well as temperatures (Ahmad and Hossain, 2020; Nichols et al., 2014; Rheinheimer et al., 2015) to accommodate specific salmonid lifecycle stages and their habitat requirements. Basin-scale hydrologic and thermal regimes that result from dam operations and impoundment may directly influence discharge and

temperature discrepancies at major river confluences, creating localized patches of physical habitat heterogeneity (Daniels and Danner, 2020; Petts, 1979).

5.1.1.2   Geology, Sediment Supply

At the broadest spatial scale, migratory habitat for salmonids is dictated by the combination of tectonic uplift and erosive forces. These act to create a topographic regime and lithological setting in which a watershed is formed. Along with climate and precipitation patterns, lithology acts as a major driver of sediment transport dynamics, drainage pattern, and spatial distribution of channel types (Dietrich et al., 2003; Howard et al., 1994; Massong and Montgomery, 2000; Sklar and Dietrich, 2001). These landscape-scale processes ultimately determine the amount and type of habitat available to a salmon population by dictating the spatial extent and distribution of alluvial channel forms in which much of the salmon lifecycle occurs (Church, 2006). Depending on the species, salmon rely on a somewhat specific range of bed sediment particle sizes in alluvial channel reaches for building redds and depositing their eggs. Due to species-specific body size limitations on their ability to move sediments of varying particle size during redd construction, it has been suggested that regional variations on lithology and geomorphic processes that control particle size may also act as controls on the geographic distribution of Pacific salmon species (Riebe et al., 2014). In cases where an impoundment blocks sediment supply, an alluvial river experiences net erosion of grain size classes that are key to redd construction which can be detrimental to reproduction and may deter migrating adults (Hauer et al., 2018; Kondolf, 2000). Confluences are hydraulically and geomorphologically complex features of fluvial channel networks. Our understanding of their dynamics has become increasingly more sophisticated since the mid-20th century (Best, 1986; Gualtieri et al., 2017; Miller, 1958; Richards, 1980). For salmon migrating upstream, each confluence that is encountered represents a critical navigational step in a sequence of decisions that must be made between entering the estuary and finally reaching their spawning grounds. Confluence hydraulics are most often dictated by regulated flows in each river, though other factors such as channel geometries and variability between

sediment particle size and transport/deposition rates may also play a role (Blettler et al., 2016; Penna et al., 2018).

5.1.1.3   Pollution, Disrupted Juvenile Imprinting

At a landscape scale, there may be multiple factors that negatively impact the ability for adult salmon to utilize olfactory navigational cues at river confluences during their upstream migration. A common practice among hatchery production facilities is to rear juveniles to a parr/smolt stage and release them off site to avoid mortality associated with downstream migration (Huber et al., 2015; Murdoch et al., 2009). This is thought to result in increased rates of straying as adults due to the interruption of olfactory imprinting at earlier life stages (Jonsson et al., 2003; Keefer and Caudill, 2014; Sturrock et al., 2019). In addition to hatchery release practices, some pollutants are known to disrupt olfaction via toxicity to the olfactory physiology of salmonids by multiple biochemical pathways (Tierney et al., 2010). Many salmon populations occur in regions that experience extensive agricultural land use and large-scale application of pesticide compounds that enter waterways via agricultural runoff. Tierney et al. (2008) demonstrated acute injury to olfactory tissue in juvenile rainbow trout (*O. mykiss*) following exposure to pesticides specifically found to occur in the Nicomekl River in British Columbia. This was an important finding, but more work is needed on identifying region-specific links between locally used pesticide mixtures and olfactory toxicity across salmonid species.

The importance of olfactory navigation in the salmonid lifecycle has been well understood for decades. In the 1950's, the first research was conducted to investigate fish olfactory cues as a means of navigation in migratory species (Hasler and Wisby, 1951; Wisby and Hasler, 1954). Since then, many salmonid specific studies have been conducted to characterize the importance of olfaction during the migratory phases of their lifecycle (Cooper et al., 1976; Dittman et al., 1996; Hasler and Scholz, 1983; Ueda, 2011). Early experimental work in hatchery facilities showed that odor imprinting in early life stages is critical for the successful return of individuals to their natal stream as spawning adults (Donaldson and Allen, 1958). Important work by Nevitt et al. (1994) also demonstrated that olfactory receptor cells in coho salmon (*O.*

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kisutch) could develop sensitization to specific odors, allowing a fish to detect not only the presence of an odor cue, but its relative concentration as well. Laboratory studies have demonstrated that amino acids elicit the strongest behavioral response in multiple species of (Ueda, 2018, 2011; Yamamoto et al., 2010). These results suggest that tissue or waste from conspecifics may be the source of odor material in an individual's natal stream habitat that is most important for olfactory imprinting. In cases where imprinted natal odor cues are not present, the "olfactory hierarchy hypotheses" suggests that odor cues from conspecifics that are first detected as adults may act as a secondary cue (Bett and Hinch, 2015).

5.1.2   Reach-scale Habitat Attributes

5.1.2.1   *Temperature, Discharge, Channel Type*

With the exception of some Alaskan chum salmon (*O. keta*) runs (which are known to occasionally spawn in intertidal areas of river mouths, see Johnson et al. 1997), most adult Pacific salmon undergo some degree of upstream migration into a watershed, encountering a sequence of tributary confluences. The distance travelled along a migration route can vary within and among species (Quinn, 2018) and the types of riverine habitats occupied by Pacific salmon species throughout their range are highly variable as well. Variability in these habitats occurs as a function of latitude, climate, regional orogeny, regional lithology and geomorphic processes, and hydrologic regime (Quinn, 2018). As they progress through their upstream migration, salmon experience variation in both channel discharge as well as channel geometry. It is this dynamic combination of flow and channel shape that dictates the hydraulic conditions that each fish experiences at any given point along their migratory corridor. At the reach scale, different geomorphic settings tend to result in generalized hydraulic conditions (such as lower, more consistent water velocity magnitudes in estuarine areas, vs. much higher, episodic velocities experienced in bedrock channels that occur higher in a watershed). Riverine habitats within the geographical range of Pacific salmon have experienced varying degrees of anthropomorphic impacts, ranging from minimal (such as some isolated coastal populations in Canada and Alaska), to highly impacted (such as the urbanized and industrialized watersheds in Washington, Oregon, and California) (Gustafson et al., 2007; Nehlsen et al., 1991).

Although watershed drainage patterns may vary within the range of Pacific salmon, (i.e. dendritic, trellis, radial, etc.), a general pattern in channel slope tends to prevail across drainages. With the exception of hillslope noses where channel formation begins, channel slope tends to decrease with increasing drainage area (Montgomery, 2001). Channel networks exhibit the following downstream progression of geomorphic processes: 1) colluvial channels (small, low-order channels dominated by colluvial sediment transport and deposition; 2) bedrock channels (steep channels dominated by episodic hydrology, sediment erosion, and bedrock incision; 3) alluvial channels (large channels with a shallow slope that experience both sediment erosion and deposition, but are dominated by unconsolidated sediment deposits; and 4) estuarine channels (very large channels dominated by tidal forces and deposition of fine material). Also, due to localized variations in underlying lithology and sediment transport dynamics, bedrock and alluvial channel forms can be longitudinally mixed, with alternating sequences of occurrence (Johnson and Whipple, 2007; Massong and Montgomery, 2000). This has important implications for the migration of adult salmon due to the geomorphic conditions necessary to provide adequate spawning habitat. Hydraulic connectivity and passage capability at knickpoints are major factors that determine how far into a mixed alluvial-bedrock channel network an individual fish can swim. From a standpoint of characterizing migratory habitat within a watershed, there are clear links between watershed geomorphology and the distance in which a spawning migration may occur. Confluences within a basin can be important drivers of reach-scale geomorphic features and resultant physical migratory habitat structure. In a review of studies on confluence effects in drainage networks, Benda et al. (2004) found a correlation between the ratio of tributary and mainstem drainage area and the probability of "confluence effects" (meaning the formation of fluvial landforms associated with confluences such as fans, bars, and terraces) occurring. They also noted that climate and disturbance regime are important drivers of these reach-scale effects with semiarid regions experiencing more frequent flash flood events, resulting in debris flows along a greater longitudinal gradient compared to humid regions. In certain cases, sediment aggradation at channel confluences may interrupt downstream sediment supply, disrupting alluvial processes that facilitate physical habitat heterogeneity downstream of

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the confluence. The extent to which this occurs within a basin is largely driven by drainage area and stream network length (Rice, 2017).

As poikilotherms, one of the most important environmental variables influencing the bioenergetics and timing of upstream migration for salmon is water temperature (Goniea et al., 2006). Temperature along the migratory corridor is driven regionally by climatic and hydrologic interactions (Johnson et al., 2020), and also at the reach scale by riparian shading (Dugdale et al., 2018) and groundwater interaction (Schmidt et al., 2006). Because migratory phenology is diverse across the salmon species and along latitudinal gradients, individual phenotypic groups have evolved to carry out the adult phase of their lifecycle in accordance with a variety of thermal regimes. A generalized relationship between average migratory swimming speed and temperature in adult Chinook salmon and steelhead trout (*O. mykiss*) in the Columbia River was characterized by Salinger and Anderson (Salinger and Anderson, 2006), identifying a temperature for peak swimming speed. For spring-run Chinook salmon, more nuanced migratory behavior has been characterized that allows them to migrate in elevated thermal conditions by selectively occupying cooler refugia. Berman and Quinn (1991) demonstrated this thermoregulatory strategy by inserting temperature-sensitive radio transmitters into the stomachs of 19 adult spring-run Chinook salmon and monitored internal body temperatures for four months as they migrated up the Yakima River in Washington State. Results showed internal temperatures to be consistently lower than ambient river temperatures, suggesting that the individuals were preferentially occupying cooler temperature refugia during that time. Torgersen et al. (1999) later showed similar patterns of thermal selectivity in upstream migrating adult Chinook salmon in disturbed areas of the Middle and North Fork John Day River in northeastern Oregon.

5.1.2.2   Water Quality, Odor Cues, Predation, Exploratory Dispersal, Density-Dependent Movement
Water quality may act as a reach-scale driver of habitat selection and focus is given to pesticide contaminants here due to their demonstrated effects to salmonid olfaction as described above. Because acute injury to olfactory organs has been demonstrated in the presence of certain pesticide compounds (Tierney et al., 2008), it is possible that it may have some influence in migratory routing at confluences

above a concentration threshold for acute toxicity. This has not yet been investigated. Dissolved and suspended contaminants that impact olfactory navigation cues may vary in presence and concentration within a basin for several reasons. Point source contamination may also have reach-scale impacts to adult salmon migratory habitat via contaminant spills, poor pesticide management practices, or concentrated discharge of agricultural runoff during dry periods (Holvoet et al., 2007; McKnight et al., 2015). The extent to which varying degrees of contaminant concentration between mainstem and tributary channels at a confluence may influence navigational choices for migrating adult salmon has not been studied.

It is also important to note that some amount of straying occurs naturally across the Pacific salmon species. Exploratory dispersal as an innate behavior appears to be expression of the portfolio effect in their life history strategy (Schindler et al., 2010). If a certain percentage of individuals home to a non-natal stream reach and the natal reach (containing the bulk of the spawning run) is destroyed through some stochastic event such as a wildlife or landslide, or an anthropogenic habitat disturbance, the population may still persist (Waples et al., 2009, 2008). Because straying dynamics have been studied at varying spatial scales, and across multiple watersheds, it is difficult to make sweeping generalizations about stray rates for a single species or across all Pacific salmon species. Keefer and Caudill (2014) examined a total of 62 studies on homing and straying and found variable straying percentages reported within and among species. Due to the presence of hatchery-origin fish examined in some of these studies, it is likely that these percentages are inflated from true natural or "background" stray rates to some degree.

Beyond biological cues at the individual level, evidence is emerging that suggests the existence of density-dependent movement of spawning cohorts. A recent study gathered evidence from sockeye salmon (*O. nerka*) indicating that adult salmon exhibit temporal pulses of migratory movements that seem to be dictated by social interactions and aggregate group dynamics that may be independent of environmental cues (Berdahl et al., 2017, 2016). Adults migrating upstream have long been known to exhibit schooling behavior, as noted in an early review of upstream migration (Banks, 1969). It is likely that group dynamics play a role in collective navigation at a confluence when group density reaches a certain threshold (Guttal

and Couzin, 2010). Further investigation is needed before a density threshold for aggregated group movement can be identified across salmonid taxa. Although much of a spawning cohort returns to their natal stream, active dispersal behavior has been shown to occur in Chinook, sockeye, and steelhead and is thought to be exploratory behavior or even a thermoregulatory strategy in some cases (Goniea et al., 2006; High et al., 2006; Peterson et al., 2016). Finally, little is known about predator avoidance dynamics in migrating adult salmon, though it is thought to be most important on or near spawning grounds (Quinn, 2018; Quinn et al., 2001). Bentley et al. (2014) observed fine-scale diel movement of Alaskan sockeye salmon between lake and spawning stream habitat suggesting avoidance of bear predation, though more work is needed to characterize this behavior across taxa. The extent to which predator avoidance influences navigation at confluences is not yet known.

5.1.3   Micro-scale Habitat Attributes

Channel discharge, geometry, and sediment composition act together to produce fine-scale physical habitat conditions commonly referred to as "microhabitats". The microhabitat spatial scale is defined by Baldes and Vincent (1969) as "the physical conditions immediately surrounding an animal at a given time and place". The term has its theoretical roots in early writings on organismal habitat selection as a function of spatial scale such as Thorpe (1945). One of its earliest uses in relation to fish ecology was in a pair of studies that investigated patterns in microhabitat selection in two species of riverine sculpin as a function of substrate type and flow velocity (Fenwick, 1968; Taylor, 1966). Wickham (1967) provided the first microhabitat investigation on a salmonid species based on velocity, depth, substrate type, and vegetation cover, and Giger (1973) compiled an influential report describing streamflow requirements for salmonids and is an early example of the microhabitat concept being applied in a regulatory context. Since then, this spatial scale has been utilized in investigations into life stage-specific habitat requirements (Carnie et al., 2016; Moir and Pasternack, 2010; Nielsen, 1992; Shirvell, 1994), restoration design and planning applications (Brown and Pasternack, 2009; Fangue et al., 2021; Favrot et al., 2018), and evaluation of passage infrastructure (Li et al., 2021; Nestler et al., 2008; Weber et al., 2006). To date, the influence of

confluence hydraulics on species-specific microhabitat distribution in space and time has not yet been studied.

The studies mentioned above are primarily concerned with physical habitat attributes including velocity magnitude and/or direction, depth, sheer stress, and sediment grain size. Channel geometry and hydraulics also influence the magnitude and distribution of turbulent flow features at spatial scales relevant to flow depth and roughness height (Franca and Brocchini, 2015). Channel confluence morphology may result in areas of high turbulence under certain conditions such as low flow periods at discordant confluences (Biron et al., 1996; Boyer et al., 2006). In turn, this may act as a deterrence to migrating adult salmon either due to bioenergetic constraints (Enders et al., 2003; Lupandin, 2005) or potentially through disruption of rheotactic cues. Even though Elder and Coombs (2015) were able to demonstrate that rheotaxis of a much smaller riverine fish (Mexican tetra, *Astyanax mexicanus*) persisted in the face of turbulent flow conditions, microscale habitat selection as a function of turbulence for migrating adult salmon is not yet fully understood.

5.2   Methods

5.2.1   Status of Chinook Salmon in the CA Central Valley

The California Central Valley is home to four phenotypically distinct populations of Chinook salmon: Sacramento River winter-run Chinook salmon, Central Valley spring-run Chinook salmon, and Central Valley fall- and late fall-run Chinook salmon (NMFS 2014). All four phenotypes have experienced precipitous population declines beginning in the mid-19th century. Yoshiyama et al. (1998) estimated average annual escapement rates of Central Valley fall-run Chinook in the mainstem Sacramento River to have declined from 192,300 to 40,900 from 1992-1997. In 2017, that number fell to 2,260 fall-run individuals in the mainstem Sacramento River (CDFW 2021). Causes of decline include passage barriers, altered hydrologic regimes, harvest pressure, disease, and water quality degradation among others (Arkush et al., 2002; Gresh et al., 2000; Yoshiyama et al., 2001; Zeug et al., 2011). Several hatchery production

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facilities have been constructed on major tributaries to the Sacramento and San Joaquin Rivers. A common practice among these hatcheries is to raise Chinook salmon to a juvenile life cycle stage and release them offsite in the San Francisco Bay-Delta estuary, thus eliminating the opportunity for olfactory imprinting during outmigration (CDFG and NMFS 2001). When this occurs, adult stray rates upon return years later may increase up to eight times their natural background rate of 5-10% of a Central Valley Chinook salmon population released onsite (Huber et al., 2015; S.P. Cramer and Associates, 1991). There is interest among fisheries managers and conservationists in California in reducing stray rates in hatchery-origin Chinook (Bett et al., 2017). One reason is that straying leads to introgression between wild- and hatchery-origin individuals, resulting in decreased wild-origin fitness due to inbreeding depression and may mask overall wild-origin population decline (Garza et al., 2008; Johnson et al., 2012; Keller and Waller, 2002; Naish et al., 2007).

5.2.2   Sediment Survey

Table A.A.1. Results of a sediment grain size distribution survey at each DIDSON deployment site throughout the project area in January 2020. Sizes were classified by ranges in diameter with percent distribution reported.

DIDSON Site	< 2mm	2mm < D < 32mm	32mm < D < 90mm	90mm < D < 128mm	128mm < D < 256mm	> 256mm
FS2	100%					
YD1	10%					90%
YS1	100%					
YD2	90%					10%
YS2	100%					
DD1	98%	2%				
DS1	5%	75%	20%			
DD2	98%	2%				
FD1	100%					
FS1	98%	2%				
FD2	100%					
			5%			
DS2	40%	45%				

5.2.3 Geometric Solution Scheme
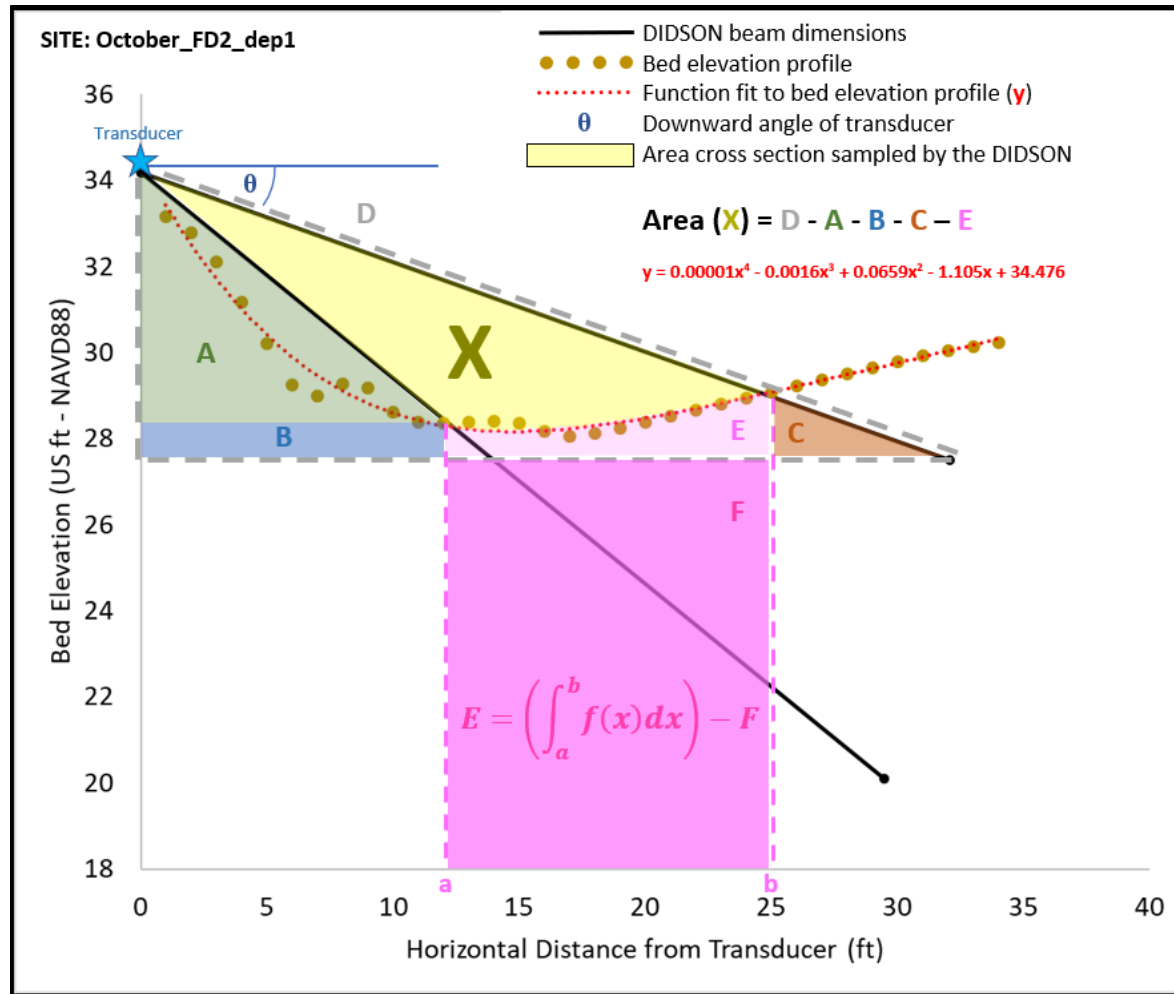
Figure A.A.1. An example geometric solution scheme used to compute the total volume sampled by the DIDSON sonar at each deployment site. The vertical area computed in this scheme was used to compute volume based on the fixed horizontal angle of the DIDSON beams.

Figure A.A.2. An image of the DIDSON sonar deployed at site "DS1".

5.2.4 DIDSON Site Attributes

Table A.A.2. A summary of DIDSON site attributes for each deployment.

Deployment Name	Detections (#)	Detection rate: [detections (#)]/[duration (min)/Volume(m^3)]	Volume Sampled (m^3)	Mean Depth (m)	ADCP Depth-averaged Vmag, mean w/in search area (ft/s)	ADCP Depth-averaged Vmag, mean w/in search area (m/s)	Vmag*d (m^2/s)	Froude number
Sept_DD1_dep1	1	0.051	1.15	2.31	2.52	0.77	1.77	0.16
Sept_DD2_dep1	13	0.053	4.10	1.75	3.01	0.92	1.61	0.22
Sept_DD2_dep2	10	0.061	4.92	1.79	3.01	0.92	1.65	0.22
Sept_DS1_dep1	6	0.087	1.16	1.50	4.05	1.23	1.85	0.32
Sept_DS1_dep2	5	0.036	4.54	1.50	4.05	1.23	1.85	0.32
Sept_FD1_dep1	3	0.104	0.75	No ADCP Data				
Sept_FD1_dep2	8	0.112	1.81	No ADCP Data				
Sept_FD2_dep1	17	0.022	23.49	2.74	1.32	0.40	1.10	0.08
Sept_FD2_dep2	109	1.870	1.22	2.61	1.32	0.40	1.05	0.08
Sept_FS1_dep1	2	0.005	6.79	2.45	1.69	0.51	1.26	0.11
Sept_FS1_dep2	4	0.194	0.60	2.12	1.69	0.51	1.09	0.11
Sept_FS2_dep1	11	0.274	1.05	1.56	1.80	0.55	0.86	0.14
Sept_FS2_dep2	4	0.094	1.09	1.58	1.80	0.55	0.86	0.14
Sept_YD1_dep1	6	0.184	0.53	No ADCP Data				
Sept_YD2_dep2	1	0.004	7.94	2.87	0.32	0.10	0.28	0.02

Sept_YS1_dep1	2	0.006	5.79	2.28	0.43	0.13	0.30	0.03
Sept_YS2_dep1	3	0.010	10.18	2.45	0.30	0.09	0.23	0.02
Oct_DD1_dep1	1	0.001	14.15	No ADCP Data				
Oct_DD2_dep2	7	0.017	6.07	1.55	1.48	0.45	0.70	0.12
Oct_DS1_dep1	2	0.075	0.92	No ADCP Data				
Oct_DS2_dep1	4	0.012	5.76	1.11	1.91	0.58	0.65	0.18
Oct_DS2_dep2	1	0.003	5.76	1.11	1.91	0.58	0.65	0.18
Oct_FD1_dep1	1	0.013	2.44	1.82	0.87	0.26	0.48	0.06
Oct_FD1_dep2	1	0.004	3.21	1.93	0.87	0.26	0.51	0.06
Oct_FD2_dep1	2	0.005	13.79	2.04	1.01	0.31	0.63	0.07
Oct_FD2_dep2	4	0.029	2.29	2.22	1.01	0.31	0.69	0.07
Oct_FS1_dep2	3	0.045	1.09	1.18	0.88	0.27	0.32	0.08
Oct_FS2_dep2	5	0.014	5.84	1.29	0.46	0.14	0.18	0.04
Oct_YD1_dep1	3	0.023	8.41	3.01	0.55	0.17	0.50	0.03
Oct_YD2_dep2	1	0.003	7.21	2.80	0.31	0.10	0.27	0.02
Oct_YS1_dep1	5	0.005	26.09	2.14	0.44	0.13	0.29	0.03
Oct_YS1_dep2	1	0.002	14.43	1.97	0.44	0.13	0.26	0.03
Oct_YS2_dep1	1	0.002	13.93	1.95	0.36	0.11	0.21	0.03
Oct_YS2_dep2	1	0.001	20.29	2.17	0.36	0.11	0.24	0.02
Sept_DS2_dep1	0	N/A	N/A	1.03	2.30	0.70	0.72	0.22
Sept_YD2_dep1	0	N/A	N/A	2.77	0.32	0.10	0.27	0.02
Sept_DD1_dep2	0	N/A	N/A	2.14	2.52	0.77	1.64	0.17

Sept_YS2_dep2	0	N/A	N/A	2.38	0.30	0.09	0.22	0.02
Sept_DS2_dep2	0	N/A	N/A	1.02	2.30	0.70	0.72	0.22
Sept_YS1_dep2	0	N/A	N/A	2.29	0.43	0.13	0.30	0.03
Sept_YD1_dep2	0	N/A	N/A	3.21	0.55	0.17	0.54	0.03
Oct_YD2_dep1	0	N/A	N/A	2.55	0.31	0.10	0.24	0.02
Oct_FS1_dep1	0	N/A	N/A	1.19	0.88	0.27	0.32	0.08
Oct_FS2_dep1	0	N/A	N/A	1.34	0.46	0.14	0.19	0.04
Oct_DD2_dep1	0	N/A	N/A	1.62	1.48	0.45	0.73	0.11
Oct_DS1_dep2	0	N/A	N/A			No ADCP Data		
Oct_DD1_dep2	0	N/A	N/A			No ADCP Data		
Oct_YD1_dep2	0	N/A	N/A	3.11	0.55	0.17	0.52	0.03

5.2.5   Checks for Sample Bias

The following data plots are included as checks for sample bias in our methods. The first was to ensure that

we were not detecting more individuals simply because we were sampling greater volumes of water with

the DIDSON sonar. As shown in Figure A.A.3, the opposite was true. This is because many of the deeper

sites where we were able to capture a greater volume of the channel occurred in slow-moving portions of

the channel that were preferentially avoided. Figure A.A.4 Figure A.A.5 show detection rates as a function

of both time of day and duration of footage. Neither show any pattern which demonstrates that there was

not a time of day (within the window of time in which all sampling occurred, ~0800 to ~1600) in which

individuals preferentially moved through the study area. Also, the amount of footage gathered during each

deployment did not affect the rate of detection. Finally, as shown in Figure A.A.6, no pattern emerged

between mean estimated body length in each deployment and the rate of detection.
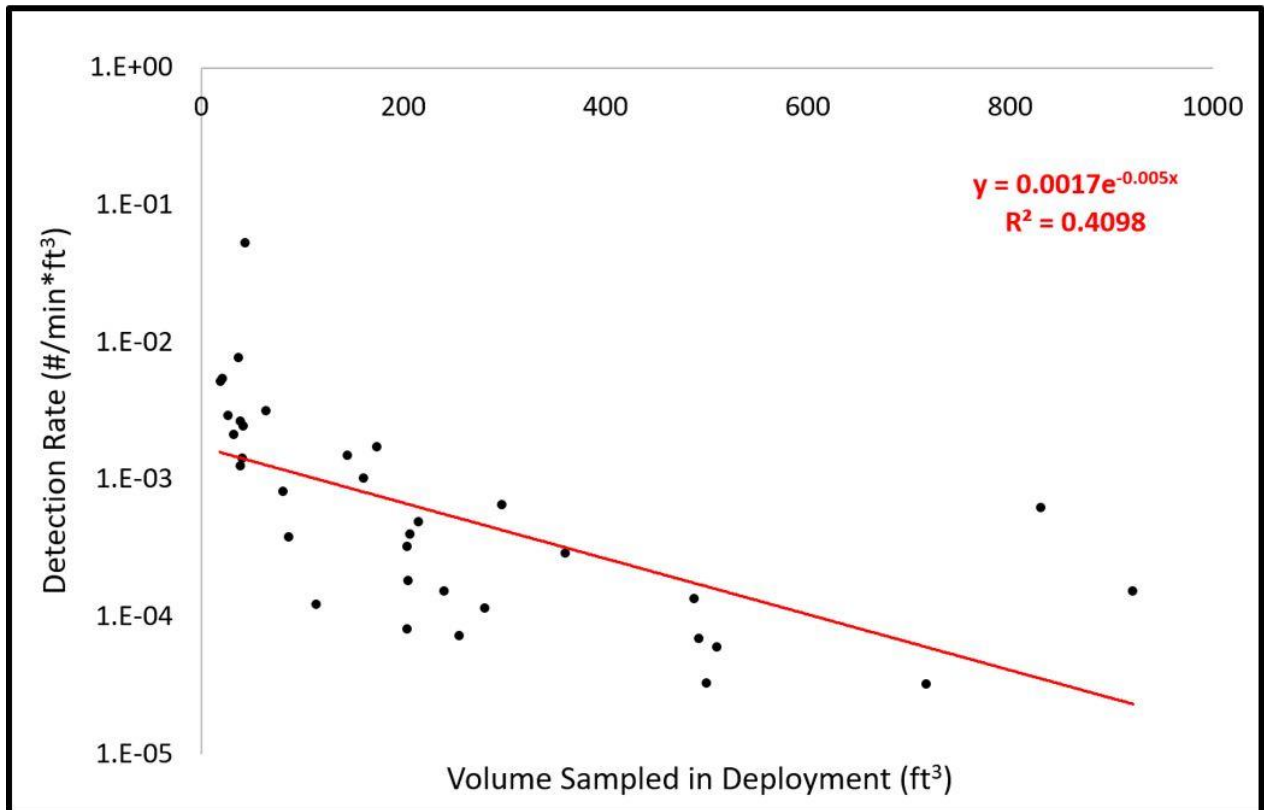
Figure A.A.3. Detection rates as a function of volume sampled in each DIDSON deployment.

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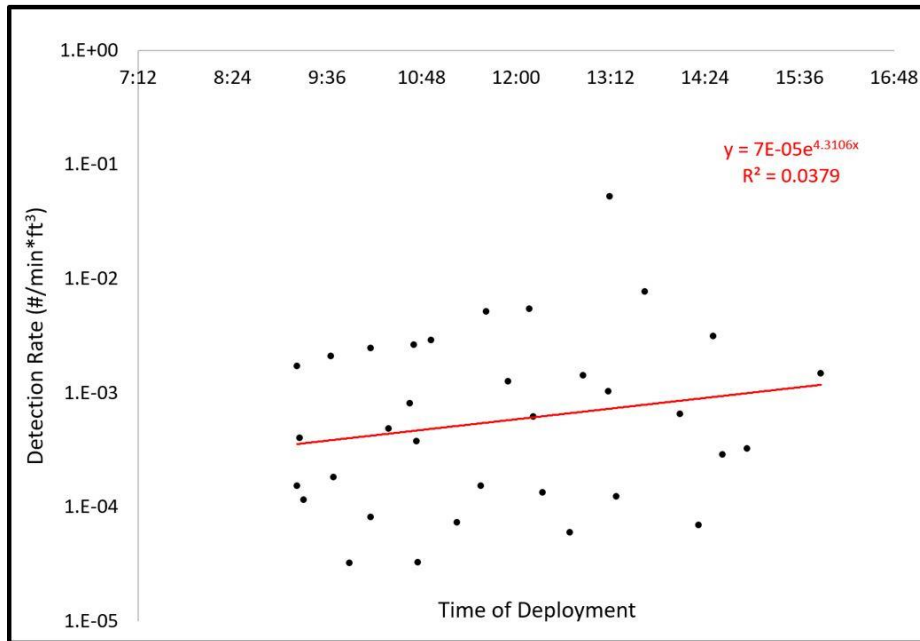
Figure A.A.4. Detection rates as a function of deployment time (time of day in which footage was captured).
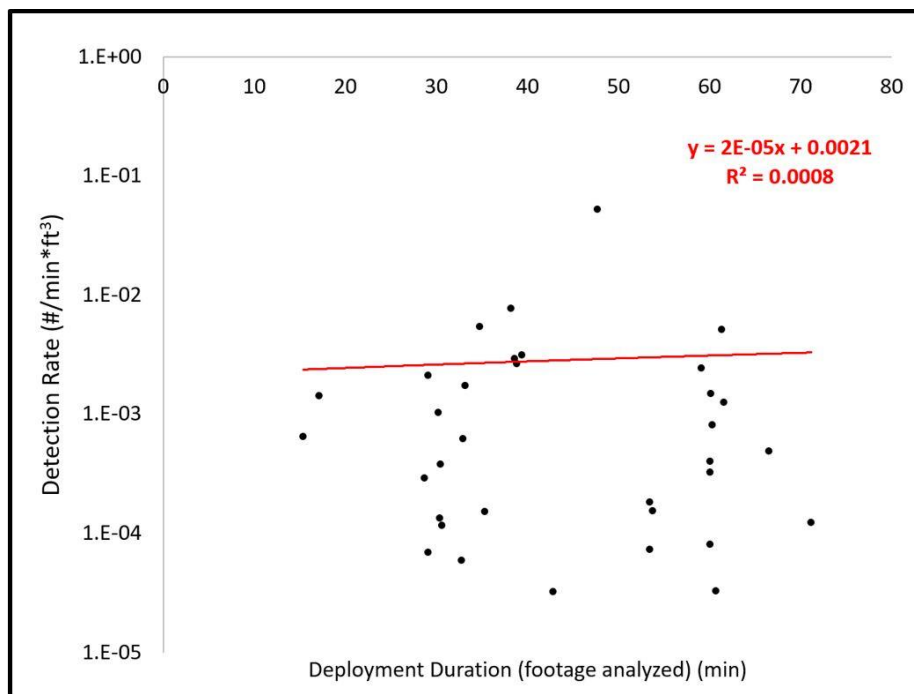
Figure A.A.5. Detection rates as a function of duration (the number of minutes in which the DIDSON sonar was capturing usable footage).

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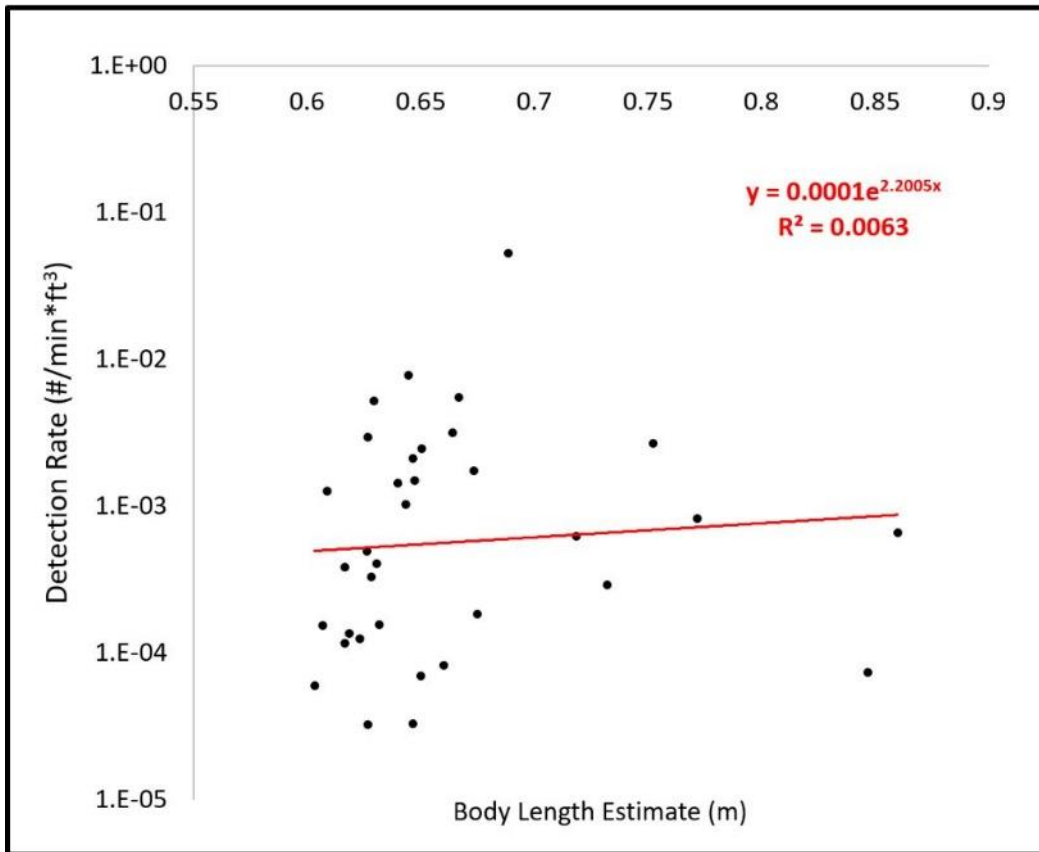
Figure A.A.6. Detection rate as a function of mean estimated body length for each deployment.

5.2.6   Species Identification Criteria

A 2012 snorkel survey conducted by YARMT indicated that the following fish species may occur in the project area: California roach (*Hesperoleucus symmetricus*, and various other species of Cyprinids), Chinook salmon (*O. tshawytscha*), steelhead trout (*O. mykiss*), riffle sculpin (*Cottus gulosus*), Sacramento pikeminnow (*Ptychocheilus grandis*), Sacramento sucker (*Catostomus occidentalis*), Tule perch (*Hysterocarpus traskii*), and largemouth bass (*Micropterus salmoides*) (YARMT, 2013). According to the PISCES database on fish community composition and species ranges in California, the following species may also occur within the project site throughout the year: white sturgeon (*Acipenser transmontanus*), green sturgeon (*Acipenser medirostris*), western brook lamprey (Lampetra richardsoni), striped bass (*Morone saxatilis*), Sacramento splittail (*Pogonichthys macrolepidotus*), Sacramento hitch (*Lavinia exilicauda exilicauda*), Sacramento blackfish (*Orthodon microlepidotus),* prickly sculpin (*Cottus asper*), Pacific

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lamprey (*Entosphenus tridentatus*), inland three-spine stickleback (*Gasterosteus aculeatus*), and hardhead (*Mylopharadon conocephalus*) (Santos et al., 2014). Criteria were generated to differentiate adult Central Valley fall-run Chinook salmon from other potential species to the best extent possible using information on body length, migration phenology, and swimming behavior.

In a study on the fecundity of Chinook salmon as a function of body length, California Department of Fish and Wildlife gathered extensive data on body lengths of spawning adult Central Valley fall-run Chinook salmon passing a video monitoring station on the Lower Mokelumne River, as well as length data from fish spawned at the Mokelumne River hatchery (Kaufman et al., 2009). 9,981 individuals were seen passing the video monitoring station and the length range was 300–1190 mm (approximate error in length data was reported to be +/- 5 cm, mean not reported). More accurate fork lengths were taken at the hatchery from 93 spawned individuals with sizes ranging from 527-991 mm (mean: 762 mm). Grilse (individuals that spend only one year in the ocean) were designated in both video data and spawner data as having body length ranges of 300–640 mm and 527–610 mm, respectively. Because Kaufman et al. (2009) examined body lengths of the same evolutionarily significant unit of Chinook salmon that is examined in this study, these data will be used as morphological criteria for discerning fall-run Chinook salmon from other fish species that may be present in the DIDSON footage. The grilse length range will be excluded here to aid in avoiding misidentification of species. A size range criterion of 600–1200 mm is used in this study.

In studies by Burwen et al. (2010) using Chinook salmon, and Hightower et al. (2013) using several other riverine fish species, R^2 values of 0.90 and 0.89 (respectively) were reported when correlating observed fish lengths with estimated lengths using the DIDSON measuring tool. These results indicate relatively accurate measuring capabilities when using the measuring tool. In a large river of comparable width and average depth to the LFR/LYR confluence, Mueller et al. (2010) observed adult Chinook salmon migrating upstream using passive DIDSON observations to develop a technique for identifying this species in the footage (and to differentiate between simultaneous observations of sockeye salmon). Using the DIDSON

measuring tool, they made every effort to ensure that each fish's length was in full display, and they measured each fish at three different frames and took the average length. The same technique is used here.

Originally proposed by Breder (1926), and later expanded upon by Domenici and Kapoor (2010), five different locomotive "styles" occur in fishes depending on body morphology (anguilliform, sub-carangiform, carangiform, thunniform, and ostraciiform). Chinook salmon (along with all other salmonids) exhibit sub-carangiform locomotion, which is characterized by a waveform swimming style in which most of the kinetic work is performed by the posterior $2/3^{rds}$ to $1/2$ of the body. However, this type of locomotion is very common in riverine fishes due to similarities in body morphology and habitat needs. Therefore, locomotive style alone cannot be used as an identifier in this case without body length data.

Of the freshwater fishes that comprise the potential community composition of the project area (based on past observational data in the LYR as well as known species ranges from the PISCES database), the species that may be confused for adult fall-run Chinook based on length, body shape, phenology, and swimming behavior are California Central Valley steelhead and striped bass. Striped bass can reach lengths in excess of 700 mm as very mature adults (it is rare, but also possible in largemouth bass), and although their body shape has a distinct vertical taper near the caudal fin, they may be confused for fall-run Chinook salmon simply based on body length (Moyle, 2002).

5.2.7 Hydrodynamic model

The following summary table includes the pertinent details of the TUFLOW models that were run and referenced in the *Hydraulic Data* section of the main article.

Table A.A.3. Hydraulic model summary

Topo-bathymetric data sources	The topographic data mosaic was sourced from the following (Figure A.A.7): • Hydrolite single beam echosounder (minimum depth of 0.3 m; depth accuracy of 1 cm; sampling frequency of 200 Hz; Seafloor Systems, Inc.) in sync with a Trimble R8 real-time kinematic GPS (horizontal and vertical accuracies of ~ 1 and 2 cm, respectively) receiving ground-based corrections on the fly at 1 Hz. • Bare-earth topography was collected at the island located at the confluence junction using a Trimble R8 RTK GPS. • A very small clip of pre-existing near-infrared and green LiDAR data was used, it accounted for 0.04% of the greatest wetted extent (September sampling period). It had been collected in 2017 by Yuba Water Agency and processed by our group to obtain a 0.9144 m (i.e., 3-ft) raster (Silva and Pasternack 2018) • Augmented points were added manually to conserve known contours in the DEM and avoid any artifacts in the DEM that might occur from surface interpolation.
Topo-bathymetric data resolution	Topo-bathymetric point density within the model domain was 1.46/3 m^2.
Topo-bathymetric uncertainty	For surveying on the LYR, RTK GPS precisions are typically within 1 cm horizontal and 2 cm vertical. Data from different collection methods are calibrated to align vertically using overlapping points, typically with ~ 3 cm standard deviation after calibration.
Model discharges	The first period occurred from September 23-26 and the second from October 22-25. During the first sampling period, mean discharges on the LFR and LYR were ~ 213 and 24 m^3/s, respectively. During the second period, discharges on the LFR and LYR were ~ 68 and 17 m^3/s, respectively (CDWR 2022).
Downstream water surface elevation (WSE) data	Figure A.A.8 shows the second order polynomial stage-discharge rating curve that was generated for our study area. WSEs were measured using a Trimble R8 RTK GPS near the downstream boundary of the study area from 2017 to 2019, capturing discharges ranging from approximately 200-1400m^3/s. We used the curve to interpolate WSEs that correspond to our modeled discharge scenarios. Discharge data was collected from the California Department of Water Resources' Data Exchange Center (CDWR 2022).
River roughness specification	We used a uniform Manning's n value of 0.03 in all model runs in this study as the sediment was dominated by sand-sized substrate with gentle bedforms and intermittent bank vegetation (Limerinos 1970, Arcement and Schneider 1989)

Eddy viscosity specification	We used the Smagorinsky formulation for eddy viscosity to account for momentum diffusion via turbulence in the model's momentum equations (BMT Commercial Australia Pty Ltd 2018). Constant coefficient and initial Smagorinsky coefficient were 0.4 and 0.5, respectively.
Hydraulic validation procedure	This study used the 2D model water velocity validation method of Barker et al. (2018). This approach is a variation of large-scale particle image velocimetry (e.g., Dramais et al. 2011). On a windless day, a kayaker moved at the speed and direction of the water around it, referencing surrounding floating debris. A Trimble R8 RTK GPS tracked kayak position at 1 Hz. The distance travelled per second was computed as a surface velocity. In addition, the method of Barker et al. (2018) was used to find a depth-average velocity constant of 0.63 and apply this to the observed data to obtain field-estimated depth-average velocities. Both the observed surface values and the estimated depth-averaged values were compared to modeled depth-average velocities at the same coordinates for the same steady flow regime that occurred during the day of the kayak survey ($28.97m^3$ in the LYR and $67.83m^3$ in the LFR for a combined discharge of $96.80m^3$). A TUFLOW model was used to simulate hydraulic conditions on the day of the kayak surveys in accordance with the methods outlined here.
Velocity magnitude prediction accuracy	The velocity validation procedure found the model predictions to be a good fit to the data on the basis of an r^2 value of 0.76 (Figure A.A.9).
Model mass conservation	Volume errors were < 1 m^3 for the September and October models and $1.93m^3$ for the validation model. All mass errors were $<0.01\%$
Model outputs	Figure A.A.10

Figure A.A.7. Sources of elevation point data used to construct the final digital elevation model used in this study.

Figure A.A.8. Stage-discharge relationship used to interpolate water surface elevations used in 2D hydrodynamic models.

The equation shown in the figure:

$$y = -4.000 \times 10^{-9}x^2 + 6.451 \times 10^{-4}x + 33.668$$
$$R^2 = 0.95$$
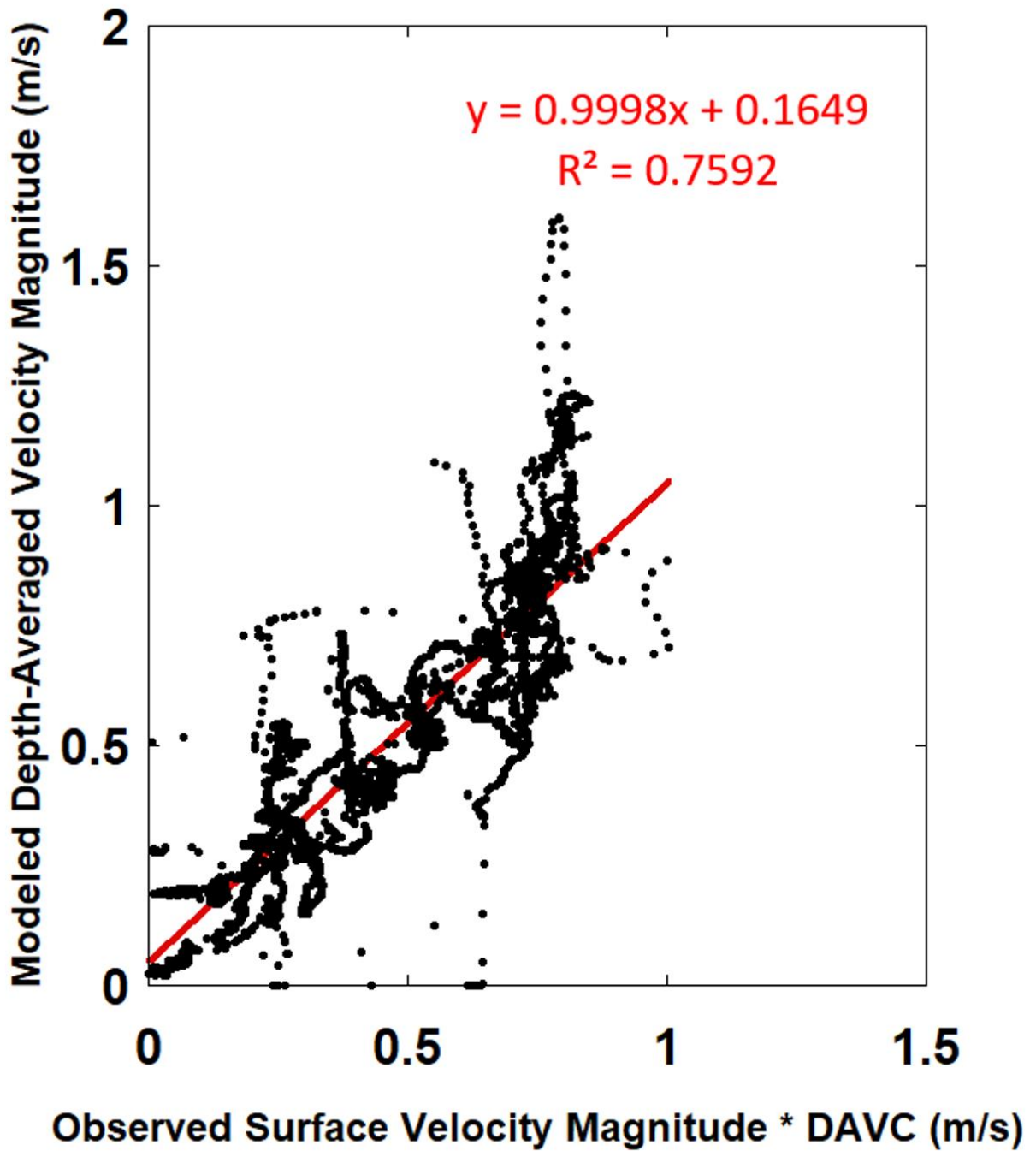
Figure A.A.9. Results of the kayak velocity validation survey. This plot compares the observed surface velocities multiplied by the depth-averaged velocity constant (DAVC) to the modeled depth-averaged velocity magnitude values from the TUFLOW model outputs to assess model accuracy and performance.
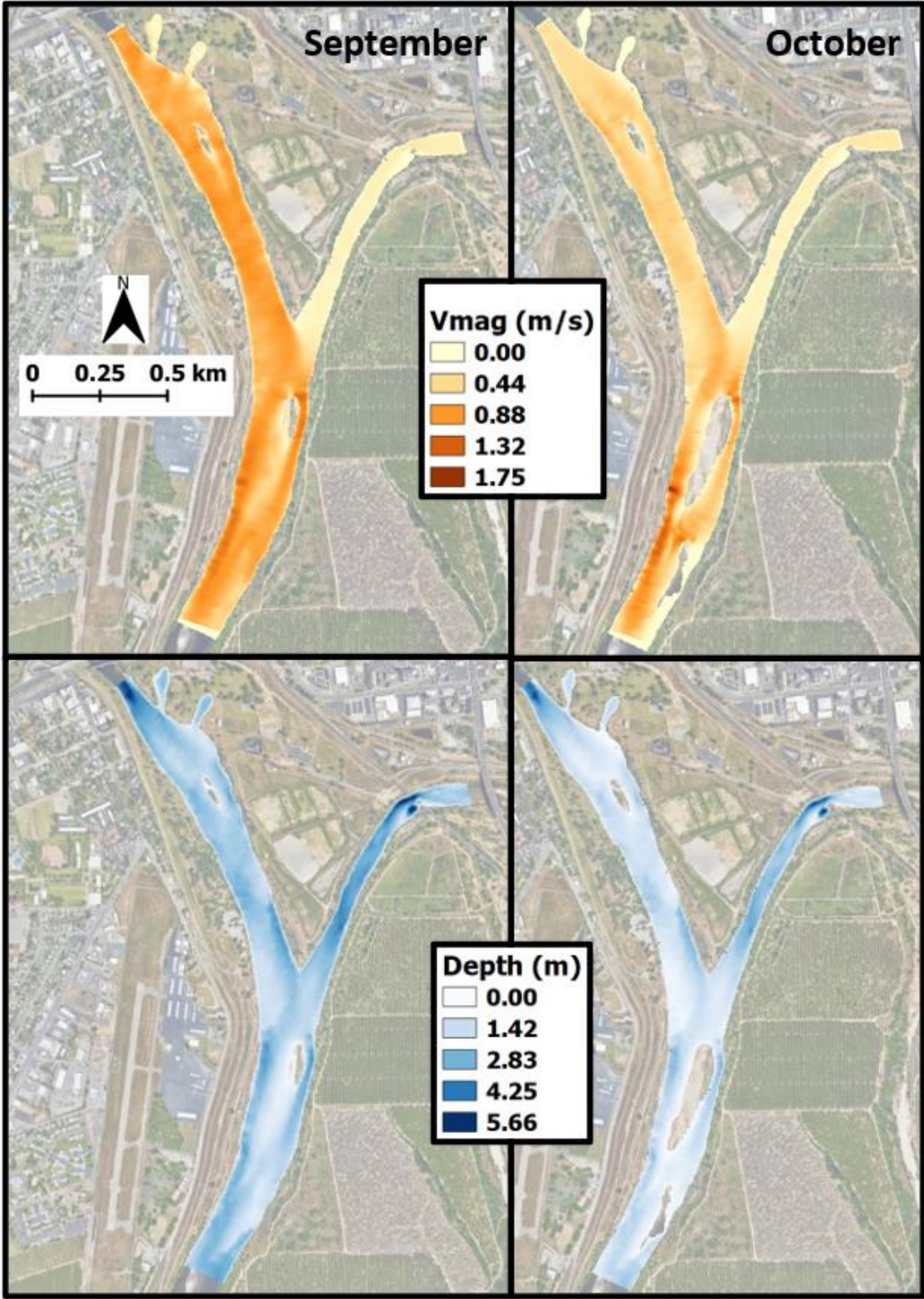
Figure A.A.10. TUFLOW hydrodynamic model outputs of velocity magnitude (Vmag) and depth for September and October DIDSON sampling periods.

Table A.A.4. Regression model descriptions and a priori rationale for inclusion in the AICc analysis.

Model	Description and A Priori Rationale
$D \sim V_{mag}$	These models test the effect of each hydraulic variable individually on DIDSON detection rate.
$D \sim d$	
$D \sim C$	
$D \sim Fr$	
$D \sim T$	These models test the individual effect of temperature and turbidity on detection rate.
$D \sim TU$	
$D \sim T + TU$	This model tests the combined effect of both temperature and turbidity on detection rate, to determine if their combined effect has more influence than their individual effects.
$D \sim C + T$	A preliminary examination of the data indicated that conveyance was the strongest predictor of detection rate among the four hydraulic variables tested. This model tests the combined effect of conveyance with temperature. Based on the range of temperature values that we observed in our surveys compared to the range of turbidity values, temperature appeared to be the more important of the two.
$D \sim C + T + TU$	This model is similar to the one above, but tests the combined effect of conveyance, temperature, and turbidity, to determine if the combined effect of temperature and turbidity, along with conveyance, has a greater influence over detection rate than conveyance and temperature alone.
$D \sim V_{mag} + d + C + Fr$	This model tests the combined effect of all hydraulic variables. This model was included to assess whether hydraulic drivers of habitat selection among DIDSON sites varied among all four of these variables or if one or more were dominant.
$D \sim V_{mag} + d + C + Fr + T + TU$	This model tests the combined effect of all variables. This model was included in the event that no single variable stood out as a strong predictor and relative influence among all six of them would need to be assessed.

D = detection rate; d = depth; V_{mag} = velocity magnitude; C = conveyance; Fr = Froude number; T = temperature; and TU = turbidity

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6 *Appendix B: Hydraulic microhabitats at a regulated river confluence influence Chinook salmon migratory routing during drought*

This file is organized by sections that correspond to the main chapter. It includes performance and validation metrics for the 2D hydrodynamic models that were generated in this study.

6.1 Methods

6.1.1 2D hydrodynamic models and model validation
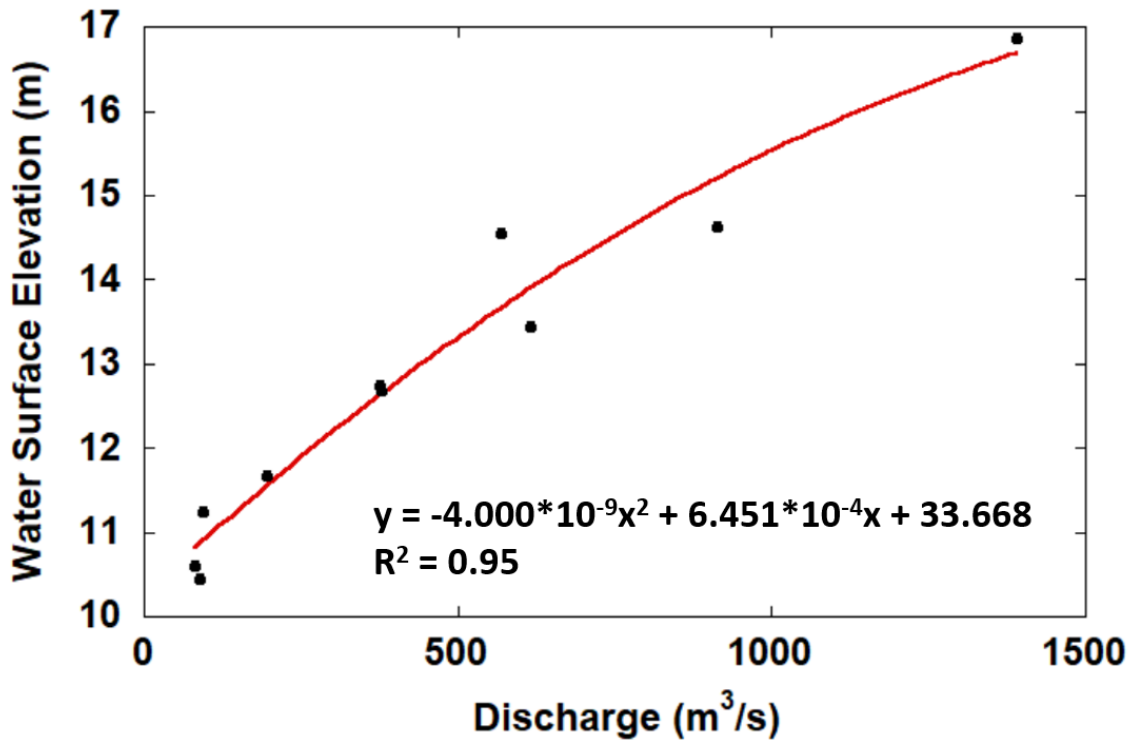
Figure A.B.1. Stage-discharge relationship used to interpolate water surface elevations used in 2D hydrodynamic models.

The equation shown in the figure:

$$y = -4.000*10^{-9}x^2 + 6.451*10^{-4}x + 33.668$$
$$R^2 = 0.95$$

Table A.B.1. Performance summary statistics for the TUFLOW model validation procedure.

Statistic	V_{diff}	$|V_{diff}|$	%error	$|\%error|$
Mean	0.05	0.09	-4.11	28.27
Standard Error	0.00	0.00	3.62	3.59
Median	0.03	0.06	-11.74	19.16
Standard Deviation	0.13	0.10	252.48	250.93
Range	1.45	0.81	17532.29	17433.42
Minimum	-0.64	0.00	-98.86	0.01
Maximum	0.81	0.81	17433.42	17433.42

V_{diff} is the difference between modeled, depth-averaged velocity and the observed surface velocity from the kayak surveys, multiplied by the depth averaged velocity constant found in our analysis (DAVC = 0.63).

7 *Appendix C: Abiotic variables are often neglected in studies of homing and straying in anadromous salmonids*

This file is organized by sections that correspond to the main chapter. It includes a complete list of articles analyzed in the literature metastudy portion of the main chapter.

7.1 Literature Metastudy

7.1.1 Systematic Literature Search

Table A.C.1. A list of the 169 articles analyzed in the metastudy portion of the main article. Sources are alphabetized by lead author and include additional attributes used in our study.

Authors	Article Title	Study Type	Location	Species	Spatial Scale	Life Stage	Abiotic variables included (#)	Abiotic HS factors tested (#)
Abe et al. 2020	Gene expression of neuronal soluble N-ethylmaleimide-sensitive factor attachment protein receptor complex components in the olfactory organ and brain during seaward and homeward migration by pink salmon (*Oncorhynchus gorbuscha*)	Phenotype/gene expression/morphometrics/endocrine response	Japan	Pink	N/A	Both	0	0
Abe et al. 2019	Chum salmon migrating upriver adjust to environmental temperatures through metabolic compensation	Lab-based/Closed system	Lab or N/A	Chum	N/A	Adult	5	2
Anderson et al. 2008	Summer distribution and growth of juvenile coho salmon during colonization of newly accessible habitat	Stationary Counts	U.S. West Coast and B.C.	Coho	Partial Catchment	Adult	0	0
Austin et al. 2021	In a warming river, natural-origin Chinook salmon spawn later but	Modeling	U.S. West Coast and B.C.	Chinook	Single Catchment	Both	1	1

	hatchery-origin conspecifics do not								
Ayllon et al. 2006	Maintenance of a small anadromous subpopulation of brown trout (*Salmo trutta L.*) by straying	Population genetics/dynamics	Europe	Brown Trout	Multiple Catchments	Adult	0	0
Bandoh et al. 2011	Olfactory Responses to Natal Stream Water in Sockeye Salmon by BOLD fMRI	Lab-based/Closed system	Lab or N/A	Sockeye	N/A	Adult	0	0
Barnett et al. 2019	Differential Marking of Embryos by Location and Date of Release Reveals Within-River Natal Homing and Parental Influence on Progeny Return Timing in Sockeye Salmon	Mark-recapture	U.S. West Coast and B.C.	Sockeye	Partial Catchment	Both	0	0
Berland et al. 2004	Movements of wild Atlantic salmon parr in relation to peaking flows below a hydropower station	Biotelemetry	Europe	Atlantic	Reach	Juvenile	2	3
Bett and Hinch 2015	Attraction of migrating adult sockeye salmon to conspecifics in the absence of natal chemical cues	Lab-based/Closed system	Lab or N/A	Sockeye	N/A	Adult	1	1
Bett et al. 2017	Causes and Consequences of Straying into Small Populations of Pacific Salmon	Population genetics/dynamics	U.S. West Coast and B.C.	Sockeye	Partial Catchment	Adult	0	0
Bett et al. 2018	Effects of natal water dilution on the migration of Pacific salmon in a regulated river	Lab-based/Closed system	U.S. West Coast and B.C.	Multiple Oncorhynchus spp.	N/A	Adult	1	1

Bett et al. 2016	Evidence of Olfactory Imprinting at an Early Life Stage in Pink Salmon (*Oncorhynchus gorbuscha*)	Lab-based/Closed system	Lab or N/A	Pink	N/A	Both	0	0
Bond et al. 2017	Combined Effects of Barge Transportation, River Environment, and Rearing Location on Straying and Migration of Adult Snake River Fall-Run Chinook Salmon	Mark-recapture	U.S. West Coast and B.C.	Chinook	Single Catchment	Adult	2	2
Bottom et al. 2005	Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon)	Mark-recapture	U.S. West Coast and B.C.	Chinook	Estuary (marine and freshwater components)	Juvenile	1	1
Bowlby et al. 2016	Applying landscape genetics to evaluate threats affecting endangered Atlantic salmon populations	Population genetics/dynamics	North American Atlantic Coast	Atlantic	Multiple Catchments	Juvenile	8	3
Bracis and Anderson 2013	Inferring the Relative Oceanic Distribution of Salmon from Patterns in Age-Specific Arrival Timing	Modeling	U.S. West Coast and B.C.	Chinook	Coastal/Off Shore	Ocean Adult	0	0
Bradbury et al. 2014	Landscape structure and climatic variation determine Atlantic salmon genetic connectivity in the Northwest Atlantic	Population genetics/dynamics	Europe	Atlantic	Multiple Catchments	Juvenile	6	7
Brannon et al. 2006	Results from a sixteen year study on the effects of oiling from the Exxon Valdez on	Mark-recapture	AK and Yukon	Pink	Multiple Catchments	Adult	1	2

	adult pink salmon returns							
Bumgarner et al. 2009	Returns of Hatchery Steelhead with Different Fin Clips and Coded Wire Tag Lengths	Mark-recapture	U.S. West Coast and B.C.	Steelhead	Partial Catchment	Adult	0	0
Burgerhout et al. 2017	Genetic background and embryonic temperature affect DNA methylation and expression of myogenin and muscle development in Atlantic salmon (*Salmo salar*)	Phenotype/gene expression/morphometrics/endocrine response	Europe	Atlantic	N/A	Juvenile	1	1
Campos et al. 2007	Spatio-temporal genetic variability in sea trout (*Salmo trutta*) populations from north-western Spain	Population genetics/dynamics	Europe	Brown Trout	Multiple Catchments	Adult	2	1
Candy and Beacham 2000	Patterns of homing and straying in southern British Columbia coded-wire tagged chinook salmon (*Oncorhynchus tshawytscha*) populations	Mark-recapture	U.S. West Coast and B.C.	Chinook	Multiple Catchments	Both	0	0
Cauwelier et al. 2018	Across rather than between river genetic structure in Atlantic salmon Salmo salar in north-east Scotland, UK: potential causes and management implications	Population genetics/dynamics	Europe	Atlantic	Single Catchment	Juvenile	1	1
Chappell et al. 2017	Sockeye salmon immunoglobulin V-H usage and pathogen	Lab-based/Closed system	Lab or N/A	Sockeye	N/A	Adult	1	1

	loads differ between spawning sites							
Ciancio et al. 2015	The invasion of an Atlantic Ocean river basin in Patagonia by Chinook salmon: new insights from SNPs	Population genetics/dynamics	South America	Chinook	Partial Catchment	Both	0	0
Clarke et al. 2013	Density Effects on Subyearling Fall Chinook Salmon During Hatchery Rearing in Raceways with Oxygen Supplementation and After Release	Mark-recapture	U.S. West Coast and B.C.	Chinook	Partial Catchment	Juvenile	0	0
Clarke et al. 2012	Performance of Spring Chinook Salmon Reared in Acclimation Ponds for Two and Four Months before Release	Mark-recapture	U.S. West Coast and B.C.	Chinook	Reach	Juvenile	0	0
Clarke et al. 2017	Increased harvest of anadromous hatchery steelhead, Oncorhynchus mykiss (Walbaum), through return timing manipulation	Mark-recapture	U.S. West Coast and B.C.	Steelhead	Partial Catchment	Both	0	0
Connor and Garcia 2006	Prespawning movement of wild and hatchery fall Chinook salmon adults in the Snake River	Biotelemetry	U.S. West Coast and B.C.	Chinook	Reach	Adult	0	0
Courtenay et al. 1997	Factors affecting the recognition of population-specific odours by juvenile coho salmon	Lab-based/Closed system	Lab or N/A	Coho	N/A	Juvenile	1	1

Crossin et al. 2007	Behaviour and physiology of sockeye salmon homing through coastal waters to a natal river	Biotelemetry	U.S. West Coast and B.C.	Sockeye	Estuary (marine and freshwater components)	Ocean Adult	0	0
Crozier et al. 1997	Comparative performance of native and non-native strains of Atlantic salmon (*Salmo salar L.*) ranched from the River Bush, Northern Ireland	Mark-recapture	Europe	Atlantic	Single Catchment	Adult	0	0
Dempson 1999	Evaluation of an alternative strategy to enhance salmon populations: Cage rearing wild smolts from Conne River, Newfoundland	Biotelemetry	North American Atlantic Coast	Atlantic	Estuary (marine and freshwater components)	Both	0	0
Dillane et al. 2007	Spatial and temporal patterns in microsatellite DNA variation of wild Atlantic salmon, Salmo salar, in Irish rivers	Population genetics/dynamics	Europe	Atlantic	Multiple Catchments	Both	1	2
Dittman et al. 2010	Homing and Spawning Site Selection by Supplemented Hatchery- and Natural-Origin Yakima River Spring Chinook Salmon	Mark-recapture	U.S. West Coast and B.C.	Chinook	Partial Catchment	Both	0	0
Dittman et al. 1996	Timing of imprinting to natural and artificial odors by coho salmon (*Oncorhynchus kisutch*)	Lab-based/Closed system	Lab or N/A	Coho	N/A	Juvenile	0	0
Dittman et al. 1997	Sensitization of olfactory guanylyl	Lab-based/Closed system	Lab or N/A	Coho	N/A	Juvenile	0	0

	cyclase to a specific imprinted odorant in coho salmon							
Drenner et al. 2018	Whole-river manipulation of olfactory cues affects upstream migration of sockeye salmon	Biotelemetry	U.S. West Coast and B.C.	Sockeye	Reach	Adult	3	1
Drenner et al. 2015	Environmental conditions and physiological state influence estuarine movements of homing sockeye salmon	Biotelemetry	U.S. West Coast and B.C.	Sockeye	Estuary (marine and freshwater components)	Adult	5	1
Ebbesson et al. 2003	Neural circuits and their structural and chemical reorganization in the light-brain-pituitary axis during parr-smolt transformation in salmon	Phenotype/gene expression/morphometrics/endocrine response	AK and Yukon	Coho	N/A	Juvenile	0	0
Ebbesson et al. 1996	Transient alterations in neurotransmitter levels during a critical period of neural development in coho salmon (*Oncorhynchus kisutch*)	Lab-based/Closed system	Lab or N/A	Coho	N/A	Juvenile	0	0
Ensing et al. 2011	Complex pattern of genetic structuring in the Atlantic salmon (*Salmo salar L.*) of the River Foyle system in northwest Ireland: disentangling the evolutionary signal from population stochasticity	Population genetics/dynamics	Europe	Atlantic	Single Catchment	Juvenile	0	0

Erdman et al. 2018	Release of hatchery adult steelhead for angler opportunity increases potential for interactions with endemic steelhead	Biotelemetry	U.S. West Coast and B.C.	Steelhead	Single Catchment	Adult	0	0
Feeken et al. 2019	Distribution and Movement of Steelhead and Anglers in the Clearwater River, Idaho	Biotelemetry	U.S. West Coast and B.C.	Steelhead	Partial Catchment	Adult	0	0
Feldhaus et al. 2016	The Influence of Size at Release on Performance of Imnaha River Chinook Salmon Hatchery Smolts	Mark-recapture	U.S. West Coast and B.C.	Chinook	Partial Catchment	Both	0	0
Fujiwara et al. 2014	The Effects of Disease-Induced Juvenile Mortality on the Transient and Asymptotic Population Dynamics of Chinook Salmon (*Oncorhynchus tshawytscha*)	Modeling	U.S. West Coast and B.C.	Chinook	Single Catchment	Both	0	0
Garvin et al. 2013	Recent physical connections may explain weak genetic structure in western Alaskan chum salmon (*Oncorhynchus keta*) populations	Population genetics/dynamics	AK and Yukon	Chum	Multiple Catchments	Adult	0	0
Gharrett et al. 2001	Use of a genetic marker to examine genetic interaction among subpopulations of pink salmon (*Oncorhynchus gorbuscha*)	Population genetics/dynamics	AK and Yukon	Pink	Multiple Catchments	Adult	0	0

Gilk et al. 2004	Outbreeding depression in hybrids between spatially separated pink salmon, *Oncorhynchus gorbuscha*, populations: marine survival, homing ability, and variability in family size	Population genetics/dynamics	AK and Yukon	Pink	Multiple Catchments	Both	0	0
Godfrey et al. 2015	Depth use and migratory behaviour of homing Atlantic salmon (*Salmo salar*) in Scottish coastal waters	Biotelemetry	Europe	Atlantic	Coastal/Off Shore	Ocean Adult	2	1
Gorsky et al. 2009	The Effects of Smolt Stocking Strategies on Migratory Path Selection of Adult Atlantic Salmon in the Penobscot River, Maine	Biotelemetry	North American Atlantic Coast	Atlantic	Reach	Adult	1	2
Gowans et al. 2003	Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland	Biotelemetry	Europe	Atlantic	Reach	Adult	3	1
Groves et al. 1968	Roles of olfaction and vision in choice of spawning site by homing adult Chinook salmon (*Oncorhynchus tshawytscha*)	Mark-recapture	U.S. West Coast and B.C.	Chinook	Partial Catchment	Adult	0	0
Gudmundsson et al. 2013	Spatio-temporal effects of stray hatchery-reared Atlantic salmon *Salmo salar* on population genetic structure	Population genetics/dynamics	Europe	Atlantic	Single Catchment	Both	0	0

	within a 21 km-long Icelandic river system							
Hamann and Kennedy 2012	Juvenile dispersal affects straying behaviors of adults in a migratory population	Microchemistry	U.S. West Coast and B.C.	Chinook	Partial Catchment	Both	0	0
Hanson et al. 2013	Reconstructing marine life-history strategies of wild Atlantic salmon from the stable isotope composition of otoliths	Microchemistry	Europe	Atlantic	Coastal/Off Shore	Ocean Adult	2	1
Hauser et al. 2017	Homing of Pacific Salmon to a Marine Release Site: A Case Study of the Homer Spit Fishing Hole, Alaska	Mark-recapture	AK and Yukon	Multiple Oncorhynchus spp.	Coastal/Off Shore	Both	0	0
Havey et al. 2017	Experimental Evidence for Olfactory Imprinting by Sockeye Salmon at Embryonic and Smolt Stages	Lab-based/Closed system	Lab or N/A	Sockeye	N/A	Juvenile	0	0
Hess and Matala 2014	Archival genetic analysis suggests recent immigration has altered a population of Chinook salmon in an unsupplemented wilderness area	Population genetics/dynamics	U.S. West Coast and B.C.	Chinook	Single Catchment	Adult	0	0
Hess et al. 2014	Monitoring Stock-Specific Abundance, Run Timing, and Straying of Chinook Salmon in the Columbia River Using Genetic Stock Identification (GSI)	Population genetics/dynamics	U.S. West Coast and B.C.	Chinook	Single Catchment	Adult	0	0
Hill et al. 2002	The effects of small dispersal rates on	Modeling	Lab or N/A	N/A	Single Catchment	Adult	0	0

	extinction times in structured metapopulation models							
Hofmann and Meyer 1993	Visual-evoked responses in the salmon telencephalon change during smolt transformation	Lab-based/Closed system	Lab or N/A	Coho	N/A	Juvenile	2	1
Horreo et al. 2011	Impact of climate change and human-mediated introgression on southern European Atlantic salmon populations	Population genetics/dynamics	Europe	Atlantic	Multiple Catchments	Adult	1	1
Horreo et al. 2018	Nature versus nurture? Consequences of short captivity in early stages	Phenotype/gene expression/morphometrics/endocrine response	Europe	Atlantic	N/A	Both	0	0
Ikediashi et al. 2012	The origins of Atlantic salmon (*Salmo salar L.*) recolonizing the River Mersey in northwest England	Population genetics/dynamics	Europe	Atlantic	Multiple Catchments	Both	0	0
Ioannidou and O'Hanley 2019	The importance of spatiotemporal fish population dynamics in barrier mitigation planning	Modeling	U.S. West Coast and B.C.	Coho	Single Catchment	Both	7	1
Jackson et al. 2013	Impact of *Lepeophtheirus salmonis* infestations on migrating Atlantic salmon, *Salmo salar L.*, smolts at eight locations in Ireland with an analysis of lice-induced marine mortality	Mark-recapture	Europe	Atlantic	Coastal/Off Shore	Ocean Adult	1	1

Jarrard 1997	Postembryonic changes in the structure of the olfactory bulb of the Chinook salmon (*Oncorhynchus tshawytscha*) across its life history	Lab-based/Closed system	Lab or N/A	Chinook	N/A	Both	0	0
Jasper et al. 2013	Source-Sink Estimates of Genetic Introgression Show Influence of Hatchery Strays on Wild Chum Salmon Populations in Prince William Sound, Alaska	Population genetics/dynamics	AK and Yukon	Chum	Multiple Catchments	Adult	0	0
Jensen et al. 2017	Rapid evolution of genetic and phenotypic divergence in Atlantic salmon following the colonisation of two new branches of a watercourse	Population genetics/dynamics	Europe	Atlantic	Partial Catchment	Adult	0	0
Johnson and Banks 2009	Interlocus variance of F-ST provides evidence for directional selection over an olfactory receptor gene in Coho salmon (*Oncorhynchus kisutch*) populations	Phenotype/gene expression/morphometrics/endocrine response	U.S. West Coast and B.C.	Coho	N/A	Adult	0	0
Johnstone et al. 2011	Expression of olfactory receptors in different life stages and life histories of wild Atlantic salmon (*Salmo salar*)	Phenotype/gene expression/morphometrics/endocrine response	North American Atlantic Coast	Atlantic	N/A	Both	0	0
Jonsson and Jonsson 2018	Egg incubation temperature affects the timing of the Atlantic	Mark-recapture	Europe	Atlantic	Partial Catchment	Both	2	1

	salmon *Salmo salar* homing migration							
Jonsson et al. 2018	Water level influences migratory patterns of anadromous brown trout in small streams	Mark-recapture	Europe	Brown Trout	Multiple Catchments	Adult	2	2
Kaitala and Getz 1995	Population-dynamics and harvesting of semelparous species with phenotypic and genotypic variability in reproductive age	Modeling	Lab or N/A	N/A	Coastal/Off Shore	Ocean Adult	0	0
Keefe and Winn 1991	Chemosensory attraction to home stream water and conspecifics by native brook trout, *Salvelinus fontinalis* from 2 southern New England streams	Lab-based/Closed system	Lab or N/A	Brook trout	N/A	Juvenile	2	1
Keefer et al. 2008	Overwintering distribution, behavior, and survival of adult summer steelhead: Variability among Columbia river populations	Mark-recapture	U.S. West Coast and B.C.	Steelhead	Single Catchment	Adult	2	2
Keefer et al. 2006	Route selection in a large river during the homing migration of Chinook salmon (*Oncorhynchus tshawytscha*)	Biotelemetry	U.S. West Coast and B.C.	Chinook	Single Catchment	Adult	0	0
Keefer et al. 2008b	Non-direct homing behaviours by adult Chinook salmon in a large, multi-stock river system	Biotelemetry	U.S. West Coast and B.C.	Chinook	Single Catchment	Adult	2	3

Keefer et al. 2008c	Transporting juvenile salmonids around dams impairs adult migration	Biotelemetry	U.S. West Coast and B.C.	Multiple Oncorhynchus spp.	Single Catchment	Both	0	0
Keefer et al. 2019	Temperature and depth profiles of Chinook salmon and the energetic costs of their long-distance homing migrations	Biotelemetry	U.S. West Coast and B.C.	Chinook	Single Catchment	Adult	3	2
Keefer et al. 2004	Hydrosystem, dam, and reservoir passage rates of adult Chinook salmon and Steelhead in the Columbia and Snake Rivers	Mark-recapture	U.S. West Coast and B.C.	Multiple Oncorhynchus spp.	Partial Catchment	Adult	2	2
Kitagawa et al. 2016	Atmospheric depression-mediated water temperature changes affect the vertical movement of chum salmon Oncorhynchus keta	Biotelemetry	Japan	Chum	Coastal/Off Shore	Adult	1	1
Kitahashi et al. 2000	Micro data logger analyses of homing behavior of chum salmon in Ishikari Bay	Biotelemetry	Japan	Chum	Coastal/Off Shore	Ocean Adult	2	1
Kock et al. 2016	Angler Harvest, Hatchery Return, and Tributary Stray Rates of Recycled Adult Summer Steelhead Oncorhynchus mykiss in the Cowlitz River, Washington	Biotelemetry	U.S. West Coast and B.C.	Steelhead	Partial Catchment	Adult	2	1
Kock et al. 2018	Responses of Hatchery- and Natural-Origin Adult Spring Chinook Salmon to a Trap-and-Haul	Biotelemetry	U.S. West Coast and B.C.	Chinook	Partial Catchment	Adult	1	1

	Reintroduction Program							
Kudo et al. 2009	Morphometry of Olfactory Lamellae and Olfactory Receptor Neurons During the Life History of Chum Salmon (*Oncorhynchus keta*)	Phenotype/gene expression/morphometrics/endocrine response	Japan	Chum	N/A	Both	0	0
Labelle 1992	Straying patterns of coho salmon (*Oncorhynchus kisutch*) stocks from southeast Vancouver Island, British Columbia	Mark-recapture	U.S. West Coast and B.C.	Coho	Multiple Catchments	Both	2	1
Lacroix 2013	Population-specific ranges of oceanic migration for adult Atlantic salmon (*Salmo salar*) documented using pop-up satellite archival tags	Biotelemetry	North American Atlantic Coast	Atlantic	Coastal/Off Shore	Ocean Adult	2	1
Lee and Ueda 2012	Effects of aggressive interaction on downstream movement and olfactory function in masu salmon, *Oncorhynchus masou*	Lab-based/Closed system	Lab or N/A	Masu	N/A	Juvenile	1	1
Lehtonen et al. 2009	Spatio-temporal genetic structuring of brown trout (*Salmo trutta L.*) populations within the River Luga, northwest Russia	Population genetics/dynamics	Europe	Brown Trout	Partial Catchment	Both	1	1
Lema and Nevitt 2004	Evidence that thyroid hormone induces	Lab-based/Closed system	Lab or N/A	Coho	N/A	Juvenile	0	0

	olfactory cellular proliferation in salmon during a sensitive period for imprinting							
Lennox et al. 2018	Biotic and abiotic determinants of the ascent behaviour of adult Atlantic salmon transiting passable waterfalls	Biotelemetry	Europe	Atlantic	Reach	Adult	5	1
Leunda et al. 2013	Homing and straying of Atlantic salmon in the Bidasoa River: report of an unusual stray from Great Britain to the Iberian Peninsula	Mark-recapture	Europe	Atlantic	Multiple Catchments	Adult	0	0
Lim et al. 2020	Elevated incubation temperature improves later-life swimming endurance in juvenile Chinook salmon, *Oncorhynchus tshawytscha*	Lab-based/Closed system	Lab or N/A	Chinook	N/A	Juvenile	1	1
Lin and Robinson 2019	How do migratory fish populations respond to barrier removal in spawning and nursery grounds?	Modeling	Lab or N/A	N/A	Partial Catchment	Adult	0	0
Lin et al. 2008	Contrasting patterns of morphological and neutral genetic divergence among geographically proximate populations of sockeye salmon Oncorhynchus nerka in Lake Aleknagik, Alaska	Phenotype/gene expression/morphometrics/endocrine response	AK and Yukon	Sockeye	Lake and Connected Streams	Adult	1	1

Lin et al. 2011	Self-sustaining populations, population sinks or aggregates of strays: chum (*Oncorhynchus keta*) and Chinook salmon (*Oncorhynchus tshawytscha*) in the Wood River system, Alaska	Population genetics/dynamics	AK and Yukon	Multiple Oncorhynchus spp.	Multiple Catchments	Adult	0	0
Lister 2014	Natural Productivity in Steelhead Populations of Natural and Hatchery Origin: Assessing Hatchery Spawner Influence	Population genetics/dynamics	U.S. West Coast and B.C.	Steelhead	Single Catchment	Both	0	0
Lohmann et al. 2008	Geomagnetic imprinting: A unifying hypothesis of long-distance natal homing in salmon and sea turtles	Modeling	Lab or N/A	N/A	Coastal/Off Shore	Both	2	1
Lower and Moore 2007	The impact of a brominated flame retardant on smoltification and olfactory function in Atlantic salmon (*Salmo salar L.*) smolts	Lab-based/Closed system	Lab or N/A	Atlantic	N/A	Juvenile	0	0
Madsen et al. 2019	Differential expression of olfactory genes in Atlantic salmon (*Salmo salar*) during the parr-smolt transformation	Phenotype/gene expression/morphometrics/endocrine response	Europe	Atlantic	N/A	Both	1	1
Martin et al. 2013	Persistence of a southern Atlantic salmon population: diversity of natal	Microchemistry	Europe	Atlantic	Single Catchment	Both	0	0

	origins from otolith elemental and Sr isotopic signatures							
McConnell et al. 2019	Is blood cortisol or vateritic otolith composition associated with natal dispersal or reproductive performance on the spawning grounds of straying and homing hatchery-produced chum salmon (*Oncorhynchus keta*) in Southeast Alaska?	Phenotype/gene expression/morphometrics/endocrine response	AK and Yukon	Chum	N/A	Both	2	1
McCormick et al. 2003	Endocrine and physiological changes in Atlantic salmon smolts following hatchery release	Phenotype/gene expression/morphometrics/endocrine response	North American Atlantic Coast	Atlantic	N/A	Juvenile	1	1
McGlauflin et al. 2011	Spawning Habitat and Geography Influence Population Structure and Juvenile Migration Timing of Sockeye Salmon in the Wood River Lakes, Alaska	Population genetics/dynamics	AK and Yukon	Sockeye	Single Catchment	Adult	1	1
McPhee et al. 2009	Genetic Diversity and Population Structure in the Kuskokwim River Drainage Support the Recurrent Evolution Hypothesis for Sockeye Salmon Life Histories	Population genetics/dynamics	AK and Yukon	Sockeye	Partial Catchment	Adult	1	1
Michael et al. 1990)	Predictability in a small commercial Atlantic salmon fishery in western Newfoundland	Stationary Counts	North American Atlantic Coast	Atlantic	Coastal/Off Shore	Both	0	0

Middleton et al. 2018	Effects of natal water concentration and temperature on the behaviour of up-river migrating sockeye salmon	Biotelemetry	U.S. West Coast and B.C.	Sockeye	Partial Catchment	Adult	4	2
Moore et al. 2007	The impact of a pesticide on migratory activity and olfactory function in Atlantic salmon (*Salmo salar L.*) smolts	Lab-based/Closed system	Lab or N/A	Atlantic	N/A	Juvenile	3	2
Morin et al. 1994	Changes in serum-free thyroxine, prolactin, and olfactory activity during induced smoltification in Atlantic salmon (*Salmo salar*)	Lab-based/Closed system	Lab or N/A	Atlantic	N/A	Juvenile	0	0
Morin and Døving 1992	Changes in the olfactory function of Atlantic salmon *Salmo-salar* in the course of smoltification	Lab-based/Closed system	Lab or N/A	Atlantic	N/A	Juvenile	0	0
Murdoch et al. 2009	Migration Patterns and Spawning Distribution of Adult Hatchery Sockeye Salmon Released as Parr from Net-Pens in Lake Wenatchee, Washington	Biotelemetry	U.S. West Coast and B.C.	Sockeye	Lake and Connected Streams	Both	0	0
Musleh et al. 2020	Mixed-stock analyses of migratory, non-native Chinook salmon at sea and assignment to natal sites in fresh water at their	Population genetics/dynamics	South America	Chinook	Multiple Catchments	Adult	1	1

	introduced range in South America							
Narum et al. 2008	Localized Genetic Structure Persists in Wild Populations of Chinook Salmon in the John Day River Despite Gene Flow from Outside Sources	Population genetics/dynamics	U.S. West Coast and B.C.	Chinook	Single Catchment	Adult	0	0
Naughton et al. 2018	Reservoir provides cool-water refuge for adult Chinook salmon in a trap-and-haul reintroduction program	Biotelemetry	U.S. West Coast and B.C.	Chinook	Partial Catchment	Adult	2	1
Negus 2003	Determination of smoltification status in juvenile migratory rainbow trout and Chinook salmon in Minnesota	Lab-based/Closed system	Lab or N/A	Multiple Oncorhynchus spp.	N/A	Juvenile	0	0
Nevitt et al. 1994	Evidence for a peripheral olfactory memory in imprinted salmon	Lab-based/Closed system	Lab or N/A	Coho	N/A	Both	0	0
Nickelson and Lawson 1998	Population viability of coho salmon, Oncorhynchus kisutch, in Oregon coastal basins: application of a habitat-based life cycle model	Modeling	U.S. West Coast and B.C.	Coho	Multiple Catchments	Both	0	0
Nordeng 2009	Char ecology. Natal homing in sympatric populations of anadromous Arctic char *Salvelinus alpinus* (L.): roles of pheromone recognition	Mark-recapture	Europe	Charr (Salvelinus spp.)	Multiple Catchments	Both	0	0

Nordeng and Bratland 2006	Homing experiments with parr, smolt and residents of anadromous Arctic char *Salvelinus alpinus* and brown trout *Salmo trutta*: transplantation between neighbouring river systems	Mark-recapture	Europe	Charr (Salvelinus spp.)	Partial Catchment	Both	0	0
Ochs et al. 2017	Organization of Glomerular Territories in the Olfactory Bulb of Post-Embryonic Wild Chinook Salmon *Oncorhynchus tshawytscha*	Lab-based/Closed system	Lab or N/A	Chinook	N/A	Juvenile	0	0
Olsen et al. 2010	The influence of hydrology and waterway distance on population structure of Chinook salmon *Oncorhynchus tshawytscha* in a large river	Population genetics/dynamics	AK and Yukon	Chinook	Single Catchment	Adult	4	2
Östergren et al. 2012	Linking genetic assignment tests with telemetry enhances understanding of spawning migration and homing in sea trout *Salmo trutta L.*	Biotelemetry	Europe	Brown Trout	Multiple Catchments	Adult	0	0
Ozerov et al. 2016	Genomewide introgressive hybridization patterns in wild Atlantic salmon influenced by inadvertent gene flow from hatchery releases	Population genetics/dynamics	Europe	Atlantic	Multiple Catchments	Juvenile	0	0
Parkinson et al. 1999	A preliminary investigation of	Biotelemetry	Europe	Grayling	Reach	Adult	3	1

	spawning migrations of grayling in a small stream as determined by radio-tracking							
Pascual et al. 1995	Factors affecting the homing of fall Chinook salmon from Columbia River hatcheries	Mark-recapture	U.S. West Coast and B.C.	Chinook	Single Catchment	Both	0	0
Pearsons and O'Connor 2020	Stray Rates of Natural-Origin Chinook Salmon and Steelhead in the Upper Columbia River Watershed	Biotelemetry	U.S. West Coast and B.C.	Multiple Oncorhynchus spp.	Multiple Catchments	Adult	0	0
Perrier et al. 2010	Natural recolonization of the Seine River by Atlantic salmon (*Salmo salar*) of multiple origins	Population genetics/dynamics	Europe	Atlantic	Multiple Catchments	Adult	0	0
Peterson et al. 2016	Exploratory behavior of dispersers within a metapopulation of sockeye salmon	Mark-recapture	AK and Yukon	Sockeye	Lake and Connected Streams	Adult	0	0
Peterson et al. 2020	Stability in reproductive timing and habitat usage of Chinook salmon across six years of varying environmental conditions and abundance	Stationary Counts	U.S. West Coast and B.C.	Chinook	Reach	Adult	4	2
Petrou et al. 2014	Fine-scale sampling reveals distinct isolation by distance patterns in chum salmon (*Oncorhynchus keta*) populations occupying a glacially dynamic environment	Population genetics/dynamics	AK and Yukon	Chum	Multiple Catchments	Adult	0	0

Poćwierz-Kotus et al. 2015	Restitution and genetic differentiation of salmon populations in the southern Baltic genotyped with the Atlantic salmon 7K SNP array	Population genetics/dynamics	Europe	Atlantic	Multiple Catchments	Both	0	0
Pollock et al. 2020	Within-river straying: sex and size influence recovery location of hatchery Chinook salmon (*Oncorhynchus tshawytscha*)	Mark-recapture	U.S. West Coast and B.C.	Chinook	Single Catchment	Adult	0	0
Powell and Campbell 2020	Contemporary genetic structure affects genetic stock identification of steelhead trout in the Snake River basin	Population genetics/dynamics	U.S. West Coast and B.C.	Steelhead	Single Catchment	Adult	0	0
Quinn et al. 2012	Population dynamics and asynchrony at fine spatial scales: a case history of sockeye salmon (*Oncorhynchus nerka*) population structure in Alaska, USA	Mark-recapture	AK and Yukon	Sockeye	Lake and Connected Streams	Both	0	0
Quinn et al. 2006	Experimental evidence of homing to site of incubation by mature sockeye salmon, Oncorhynchus nerka	Mark-recapture	AK and Yukon	Sockeye	Partial Catchment	Both	1	1
Quinn et al. 1999	Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*)	Phenotype/gene expression/morphometrics/endocrine response	AK and Yukon	Sockeye	N/A	Both	1	1

Quiñones et al. 2014	Hatchery practices may result in replacement of wild salmonids: adult trends in the Klamath basin, California	Mark-recapture	U.S. West Coast and B.C.	Multiple Oncorhynchus spp.	Single Catchment	Adult	0	0
Richins and Skalski 2018	Steelhead Overshoot and Fallback Rates in the Columbia-Snake River Basin and the Influence of Hatchery and Hydrosystem Operations	Biotelemetry	U.S. West Coast and B.C.	Steelhead	Single Catchment	Adult	1	1
Santaquiteria et al. 2016	Contrasting levels of strays and contemporary gene flow among anadromous populations of Arctic charr, *Salvelinus alpinus* (L.), in northern Norway	Population genetics/dynamics	Europe	Charr (Salvelinus spp.)	Multiple Catchments	Both	0	0
Saura et al. 2008	Are there atlantic salmon in the river tambre?	Population genetics/dynamics	Europe	Atlantic	Single Catchment	Adult	0	0
Schroeder et al. 2001	Origin and straying of hatchery winter steelhead in Oregon coastal rivers	Mark-recapture	U.S. West Coast and B.C.	Steelhead	Multiple Catchments	Both	0	0
Shrimpton et al. 2014	Freshwater movement patterns by juvenile Pacific salmon Oncorhynchus spp. before they migrate to the ocean: Oh the places you'll go!	Microchemistry	U.S. West Coast and B.C.	Coho	Partial Catchment	Both	0	0
Small et al. 2011	Does Lower Crab Creek in the Eastern Washington Desert Have a Native	Population genetics/dynamics	U.S. West Coast and B.C.	Chinook	Partial Catchment	Both	0	0

	Population of Chinook Salmon?							
Small et al. 2006	Genetic structure of chum salmon (*Oncorhynchus keta*) populations in the lower Columbia River: are chum salmon in Cascade tributaries remnant populations?	Population genetics/dynamics	U.S. West Coast and B.C.	Chum	Partial Catchment	Adult	0	0
Stewart et al. 2003	Evidence for fine-scale natal homing among island beach spawning sockeye salmon, Oncorhynchus nerka	Population genetics/dynamics	AK and Yukon	Sockeye	Lake and Connected Streams	Adult	0	0
Tanaka et al. 2000	Behavioural thermoregulation of chum salmon during homing migration in coastal waters	Biotelemetry	Japan	Chum	Coastal/Off Shore	Adult	3	1
Tattam and Ruzycki 2020	Smolt Transportation Influences Straying of Wild and Hatchery Snake River Steelhead into the John Day River	Mark-recapture	U.S. West Coast and B.C.	Steelhead	Single Catchment	Both	2	2
Tentelier et al. 2016	Space use and its effects on reproductive success of anadromous Atlantic salmon	Biotelemetry	Europe	Atlantic	Single Catchment	Adult	0	0
Thedinga et al. 2000	Effects of stock, coded-wire tagging, and transplant on straying of pink salmon (*Oncorhynchus gorbuscha*) in southeastern Alaska	Mark-recapture	AK and Yukon	Pink	Multiple Catchments	Both	0	0
Turcotte and Shrimpton 2020	Assessment of spawning site fidelity in interior Fraser River	Microchemistry	U.S. West Coast and B.C.	Coho	Partial Catchment	Both	0	0

	Coho salmon Oncorhynchus kisutch using otolith microchemistry, in British Columbia, Canada							
Ueda et al. 2016	Involvement of hormones in olfactory imprinting and homing in chum salmon	Phenotype/gene expression/morphometrics/endocrine response	Japan	Chum	N/A	Both	0	0
Unwin and Quinn 1993	Homing and straying patterns of Chinook salmon (*Oncorhynchus tshawytscha*) from a New Zealand hatchery – spatial distribution of strays and effects of release date	Mark-recapture	New Zealand	Chinook	Multiple Catchments	Adult	1	1
Vähä et al. 2007	Life-history and habitat features influence the within-river genetic structure of Atlantic salmon	Population genetics/dynamics	Europe	Atlantic	Single Catchment	Adult	5	1
Walter et al. 2009	Gene flow increases temporal stability of Chinook salmon (*Oncorhynchus tshawytscha*) populations in the Upper Fraser River, British Columbia, Canada	Population genetics/dynamics	U.S. West Coast and B.C.	Chinook	Partial Catchment	Adult	0	0
Wellband et al. 2012	Fine-Scale Population Genetic Structure and Dispersal of Juvenile Steelhead in the Bulkley-Morice River, British Columbia	Population genetics/dynamics	U.S. West Coast and B.C.	Steelhead	Single Catchment	Juvenile	0	0
Wertheimer et al. 2000	Straying of adult pink salmon from their	Mark-recapture	AK and Yukon	Pink	Multiple Catchments	Both	2	1

	natal stream following embryonic exposure to weathered Exxon Valdez crude oil							
Westley et al. 2015	Signals of climate, conspecific density, and watershed features in patterns of homing and dispersal by Pacific salmon	Mark-recapture	U.S. West Coast and B.C.	Chinook	Single Catchment	Adult	9	5
Westley et al. 2013	Rates of straying by hatchery-produced Pacific salmon (*Oncorhynchus spp*.) and steelhead (*Oncorhynchus mykiss*) differ among species, life history types, and populations	Mark-recapture	U.S. West Coast and B.C.	Multiple Oncorhynchus spp.	Single Catchment	Adult	0	0
Wilson et al. 2014	Coastal marine and in-river migration behaviour of adult sockeye salmon en route to spawning grounds	Biotelemetry	U.S. West Coast and B.C.	Sockeye	Estuary (marine and freshwater components)	Adult	7	2
Wirth et al. 2012	A Remote-Sensing, GIS-Based Approach to Identify, Characterize, and Model Spawning Habitat for Fall-Run Chum Salmon in a Sub-Arctic, Glacially Fed River	Modeling	AK and Yukon	Chum	Reach	Adult	4	2
Withler et al. 2000	Intact genetic structure and high levels of genetic diversity in bottlenecked sockeye salmon (*Oncorhynchus nerka*) populations of	Population genetics/dynamics	U.S. West Coast and B.C.	Sockeye	Single Catchment	Adult	0	0

Author	Title	Theme/Method	Country	Species	System	Life stage		
	the Fraser River, British Columbia, Canada							
Yamaguchi et al. 2016	Population structure and conservation genetics of anadromous white-spotted char (*Salvelinus leucomaenis*) on Hokkaido Island: Detection of isolation-by-distance	Population genetics/dynamics	Japan	Charr (Salvelinus spp.)	Multiple Catchments	Adult	0	0
Yamamoto et al. 2010	Olfactory Imprinting of Amino Acids in Lacustrine Sockeye Salmon	Lab-based/Closed system	Lab or N/A	Sockeye	N/A	Juvenile	0	0
Yamamoto et al. 2013	Olfactory Homing of Chum Salmon to Stable Compositions of Amino Acids in Natal Stream Water	Lab-based/Closed system	Lab or N/A	Chum	N/A	Adult	3	1
Yano and Nakamura 1992	Observations on the effect of visual and olfactory ablation on the swimming behavior of migrating adult chum salmon Oncorhynchus keta	Biotelemetry	Japan	Chum	Coastal/Off Shore	Ocean Adult	4	1
Yeakel et al. 2018	Eco-evolutionary dynamics, density-dependent dispersal and collective behaviour: implications for salmon metapopulation robustness	Modeling	Lab or N/A	N/A	Single Catchment	Adult	0	0

| Zimmerman et al. 2013 | Species and Life History Affect the Utility of Otolith Chemical Composition for Determining Natal Stream of Origin for Pacific Salmon | Microchemistry | AK and Yukon | Multiple Oncorhynchus spp. | Multiple Catchments | Both | 0 | 0 |

Table A.C.2. Frequency of abiotic variable type per study attribute class.

		N	Temperature or temperature proxy	Discharge	Depth	Spatial Dimensions (distances, areas, elevation, etc.) and geomorphic classification	Oceanographic/Geophysical/Climatic Condition (tides, magnetic field, PDO, ENSO, etc.)	Photoperiod	Passage Barriers	Other habitat disturbance (infrastructure, land use, parasite, etc.)	Other water chemistry (natal water concentration, salinity, turbidity, pH, DO, contaminants)
Study method category	Biotelemetry	21	13	13	11	8	4	1	3	0	5
	Stationary Counts	1	1	1	0	2	0	0	0	0	0
	Lab/Closed System	12	5	0	0	4	0	2	0	1	11
	Microchemistry	1	2	0	0	0	0	0	0	0	0
	Modeling	4	1	0	0	3	4	0	6	0	0
	Mark-Recapture	14	11	11	1	1	1	0	0	1	4
	Pheno/genotype	5	4	0	0	1	0	0	0	0	0
	Population Genetics	12	1	1	0	16	2	0	2	7	3
Study location	AK and Yukon	9	2	1	0	8	2	0	0	0	3
	Europe	18	9	7	4	11	2	0	4	1	3
	Japan	4	4	0	4	1	0	0	0	0	1
	Lab or N/A	12	5	0	0	4	0	2	0	1	10
	New Zealand	1	0	1	0	0	0	0	0	0	0
	NA Atlantic Coast	4	1	1	2	0	0	0	0	7	1

	South America	1	0	0	0	1	0	0	0	0	0
	US West Coast	21	17	16	2	10	5	1	7	0	5
Study species	Atlantic	19	7	7	2	9	2	0	3	1	5
	Brook Trout	1	0	0	0	0	0	0	0	0	2
	Brown Trout	3	1	0	1	2	0	0	1	0	0
	Chinook	13	10	11	0	10	1	0	0	0	0
	Chum	8	0	0	4	6	2	0	0	0	4
	Coho	4	0	0	0	1	0	0	6	0	1
	Grayling	1	1	0	1	0	0	0	0	0	1
	Masu	1	0	0	0	1	0	0	0	0	0
	N/A (theoretical model)	1	0	0	0	0	2	0	0	0	0
	Multiple Oncorhynchus	2	1	1	0	0	0	0	0	0	1
	Pink	2	0	0	0	0	0	0	0	0	3
	Sockeye	11	6	1	2	6	4	1	1	1	4
	Steelhead	4	3	4	0	0	0	0	0	0	0

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