Impacts of Environmental and Social Factors on Fish Movement and Behavior Over Three Timescales

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Abstract

Impacts of Environmental and Social Factors on Fish Movement and Behavior Over Three Timescales

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The ability to move influences essential behaviors in fish, including foraging, predator escape, migration, mating, and breeding. These behaviors occur over various timescales, from the immediate response to predators to migrations over a longer timescale. Environmental factors like temperature impact both instantaneous and long-term behaviors. Additionally, social factors, such as the presence and behavior of other fish, also play a significant role in these behaviors. This dissertation explores the impacts of environmental and social factors on fish movement and behavior across three distinct timescales. In the first chapter, I examine how temperature affects the collective response of fish to a predation threat in the timescale of seconds. Using lab experiments I found that while fish can move faster in higher temperatures, during a predation threat, fish at lower temperatures are able to compensate for the lower speeds by increasing their probability to startle. In the second chapter, I explore the influence of social cues on the juvenile migration of salmon on a daily timescale in three rivers in Washington state. I use hatchery releases as a way to test the ‘pied-piper’ hypothesis that the large number of hatchery salmon moving downstream motivates wild salmon to migrate along with them. Our findings support the ‘pied-piper’ hypothesis, demonstrating that both environmental and social cues stimulate downstream migration in salmon. In the third chapter, I investigate the influence of temperature, cumulative flow, and hatchery releases on the timing of peak migration and the duration of migration of juvenile salmon at the seasonal timescale. The results show that increased temperatures have a negative effect on the timing of migration of sub-yearling Chinook salmon and sub-yearling chum salmon. Similarly, increased flow has a negative effect on the timing of migration of coho salmon. Larger and earlier hatchery releases have a negative effect on the duration of migration of coho salmon. Broadly, this research shows us both environmental factors and social factors influence the movement and behavior of fish in nuanced ways. By understanding these relationships across various timescales, we can make better management strategies to reduce the impact of various anthropogenic stressors on fish populations.

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DEDICATION

To the fish. To Nicole and Oscar for believing in the fish. To Kesav for believing in me.

Chapter 1. THE EFFECT OF TEMPERATURE ON FISH SWIMMING AND SCHOOLING IS CONTEXT DEPENDENT

Publication history: This study was co-authored with Anthony Dell, Ashley R. Olson, Jason Knouft, John Grady, Jacob Forbes, and Andrew M. Berdahl. At the time this dissertation was published, this chapter was published in Oikos.

1.1 ABSTRACT

Temperature is highly influential on the physiology and behavior of ectotherms. In fish, temperature affects social interactions such as schooling behavior, a common defense against predation. However, the effect of temperature on the ability of schooling fish to collectively respond to a predator is unknown. Here we used a loom stimulus to simulate an approaching predator that elicited a fleeing response in schooling fish over a range of water temperatures (9–29°C) and group sizes (1–16 fish). While speed and acceleration always exhibited a positive curvilinear response to temperature, the optimal temperature at which performance peaked was different during the predation threat versus when they were unperturbed. Similarly, group-level metrics were sensitive to temperature immediately after a loom stimulus but showed no response to temperature during unperturbed swimming. The time taken for fish to respond to the loom stimulus was minimal at 20°C. The proportion of fish that startled, during a loom, peaked at 13°C – around the same temperature at which speed, and acceleration was maximum. Taken together, our results suggest that ectothermic fish may be able to compensate for their slower swim speeds at lower temperatures during unperturbed swimming by increasing their sensitivity to startle in response to a predation threat. More generally, we show that in ectotherms the qualitative and quantitative effect of temperature on a behavioral trait may be dependent on the context.

1.2 INTRODUCTION

Ectothermic animals are especially sensitive to changes in external temperatures compared to endotherms because ambient temperature controls physiological rates in ectotherms. Ambient temperature not only affects the growth and development of ectotherms (Brett et al. 1969, Zuo et al. 2012) but also their movement (Payne et al. 2016). Biological responses to temperature are often characterized by thermal performance curves in which performance (e.g. metabolic rate, development time, movement) increases gradually with temperature, peaks at some optimum and then decreases rapidly at higher temperatures (Huey and Stevenson 1979, Angilletta Jr and Angilletta 2009, Dell et al. 2011, Clarke 2017). Ectothermic species encounter varying temperatures due to daily and seasonal temperature cycles, the range and predictability of which may be altered due to directional changes in climate (Deutsch et al. 2008).

As ectotherms, many aspects of fish behavior are influenced by temperature. In the presence of predators, guppies *Poecilia reticulata* increase both the time spent in predator inspection and foraging activities at higher temperatures than at lower temperatures (Weetman et al. 1998). Additionally, there is evidence for behavioral regulation of activity levels as water temperatures rise. For example, the routine swimming speed of juvenile walleye pollock *Gadus chalcogrammus* decreases as temperature increases, but their maximum swimming speed increases as temperature increases (Hurst 2007). This suggests a behavioral rather than physiological regulation of their swimming speed.

Temperature also affects fish social behavior. Some previous studies have shown that the average nearest neighbor distances increases (fish become more dispersed) with increasing temperature (Hurst 2007, Bartolini et al. 2015, Colchen et al. 2017), but this is not always the case as Weetman et al. (1998) found that average nearest neighbor distance was higher for guppies at 22°C than at 26°C. The contrasting results of these studies suggests either non-monotonic, or taxa-specific, behavioral responses to thermal conditions and merits further investigation.

Schooling is a wide-spread behavior in fishes that yields a tradeoff of fitness benefits and costs. Schooling helps fish to avoid predation, forage, navigate, find mates more easily and, conserve energy by exploiting hydrodynamic factors and offers protection from predators (Krause et al. 2002, Ioannou 2017, Berdahl et al. 2018, Li et al. 2020, Polyakov et al. 2022). However, schooling can incur costs, including increased intraspecific competition for food (Polyakov et al. 2022) and increased parasites and disease transfer (Polyakov et al. 2022, Walsman et al. 2022). The size of the group can influence the behavior of individual fish within that group. For instance, Gil and Hein (2017a) found that each fish spends less time feeding when fewer fish are present. However, given the abundance of factors promoting and discouraging grouping listed above, the effect of group size on the behavior of fish is context specific. Group size and temperature both influence fish behavior and are biotic and abiotic factors, respectively. Considered together, group size and temperature may create a multi-stressor effect on the behavior of fish, with unknown interactions between these factors.

Since schooling is one of the primary ways in which many fish species avoid predation (Foster and Treherne 1981, Ioannou 2017), and schooling is ultimately driven by the movement of individual fish, there is a need to understand how temperature affects the ability of prey fish to collectively escape from a predator. Moreover, fish can be preyed upon by endotherms, whose performance may be much more robust to changes in temperature, creating an asymmetry in performance with changing temperatures that shape ecological interactions (Grady et al. 2019). Thus, thermally-mediated changes in ectotherms' individual and collective responses to predation may be critical to their survival and fitness.

We addressed the knowledge gap of how water temperature and group size affect the behavior of schooling fish both during unperturbed swimming and during response to a potential predation event. We simulated predation events with looming stimuli and quantified fish behavior via automated tracking of overhead videos. We hypothesized that: 1) following simulated predation events, many responses relevant to escape (e.g. speed, acceleration and proportion of individuals that startle) would exhibit a positive curvilinear response to temperature, indicating an optimal temperature for predation response; 2) during unperturbed swimming, speed and acceleration would follow a similar positive curvilinear response to temperature, but it would be attenuated, since fish would be less likely to push their performance limits in non-life-threatening situations; 3) collective behavioral traits like average nearest neighbor distance exhibit a positive curvilinear response to temperature during unperturbed swimming as well as following simulated predation events; and 4) there would be an interaction between the effect of group size and the effect of temperature on fish behavior during a predation threat.

We used golden shiners *Notemigonus crysoleucas*, a small cyprinid fish species, as they have been used in other collective behavior experiments (Katz et al. 2011, Berdahl et al. 2013, Polverino et al. 2013), including those on collective escape responses (Rosenthal et al. 2015). Golden shiners aggregate when faced with risk of predation in the wild (Johannes 1993), which renders them ideal to study collective escape responses. In Missouri, where our fish were sourced, water temperatures in golden shiner habitat ranges from 2 to 25°C and is approximately 15°C when golden shiners spawn (Supporting information). By the peak of winter, water temperatures are as low as 2°C. We chose experimental water temperatures of 9–29°C to reflect the large range of temperatures golden shiners experience and to study how warmer temperatures will affect their ability to escape predators.

Studies of golden shiners in the wild observed single species shoal size from 6 to 110 individuals with a mean of 31 (Krause et al. 1998). While group sizes are highly variable in the wild, they tend to be distributed either exponentially or as a power-law, and in each case the mode of the distribution is at small group sizes (Bonabeau et al. 1999). We chose group sizes of 1, 2, 4, 8 and 16 fish which span a 16-fold range in increments of 2_n, which is thought to be distinguishable by fish (Wong et al. 2007).

1.3 MATERIAL AND METHODS

1.3.1 *Study system*

We obtained juvenile golden shiners from Welpman Springs Goldfish Hatchery, in Stover, MO, USA, and transported them to the laboratory at Saint Louis Univ. in St. Louis, MO, USA. In the laboratory, the fish were housed in approximately equal numbers in 24 aquaria, which we will call housing tanks, with dimensions of 60 × 30 × 40 cm and a maximum volume of 72 l. Fish were fed a uniform commercial fish food (Purina Aquamax Premium Fish Food) daily and leftover food was removed after each feeding session. Approximately a quarter of the water in each housing tank was replaced every day with new dechlorinated water matching the temperature of the housing tank to remove nitrogenous waste. We tested the concentration of nitrogenous waste products (ammonia, nitrite and nitrate) approximately every 48 h using commercial test kits (API brand). Concentrations of ammonia and nitrite were maintained at undetectable levels and the concentration of nitrate was maintained at five ppm or less according to our tests. We also treated each tank with the instructed dose of Seachem ‘Prime’, a commercially available product designed to neutralise the toxicity of all three forms of nitrogenous waste in aquariums and aquaculture systems. We maintained a pH of 7.2 in each tank and light was provided on a 14L:10D cycle, matching the approximate conditions of the hatchery during the boreal summer. To avoid fish becoming acclimatised to looming stimuli, the housing tanks were covered on all sides by white curtains, which were only drawn for feeding and tank cleaning.

Water temperature in the housing tanks was controlled by aquarium chillers (JBJ 1/10 HP Titanitum Arctica Chiller DBA-075) and for warmer housing tanks also heaters (EHEIM Jager Aquarium Thermostat Heater 100W). Supplemental water circulation and aeration was provided by a small aquarium air pump (100 l h−1) connected to each housing tank. When the fish first arrived, all housing tanks were set to 15°C (the approximate water temperature at the fish hatchery). Water temperature was then increased or decreased by ≤ 3°C per day until the desired final temperature for that housing tank was attained. The final six temperatures ranged from were 9 ± 0.6, 13 ± 0.4, 17 ± 0.4, 21 ± 0.3, 25 ± 0.3 and 29 ± 0.3°C, with four housing tanks per temperature. The maximum temperature was lower than the temperature at which heat stress is observed in golden shiners (34°C) (Chen et al. 2003). All fish had two weeks to acclimate in the lab, of which at least one week was at their final acclimation temperature. Experiments were conducted over two weeks in July–August 2019. The body length (estimated by considering the median of the diagonal of the images associated to each individual (Romero-Ferrero et al. 2019)) of a subset (33) of the fish were measured by idtracker.ai for which the mean was 4.03 ± 0.29 cm. See the Supporting Information for median body length of fish in each combination of group size and temperature.

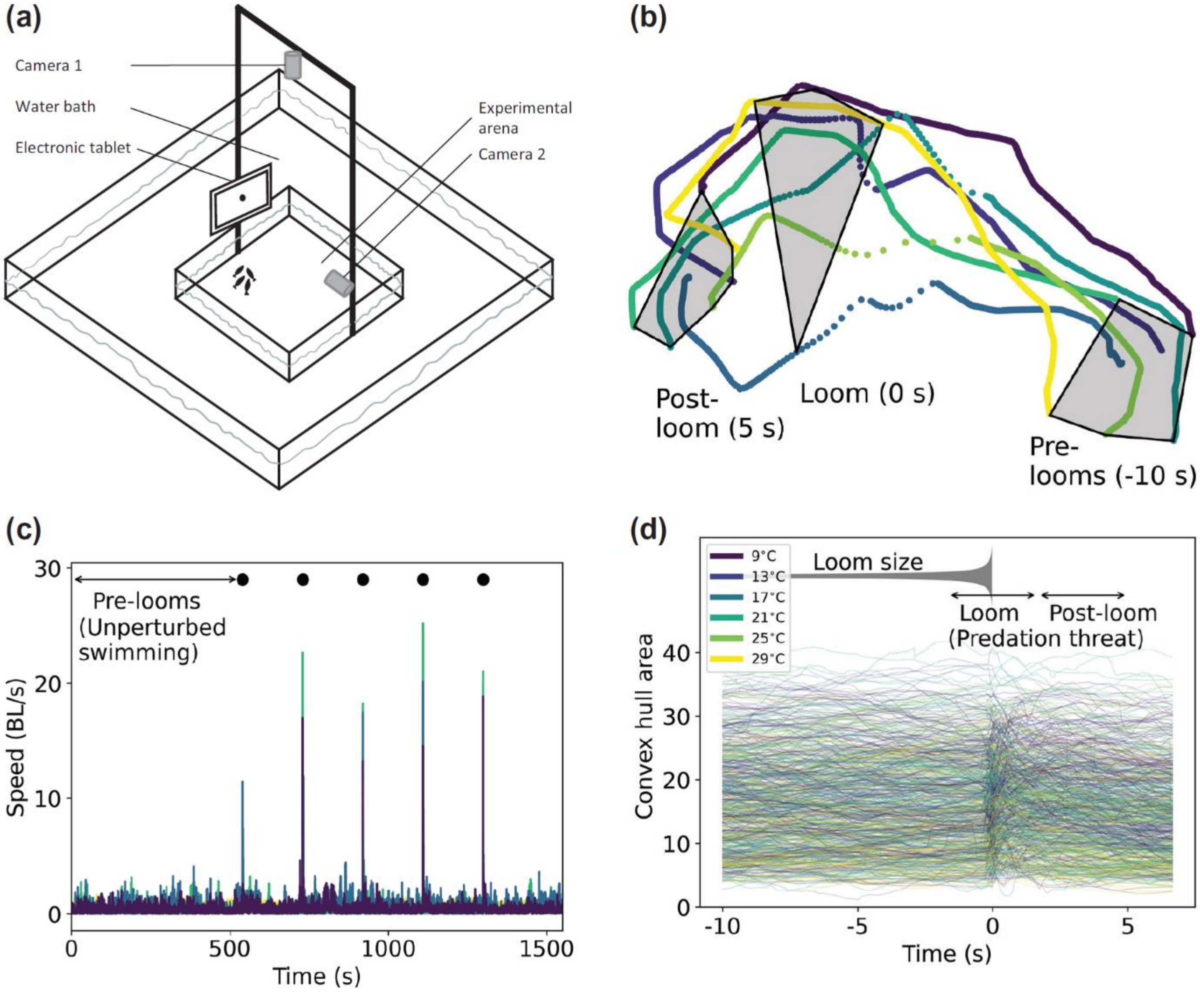

Figure 1.1. Experimental overview. (a) Schematic of one of our six experimental setups. Each experimental arena was contained in a larger water bath to help with temperature control. Experiments were recorded using a near-IR camera positioned directly above the experimental arena. A loom stimulus was displayed periodically on an electronic tablet located above the surface of the water on one side of the arena, but angled downward. A second camera recorded the tablet so we could synchronize the timing of the loom with the fish tracking. (b) Trajectory of each fish during a single loom event. Each trajectory is constructed with a marker every 0.033 s, so that the distance between the markers is proportional to body speed. The dotted section of each trajectory indicated the fish is moving fast after being startled (either by the loom directly, or by other fish in the arena). The polygons indicate the convex hull area of the group three times during the event (pre-looms, loom, post-loom). (c) An example of a time series of body speed of each fish in the group during one trial, showing startles during each stimulus. We define unperturbed swimming as the pre-looms period which occurs before any loom stimulus. The

black circles indicate loom events, with each experimental trial consisting of five loom stimuli separated by three minutes. (d) Each line represents the convex hull area of a school of fish during a single loom event. The time axis is re-scaled for all loom events, so that 0 s coincides with the end of the loom stimulus. ‘Loom’ is defined as the period from −1.67 s to 1.67 s. ’Post-loom’ is defined as period from 1.67 s to 5 s after the end of the loom stimulus. The loom stimulus started growing at frame −10 s and increased in size at a rate that mimicked an object approaching at a constant speed (500 cm s−1).

Table 1.1. Total number of trials for each combination of group size and temperature.

	Number of trials				
	Group size				
Temperature	1	2	4	8	16
29	8	9	8	7	7
25	7	6	6	6	9
21	6	8	6	6	6
17	4	9	8	9	9
13	6	8	9	7	7
9	7	8	10	10	9

1.3.2 *Experimental design and procedure*

We used a factorial design in which we independently varied water temperature and group size (number of fish). We investigated the five different group sizes at each of the six temperatures (listed above), for a total of 30 different treatments. We performed 10 replicates of each combination of water temperature and group size, for a total of experimental 300 trials. Within each replicate/trial the fish were presented with five evenly spaced replicate loom stimuli (Fig. 1.1c), such that in total we had response data from 1500 looms.

Trials took place simultaneously in six approximately square (46 × 47 cm), shallow (~ 5 cm water depth) experimental arenas (Fig. 1.1). The shallow arenas constrained the fish to move in mostly two-dimensions, greatly simplifying our ability to track movement with a single camera from above. Each experimental arena was situated in a larger (110 × 75 × 30 cm) water bath, in which the water was controlled by either 1) a chiller (temperatures < 21°C), 2) a chiller and heater (temperatures > 21°C) or 3) the ambient room temperature (21°C). These experimental arenas were filled with water from the housing tanks prior to the experiments and the temperature in each arena was recorded with aquarium thermometers to ensure that water temperature did not vary more than 1°C.

Each experimental arena was backlit by an infra-red (IR) LED panel and trials were filmed from directly above with an IR light sensitive video camera (Basler acA1300-60-gm-NIR). An electronic tablet (YUNTAB, 10.1 inch) was placed beside each arena with the bottom edge of the tablet one inch above the arena and tilted down at an angle of 10–15°. Additional, visible-light cameras (Basler acA1300-60-gm-NIR without the IR pass filter) were placed beside the arenas facing the screens to record the loom stimulus. To make the loom stimuli more apparent, the lights in the experimental room were dimmed so that the surface of each experimental arena was approximately 400 lux (measured with a light meter). This 400 lux light level corresponds to sunrise/sunset conditions – times of heavy activity for golden shiners, which are crepuscular.

During the experiments, the electronic tablets displayed a video featuring a series of loom stimuli that had been generated using the R package loomeR (Carey 2019). Each loom stimulus consisted of a black disk increasing in size at an increasing rate that simulated an object (predator) approaching at 500 cm s^{-1}. This method has been used previously (Dill 1974, 1990) and allowed us to control the timing and speed of approach of the ‘predator’. The loom video began with a ten-minute pre-looms period that we used to quantify the base-line fish behavior. This was followed by a series of five looms events each spaced three minutes apart, allowing ample time for the fish to resume normal activity (Gil and Hein 2017b). Each trial lasted for about thirty minutes with recording being stopped five minutes after the final loom (Fig. 1.1c).

The order of trials was randomized to reduce any influence of the timing of a trial. We randomly assigned group sizes to each of the six experimental arenas. To transfer the fish from the housing tank to the experimental arena, we first filled portable containers with water from the housing tank. We then transferred the desired number of fish from the housing tank to the container with a net. We then transferred the fish along with the water to the experimental arena. Once fish were in the arenas, the curtains that separate the experimental arena from the rest of the lab were drawn and the fish were allowed to acclimate for 20 min. Following this, the loom video on each tablet was started and we commenced filming, signifying the beginning of one experimental trial. At the end of the trial, we transferred all the fish to a portable container with a net and then transferred them to a different housing tank to keep them separate from fish that have not yet been through an experimental trial. No individual fish was used in the experiment more than once. All experimental trials were conducted between 9:00 and 19:00.

1.3.3 *Fish tracking*

Overhead video recordings of the experimental trials were converted to pseudo 2D trajectories using idtracker.ai, which allows tracking of large number of unmarked animals using deep neural networks to maintain identities and prevent error propagation after crossovers (Romero-Ferrero et al. 2019). Distance-related metrics, such as speed and acceleration, were scaled by the body length (BL) of the fish (Romero-Ferrero et al. 2019). All the videos used for analyses had a tracking accuracy above 98%, which is calculated by idtracker.ai based on the average probability of assigning an identity to the fish. While idtracker.ai performed well with detections, in videos with larger group sizes there were occasional temporary mismatches in identities, which resulted in artificially elevated spikes in velocity and acceleration when idtracker.ai corrected these swapped identities. In order to avoid incorrectly classifying these spikes in kinematic variables as real fish movement, we created a filter that removed all frames in which the speed or acceleration were above a certain threshold. Since mismatched identities do not occur in videos with a single fish, the threshold was determined by the maximum speed (30 BL s^{-1}) and maximum acceleration (3338 BL s^{-2}) in all the single fish videos. The sensitivity of our models to these thresholds were determined in all our analyses. 75 videos were excluded from analyses due to tracking failures (n = 38), fish/debris in water bath (n = 19), dropped frames and corrupted video files (n = 10) or fish jumping from the experimental arena (n = 8). We were left with 225 videos with approximately 113 h of recording in total. See Table 1.1 for the total number of trials for each combination of group size and temperature.

1.3.4 *Behavioral metrics*

We calculated all behavioral parameters using the trajectory data output from idtracker.ai and the trajectorytools package in Python (Romero-Ferrero et al. 2019). We examined the relationship between temperature and various behavioral metrics during two different types of movement. The first type of movement was unperturbed swimming, for which we used the data from the ten-minute period before any loom stimulus was presented to the fish, also known as the prelooms period (Fig. 1.1c). The second type of movement was the predation threat escape, which we further divided into two phases. The first phase was during the loom stimulus (−1.67 to 1.67 s) and the second phase was after the loom stimulus or post-loom (1.67–5 s) (Fig. 1.1b). In both the unperturbed swimming and predation threat escape, we measured several individual movement and collective spatial metrics that we list below.

We explored how the 99th percentile of speed and acceleration changes as a function of temperature. We also calculated the mean and median speed and acceleration of all fish over all frames, but found that the 99th percentile better captured performance limits (Gannon et al. 2014), without being sensitive to thresholds (30 BL s−1, 3338 BL s−2 respectively) that we used to eliminate tracking errors. Since this was an estimate of the maximum speed/acceleration, henceforth, we refer to the 99th percentile of speed/acceleration as the maximum speed/acceleration. Maximum speed is a measure of swimming performance that determines how fast the fish can get away from the predator, but how quickly a fish can accelerate to that speed also influences the outcome of the interaction (Walker et al. 2005). We also examined the role of temperature on several collective behavior metrics of a school during both unperturbed swimming and predation threat escape. The first collective behavior trait, local polarization, is a measure of alignment of swimming direction between the focal individual and its nearest neighbor ranging continuously from 0 (when fish are swimming in perpendicular directions) to 1(when fish are swimming in parallel directions). Secondly, we considered the average distance between the focal individual and its nearest neighbor, known as average nearest neighbor distance (ANND). Finally, we quantified the convex hull area, which is the area of the smallest polygon enclosing all the fish in the group. Convex hull area and ANND are complementary measures of the spatial distribution of fish. For example, if fish are distributed in several clusters around the experimental arena, ANND will be small but the convex hull area will be large. In addition to the parameters listed above, we measured two parameters specific to the predation threat escape behavior. Since the time taken to respond to a threat is an important factor in escaping predators, we measured latency of response, which we defined as the time between the end of the loom stimulus and the first fish in the experimental arena to exhibit an escape response. Fish often startled before the end of the loom, so this metric had potentially negative values. The probability of responding to a predation threat is also an important factor that determines survival, and so we calculated the ’startle probability' which we defined as the proportion of individuals in the group that startled during the loom. Latency and probability to startle are both important but complementary parameters that determine the outcome of predator evasion. For example, if a fish has a high probability of responding to predation threats but takes a long time to respond, the chances of evading a predator are low. For both latency and startle probability, we defined a startle response to occur when an individual's speed exceeded a threshold of 10 BL s−1. We examined the sensitivity of our results to the startle threshold (10 BL s−1), speed threshold (30 BL s−1) and acceleration threshold (3338 BL s−2). However, our results were largely insensitive to the specific value of these thresholds. Sensitivity analysis can be found in the Supporting information.

Since in each trial the unperturbed swimming occurred before the predation threat (Fig. 1.1c) the differences between unperturbed swimming and predation threat escape are potentially confounded with time. However, we examined the effect of temperature on all the behavioral metrics immediately before each loom stimulus (−11.67 to −10 s) and found the same results as the effect of temperature on unperturbed swimming. Thus, we used the period before any loom stimulus as the unperturbed swimming phase, since it had more data and loom number was not a significant predictor in these models.

1.3.5 *Statistical methods*

We used linear models (LMs) (<www.r-project.org>) to investigate the effect of temperature, the effect of group size and the interaction between temperature and group size on each behavioral metric described in section (d), during both unperturbed swimming and behavior following a predation threat stimulus. Since performance traits in ectotherms generally show a curvilinear response to temperature (Huey and Stevenson 1979, Angilletta Jr. and Angilletta 2009, Dell et al. 2011, Clarke 2017), we also included a nonlinear temperature term (temperature^2) as a covariate in all the statistical models.

1.3.5.1 Unperturbed swimming

The general form of the equation we used for all behavioral metrics during unperturbed swimming is given in Eq. 1. We examined the residuals for heteroscedasticity and nonlinearity (<www.r-project.org>, Gelman and Su 2020) and we transformed the response variable when appropriate (Venables and Ripley 2002) as shown in Table 1.2. We also log transformed the group size variable in all the models. In addition to investigating the effect of temperature and group size on unperturbed swimming behavior, we also examined whether group size mediates the way temperature affects behavior by testing a model with an additional interaction term between temperature and group size (Eq. 2). We used a likelihood ratio test (LRT) (Zeileis and Hothorn 2002) to determine if the inclusion of the interaction term improved the fit of our model. If the p-value of the LRT was < 0.05, we used the more complicated model with the interaction term to make predictions for that behavioral metric and to test for the significance of each of the parameters. We examined normality using QQ plots (Wilk and Gnanadesikan 1968). For all the models used on unperturbed swimming, the errors were normally distributed. We used these models to make predictions with 95% confidence intervals to visualize the relationship of the behavioral metrics with temperature.

$$Behaviour_i = \beta_0 + \beta_1 Temperature_i + \beta_2 Temperature_i^2 + \beta_3 \log_2(Group\ size_i) + \epsilon_i \quad 1.1$$

$$\begin{aligned} Behaviour_i = \beta_0 + \beta_1 Temperature_i + \beta_2 Temperature_i^2 + \beta_3 \log_2(Group\ size_{i)} \\ + \beta_4 Temperature_i \times \log_2 Group\ size_i + \epsilon_i \quad 1.2 \end{aligned}$$

1.3.5.2 Predation threat

For behavior following a predation threat stimulus, in addition to temperature and group size, we investigated the effect of loom number on different behavioral metrics (Eq. 3). We examined normality using QQ plots (Wilk and Gnanadesikan 1968). All the errors were normally distributed for all behavioral metrics except for proportion of individuals that startled. Since the data for proportion of individuals that startled were proportions (between 0 and 1), we used generalized linear model (GLM) with binomial distribution and logit link function (logistic regression). We used Pearson's X2 for goodness of fit to test whether the GLM was correctly specified (Pearson 1900). We used residual plots to examine for heteroscedasticity and nonlinearity for all the models except for logistic regression where we used binned residual plots (<www.r-project.org>, Gelman and Su 2020). We transformed the response variable when appropriate (Venables and Ripley 2002) as shown in Table 1.2. Since latency was the only behavioral metric for which we could easily determine errors caused due to tracking by watching the videos, we investigated influential points with Cook's distance (Cook 1977, Faraway 2016). We removed four influential points after the raw videos proved that they were affected by tracking errors. Similar to unperturbed swimming, we also included the interaction term between group size and temperature and used the more complicated model with the interaction term for predictions and significance of parameters, if the value of the LRT was < 0.05. For maximum acceleration during the loom, we used Eq. 4 since that model performed better than the model without the interaction term. We used Eq. 4 to make predictions with 95% confidence intervals to visualize the relationship of these two behavioral metrics with temperature and to test for the significance of each parameter. For all other behavioral metrics under predation threat, we used Eq. 3 to make predictions and test for significance. The R2 value for each model and the significance of each predictor variable is shown in Table 1.2 (<www.r-project.org>, Zhang 2021).

We also tried an alternate statistical modeling approach where we used different candidate models for each behavioral metric and chose the best fitting model using AIC (Supporting information). Since there were minimal differences between the results of both modeling approaches, we ultimately used the results of the simpler approach with the same model for all behavioral metrics.

$$Behaviour_i = \beta_0 + \beta_1 Temperature_i + \beta_2 Temperature_i^2 + \beta_3 \log_2(Group\ size_i) + \beta_4 Loom_i + \epsilon_i \qquad 1.3$$

$$Behaviour_i = \beta_0 + \beta_1 Temperature_i + \beta_2 Temperature_i^2 + \beta_3 \log_2(Group\ size_i) + \beta_4 Loom_i + \beta_5 Temperature_i \times \log_2(Group\ size_i) + \epsilon_i \qquad 1.4$$

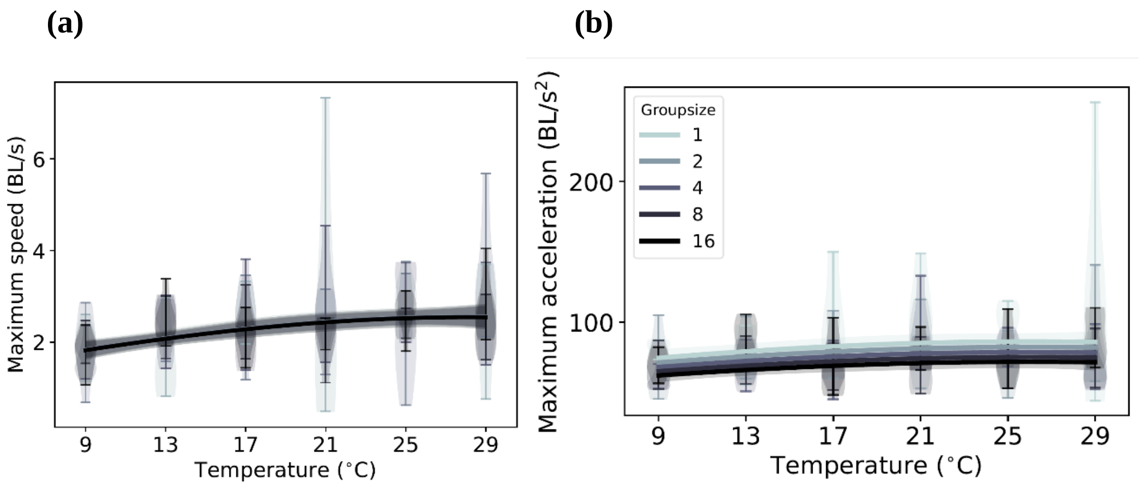

Figure 1.2 Individual behavior during unperturbed swimming. (a) Maximum speed and (b) acceleration had a positive curvilinear relationship with temperature but with the peak towards the highest temperatures in this range. The same legend holds for both figures.

Table 1.2. Summary of model results for each behavioral metric. The significance level of each of the variables is given beside each coefficient such that ***, ** and * corresponds to < 0.001, < 0.01 and < 0.05 respectively. The last column specifies the temperature at which the response variable (x) is maximum or minimum (within the range of temperatures used in the experiment) according to model predictions. A range is given when the maximum or minimum varies with group size.

Response variable (x)	Transformation/ Link function	*Intercept*	*Temperature*	*Temperature^2*	*Group size*	*Loom*	*Temperature x Group size*	*R^2*	*Min/Max temperature (°C)*
Unperturbed swimming									
Maximum speed	*log*(x + 1)	0.781***	0.034*	−0.001	−0.001	−	−	0.128	28
Maximum acceleration	*log*(x + 1)	4.131***	0.026	−0.001	−0.045***	−	−	0.105	26
ANND	*log(x)*	0.770***	0.023	−0.001	−0.567***	−	−	0.764	-
Convex hull area	$\sqrt{x}$	1.606***	0.037	−0.002	0.706***	−	−	0.574	-
Polarization	$\sqrt{x}$	0.551***	−0.003	0.	0.002	−	−	0.011	-
Predation threat									
Maximum speed	$\sqrt{x}$	2.358***	0.05*	−0.002**	0.231***	−0.078***	−	0.174	12
Maximum acceleration	*log*(x + 1)	4.577***	0.082***	−0.003***	0.236***	−0.056***	−0.004*	0.185	13-16
Latency	1	0.059	−0.025***	0.001***	−0.035***	0.01	−	0.064	20
Proportion of individuals startling	logit link	-0.881	0.124*	−0.005**	0.064	−0.105*	−	0.039	13
ANND	*log(x)*	1.508***	−0.072**	0.001	−0.630***	0.001	0.007*	0.413	-
Convex hull area	$\sqrt{x}$	2.502***	−0.049*	0.001	0.684***	0.009	−	0.418	-
Polarization	$\sqrt{x}$	0.842***	−0.019**	0.001**	−0.034***	−0.013*	−	0.043	19

1.4 RESULTS

1.4.1 *Unperturbed swimming*

1.4.1.1 Individual behavior

Temperature was the only significant predictor of near-maximum speed during the unperturbed swimming phase (Table 1.2). The near-maximum swimming speed had a positive curvilinear relationship with temperature, with the peak speed occurring at 28°C (Fig. 1.2a, Table 1.2). In contrast, only group size was significant predictors of near-maximum acceleration during the unperturbed swimming phase. Although the effect was not significant, the near-maximum acceleration had a positive curvilinear relationship with temperature with the peak approximately 26°C (Fig. 1.2a, Table 1.2). While the same relationship observed for all group sizes, the intercept decreased for larger group sizes (Table 1.2). The mean and median of acceleration also exhibited a positive curvilinear relationship with temperature (Supporting information).

1.4.1.2 Collective behavior

We did not observe a significant effect of temperature on average nearest neighbor distance, convex hull area or polarization during the unperturbed swimming portion of the trials (Table 1.2).

1.4.2 *Predation threat*

1.4.2.1 Individual behavior

Temperature, temperature^2, group size and loom were all significant predictors of maximum speed during the predation threat (Table 1.2). The maximum speed during the loom stimulus had a positive curvilinear relationship with temperature with the maximum at approximately 12°C (Fig. 1.3a, Table 1.2). While the same relationship was observed for all group sizes and looms, the intercept increased with higher group sizes and decreased with subsequent looms (Table 1.2). The optimal temperature at which speed was maximum during an escape response (12°C) was much lower than the temperature at which speed peaks during the unperturbed swimming phase (28°C) (Fig. 1.2a, Table 1.2). In addition to temperature, temperature^2, group size and loom, the interaction between temperature and group size was also a significant predictor of maximum acceleration during the predation threat (Table 1.2). Maximum acceleration had a positive curvilinear relationship with temperature and reached a maximum at 13–16°C (Fig. 1.3b), which was 10–13°C lower than the optimal temperature during unperturbed swimming (Fig. 1.2b, Table 1.2). As group size decreased, the optimal temperature at which maximum acceleration peaks during predation threat increased (Fig. 1.3b). For group size = 1, the optimal temperature was approximately 16°C, which was still 10°C lower than the optimal temperature during unperturbed swimming (Fig. 1.2b). While the same relationship between acceleration, temperature and group size was observed for every loom, the intercept decreased with subsequent looms (Table 1.2).

As shown in Table 2 temperature, temperature^2 and group size were significant predictors of latency. Latency exhibited a negative curvilinear relationship with temperature and had a minimum at approximately 20°C. Although we observed the same relationship with temperature for all group sizes, the intercept decreased with increased group size (Table 1.2). temperature, temperature^2 and loom were significant predictors of the proportion of individuals startling during the loom stimulus (Table 1.2). While the proportion of individuals startling had a positive curvilinear relationship with temperature with a maximum at approximately 13°C (though this exact value varied slightly with the startle threshold as shown in the Supporting information), we did not observe an effect of group size (Fig. 1.3d, Table 1.2). While the same relationship held for all loom stimuli, the intercept again decreased for subsequent looms, suggesting an acclimation to the loom stimuli or learning (Table 1.2).

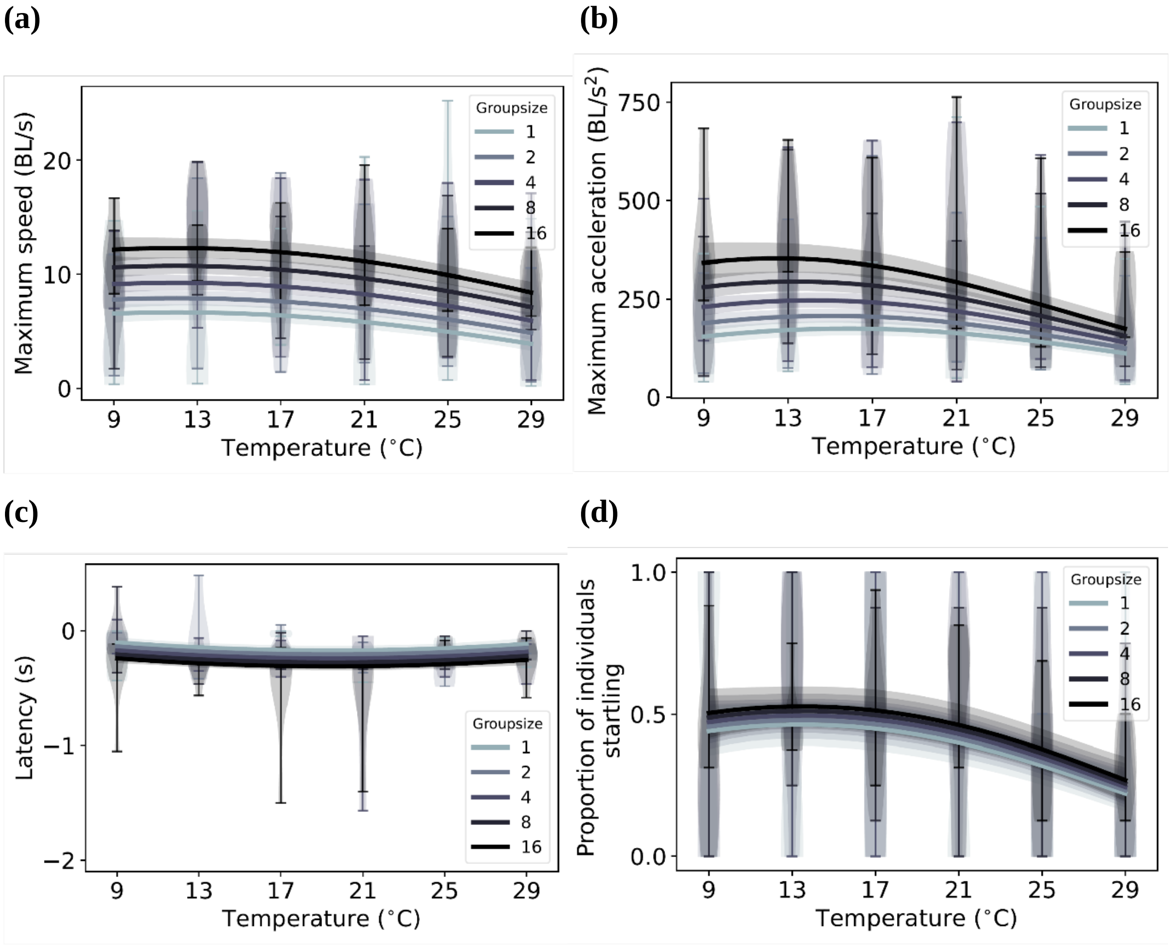

Figure 1.3. Individual behavior during the predation threat. (a) Maximum speed and (b) maximum acceleration during the loom stimulus exhibited a positive curvilinear relationship with temperature. However, the value of that optimal temperature at which acceleration peaked varied with group size. (c) Latency (reaction time in seconds after end of loom) also exhibited a minimum at an ostensibly optimal temperature. (d) The proportion of individuals that startled peaked at an optimal temperature. The same legend holds for all four figures.

1.4.2.2 Collective behavior

During the post-loom period, the average distance between individuals and their nearest neighbor decreased as group size increased and as temperature increased (Table 1.2). The interaction effect of group size and temperature was also significant and there was a reduced effect of temperature on ANND in larger group sizes (Fig. 1.4a). We also found that the convex hull area decreased monotonically as temperature increased (Fig. 1.4b). While the same relationship with temperature was observed for all group sizes, the convex hull area increased with increased group sizes (Table 1.2). Although the model with local polarization explained less than 5% of the variance in our data, we found that temperature, temperature^2, group size and loom were significant predictors of local polarization (Table 1.2). Local polarization was minimum at 19°C (Fig. 1.4c, Table 1.2) for all group sizes and loom stimuli, although the intercept decreased with increased group sizes and subsequent looms (Table 1.2).

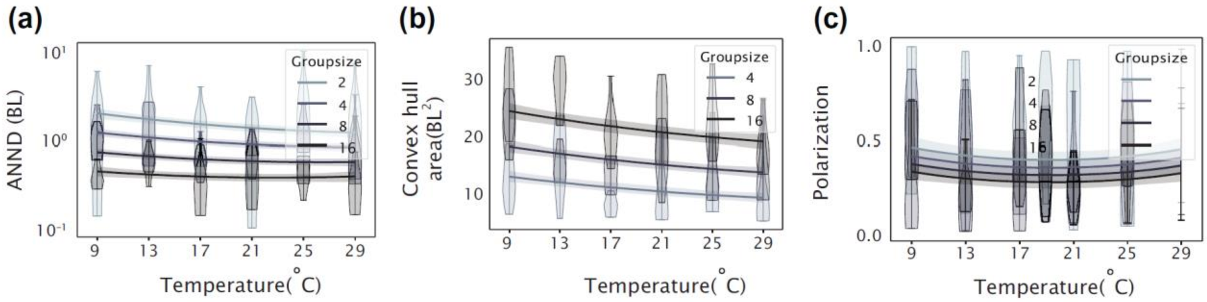

Figure 1.4. Collective behavior during the predation threat. (a) Average nearest neighbor distance during post-loom phase decreased with increasing temperature. The effect of temperature was less pronounced for larger group sizes as shown by the black curve for group size 16. (b) Convex hull area of the group during post-loom phase decreased with temperature. (c) Local polarization of the group following a predation stimulus has a minimum at 19°C. The same legend holds for all three figures, but convex hull area was calculated only for group size 4, 8 and 16.

1.5 DISCUSSION

1.5.1 *Context dependence*

While the importance of water temperature to the performance of freshwater ectotherms has long been recognized, ongoing and directional changes in climate have elevated the importance of understanding these relationships due to the likely novel thermal conditions that will be experienced by freshwater taxa in the coming decades (Whitney et al. 2016, Knouft and Ficklin 2017). In our experiments, temperature had a context-dependent effect on the movement of individual fish and the collective dynamics of schools. We found support for our first hypothesis that traits relevant to escape would exhibit a positive curvilinear response to temperature. However, we found that the optimal temperature to escape from their predators – the temperature at which speed and acceleration were maximized – was different from their optimal temperature during unperturbed swimming.

During unperturbed swimming, individual speed and acceleration both increased with temperature, reaching a maximum only at and beyond 25°C, respectively. This pattern is consistent with the fact that biochemical reaction rates, and thus metabolic rates increase exponentially with temperature in ectotherms (Brown et al. 2004). However, the increase was far lower than predicted by metabolic theory of ecology, pointing to the considerable variance that accompanies macro ecological patterns. This was in support of our second hypothesis that the effect of temperature on unperturbed swimming would be attenuated since fish would be less likely to push their performance limits in non-life-threatening situations. In contrast to unperturbed swimming, during a predation threat, individual speed increased with temperature up to 12°C for speed and acceleration increased with temperature up to 13–16°C, after which these response variables then decreased as temperature continued to rise. Most studies have examined the influence of external factors on only unperturbed swimming at the individual and collective level (Herbert-Read et al. 2017, Ginnaw et al. 2020). In this study, however, we compared the unperturbed swimming and escape response. We found an asymmetry in the effect of temperature between these two behaviors, demonstrating that the effect of temperature on one measure of behavior may not extend to other behaviors and rates.

1.5.2 *Behavioral regulation*

Our results are consistent with findings from other species that activity levels can be regulated by behavior as temperature changes (O'Steen and Bennett 2003). First, since temperature affects maximum speed and acceleration differently depending on whether the fish are trying to evade a predator or not, the fish may be behaviorally regulating their maximum speed or acceleration as opposed to a physiological change caused due to external temperature. Second, the proportion of fish that startle during predation also peaks at 13°C, around the same temperature at which maxi mum speed and acceleration of the fish peaks. Speed, acceleration and probability to startle are also highly correlated during predation threat (Supporting information) indicating that maximum speed and acceleration might be driven by the probability to startle. For example, the maximum speed and maximum acceleration are more likely to be higher when 50% of the fish are startling than if 25% of the fish are startling. If the trends in speed and acceleration during predtion are being driven by the fish that startle, then the fish may be compensating for their inability to swim faster at lower temperatures by being more responsive to potential threats at lower temperatures. However, there might be physiological effects of temperature, such as lower metabolic rate, that are influencing their swimming speeds below 13°C.

1.5.3 *Collective behavior*

In contrast to previous results (Bartolini et al. 2015, Colchen et al. 2017), we did not observe a significant effect of temperature on average nearest neighbor distance, convex hull area or polarization during the unperturbed swimming. While we did observe a significant effect of temperature on average nearest neighbor distance during post-loom phase, the effect of temperature was monotonic and opposite to that found by Bartolini et al. (2015) and Colchen et al. (2017). Polarization had a negative curvilinear response to temperature following simulated predation events. The effect of temperature on all the collective behavior traits contrasted with our third hypothesis that the traits would exhibit a positive curvilinear response to temperature during unperturbed swimming as well as following simulated predation events. We also found that ANND and convex hull area decreases with increasing temperatures after each loom stimulus. These results add to the existing literature about how temperature affects social behavior, but also provide insight on the asymmetry in the effect of temperature on social behavior in the context of predation.

1.5.4 *Multistress response*

The presence, decisions and performance of other animals can act as social information to guide the behavior of the focal individual (Doligez et al. 2010). For species that use social information, the effect of temperature on behavior might not be simple extensions of the effect of temperature on individuals. Maximum acceleration had an optimal temperature that shifted to a lower temperature for larger group sizes (Fig. 1.3b). This supports our fourth hypothesis that there would be an interaction between the effect of group size and the effect of temperature on fish behavior during a predation threat. There is growing awareness about how multiple stressors can have an interactive effect on animals (Darling and Côté 2008) and this study provides empirical data to the ecology of multistress responses in fish.

1.5.5 *Dampened response to temperature*

Temperature was a significant parameter in most of the models we fit to the data, however temperature explained only a modest percentage of the variance. This dampened response to temperature could be due to the large range of temperatures throughout the year that golden shiners experience in the Missouri region (Jones et al. 2011, Knouft et al. 2021). Despite this large range in temperature tolerance we still found a significant effect of temperature, suggesting that temperature could have a stronger effect on fish species with tolerance to a smaller range of temperature. Another possible reason why we did not observe a stronger effect of temperature is that we gave the fish at least one week to acclimatize to the respective temperatures. Beitinger and Bennett (2000) showed that acclimation can effectively double thermal tolerance for some species and acclimation played a larger role at lower temperatures than higher thermal tolerance temperatures. This suggests that future research should incorporate a wider range of temperatures range and also test the effects of more abrupt changes in temperature.

1.5.6 *Laboratory conditions*

In this study, like in many collective behavior studies, fish were restricted to mostly swimming in one plane (shallow water) to ensure easy detection and tracking of individuals and easier analysis of the data. Since many animal groups move in three-dimensional space, more studies have extended the models to three dimensions. These studies have shown that many of the qualitative results obtained in 2D also hold in 3D (Giardina 2008). Additionally, golden shiners are often found in the littoral zone of shallow lakes (Krause et al. 1996). Hence, while swimming in shallow water is not uncommon for this species, it could change their schooling dynamics. In this study, we found that the optimal temperature for golden shiners to escape from predators is different from their optimal temperature during unperturbed swimming. Future research should test this result in wild conditions.

1.5.7 *Rate asymmetry*

Unperturbed swimming and predator escape responses both play a major role in determining the strength and outcome of consumer–resource interactions. Unlike previous work examining the effects of thermal asymmetries on different ecological rates (Dell et al. 2014, Amarasekare 2015), our study reveals evidence of rate asymmetry within the same species. Differences in thermal sensitivity of different behaviors of the same species can affect ecological dynamics and food web structure. If fish are indeed able to compensate for lower speeds at lower temperatures, this could indicate more resistance to temperature changes and a more stable food web structure (Vallina and Le Quéré 2011). On the other hand, increasing global temperatures are likely to push prey fish towards a temperature at which their speed and acceleration are less than optimal when they are escaping from predators. Our results suggest that these changes may be more nuanced than macro metabolic models, reflecting the variable role temperature plays across traits and social structures.

1.6 REFERENCES

Amarasekare, P. 2015. Effects of temperature on consumer–resource interactions. – J. Anim. Ecol. 84: 665–679.

Angilletta Jr., M. J. and Angilletta, M. J. 2009. Thermal adaptation: a theoretical and empirical synthesis. – Oxford Univ. Press.

Bartolini, T. et al. 2015. Temperature influences sociality and activity of freshwater fish. – Environ. Biol. Fish. 98: 825–832.

Beitinger, T. L. and Bennett, W. A. 2000. Quantification of the role of acclimation temperature in temperature tolerance of fishes. – Environ. Biol. Fish. 58: 277–288.

Berdahl, A. et al. 2013. Emergent sensing of complex environments by mobile animal groups. – Science 339: 574–576.

Berdahl, A. M. et al. 2018. Collective animal navigation and migratory culture: from theoretical models to empirical evidence. – Phil. Trans. R. Soc. B 373: 20170009.

Bonabeau, E. et al. 1999. Scaling in animal group-size distributions. – Proc. Natl Acad. Sci. USA 96: 4472–4477.

Brett, J. et al. 1969. Growth rate and body composition of fingerling sockeye salmon, Oncorhynchus nerka, in relation to temperature and ration size. – J. Fish. Board Canada 26: 2363–2394.

Brown, J. H. et al. 2004. Toward a metabolic theory of ecology. – Ecology 85: 1771–1789.

Carey, N. 2019. nicholascarey/loomeR: looping, custom frame numbers and filenames! – Zenodo, <https ://do i.org /10.5 281/z enodo .3279 092>.

Chen, R. et al. 2003. Alternative complement activity and resistance to heat stress in golden shiners Notemigonus crysoleucas are increased by dietary vitamin C levels in excess of requirements for prevention of deficiency signs. – J. Nutr. 133: 2281–2286.

Clarke, A. 2017. Principles of thermal ecology: temperature, energy and life. – Oxford Univ. Press.

Colchen, T. et al. 2017. Temperature modifies activity, inter-individual relationships and group structure in a fish. – Curr. Zool. 63: 175–183.

Cook, R. D. 1977. Detection of influential observation in linear regression. – Technometrics 19: 15–18.

Darling, E. S. and Côté, I. M. 2008. Quantifying the evidence for ecological synergies. – Ecol. Lett. 11: 1278–1286.

Dell, A. I. et al. 2011. Systematic variation in the temperature dependence of physiological and ecological traits. – Proc. Natl Acad. Sci. USA 108: 10591–10596.

Dell, A. I. et al. 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. – J. Anim. Ecol. 83: 70–84.

Deutsch, C. A. et al. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. – Proc. Natl Acad. Sci. USA 105: 6668–6672.

Dill, L. M. 1974. The escape response of the zebra danio Brachydanio rerio I. The stimulus for escape. – Anim. Behav. 22: 711–722.

Dill, L. M. 1990. Distance-to-cover and the escape decisions of an African cichlid fish, Melanochromis chipokae. – Environ. Biol. Fish. 27: 147–152.

Doligez, B. et al. 2010. Social information use. – Encycl. Anim. Behav. 3: 242–250.

Faraway, J. 2016. faraway: functions and datasets for books by Julian Faraway. – R package ver. 1.0.7, <https ://CR AN.R- proje ct.or g/pac kage=faraway>.

Foster, W. and Treherne, J. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. – Nature 293: 466–467.

Gannon, R. et al. 2014. Thermal limitation of performance and biogeography in a free-ranging ectotherm: insights from accelerometry. – J. Exp. Biol. 217: 3033–3037.

Gelman, A. and Su, Y. S. 2020. Arm: data analysis using regression and multilevel/hierarchical models. – R package ver. 1.11-2, <https ://CR AN.R- proje ct.or g/pac kage=arm>.

Giardina, I. 2008. Collective behavior in animal groups: theoretical models and empirical studies. – HFSP J. 2: 205–219.

Gil, M. A. and Hein, A. M. 2017. Social interactions among grazing reef fish drive material flux in a coral reef ecosystem. – Proc. Natl Acad. Sci. USA 114: 4703–4708.

Ginnaw, G. M. et al. 2020. Effects of multiple stressors on fish shoal collective motion are independent and vary with shoaling metric. – Anim. Behav. 168: 7–17.

Grady, J. M. et al. 2019. Metabolic asymmetry and the global diversity of marine predators. – Science 363: eaat4220.

Herbert-Read, J. E. et al. 2017. Anthropogenic noise pollution from piledriving disrupts the structure and dynamics of fish shoals. – Proc. Natl Acad. Sci. USA 284: 20171627.

Huey, R. B. and Stevenson, R. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. – Am. Zool. 19: 357–366.

Hurst, T. P. 2007. Thermal effects on behavior of juvenile walleye pollock Theragra chalcogramma: implications for energetics and food web models. – Can. J. Fish. Aquat. Sci. 64: 449–457.

Ioannou, C. 2017. Grouping and predation. – In: Shackelford, T. K. and Weekes-Shackelford, V. A. (eds), Encyclopedia of evolutionary psychological science. Springer, p. 1–6.

Johannes, M. R. 1993. Prey aggregation is correlated with increased predation pressure in lake fish communities. – Can. J. Fish. Aquat. Sci. 50: 66–73.

Jones, J. R. et al. 2011. Temperature and oxygen in Missouri reservoirs. – Lake Reservoir Manage. 27: 173–182.

Katz, Y. et al. 2011. Inferring the structure and dynamics of interactions in schooling fish. – Proc. Natl Acad. Sci. USA 108: 18720–18725.

Knouft, J. H. and Ficklin, D. L. 2017. The potential impacts of climate change on biodiversity in flowing freshwater systems. – Annu. Rev. Ecol. Evol. Syst. 48: 111–133.

Knouft, J. H. et al. 2021. Forested riparian buffers as climate adaptation tools for management of riverine flow and thermal regimes: a case study in the Meramec River Basin. – Sustainability 13: 1877.

Krause, J. et al. 1996. Phenotypic variability within and between fish shoals. – Ecology 77: 1586–1591.

Krause, J. et al. 1998. Body length variation within multi-species fish shoals: the effects of shoal size and number of species. – Oecologia 114: 67–72.

Krause, J. et al. 2000. Fish shoal composition: mechanisms and constraints. – Proc. R. Soc. B 267: 2011–2017.

Krause, J. et al. 2002. Living in groups. – Oxford Univ. Press.

Kuruvilla, M. et al. 2022. Data from: The effect of temperature on fish swimming and schooling is context dependent. – Dryad Digital Repository, <https ://do i.org /10.5 061/d ryad. XXXX>.

Li, L. et al. 2020. Vortex phase matching as a strategy for schooling in robots and in fish. – Nat. Commun. 11: 5408.

O’Steen, S. and Bennett, A. F. 2003. Thermal acclimation effects differ between voluntary, maximum and critical swimming velocities in two cyprinid fishes. – Physiol. Biochem. Zool. 76: 484–496.

Payne, N. L. et al. 2016. Temperature dependence of fish performance in the wild: links with species biogeography and physiological thermal tolerance. – Funct. Ecol. 30: 903–912.

Pearson, K. X. 1900. On the criterion that a given system of deviations from the probable in the case of a correlated system of variables is such that it can be reasonably supposed to have arisen from random sampling. – Lond. Edinb. Dublin Phil. Mag. J. Sci. 50: 157–175.

Polverino, G. et al. 2013. Fish and robots swimming together in a water tunnel: robot color and tail-beat frequency influence fish behavior. – PLoS One 8: e77589.

Polyakov, A. Y. et al. 2022. Group size affects predation risk and foraging success in Pacific salmon at sea. – Sci. Adv. 8: eabm7548.

Romero-Ferrero, F. et al. 2019. Idtracker.ai: tracking all individuals in small or large collectives of unmarked animals. – Nat. Methods 16: 179–182.

Rosenthal, S. B. et al. 2015. Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. – Proc. Natl Acad. Sci. USA 112: 4690–4695.

Vallina, S. M. and Le Quéré, C. 2011. Stability of complex food webs: resilience, resistance and the average interaction strength. – J. Theor. Biol. 272: 160–173.

Venables, W. N. and Ripley, B. D. 2002. Modern applied statistics with S, 4th edn. – Springer, <www.stats.ox.ac.uk/pub/MASS4/>.

Walker, J. et al. 2005. Do faster starts increase the probability of evading predators? – Funct. Ecol. 19: 808–815.

Walsman, J. C. et al. 2022. Shoaling guppies evade predation but have deadlier parasites. – Nat. Ecol. Evol. 6: 945–954.

Weetman, D. et al. 1998. Effects of temperature on anti-predator behavior in the guppy, Poecilia reticulata. – Anim. Behav. 55: 1361–1372.

Whitney, J. E. et al. 2016. Physiological basis of climate change impacts on North American inland fishes. – Fisheries 41: 332–345.

Wilk, M. B. and Gnanadesikan, R. 1968. Probability plotting methods for the analysis for the analysis of data. – Biometrika 55: 1–17.

Wong, B. et al. 2007. Shoaling decisions in female swordtails: how do fish gauge group size? – Behavior 144: 1333–1346.

Zeileis, A. and Hothorn, T. 2002. Diagnostic checking in regression relationships. – R News 2: 7–10. <https ://CR AN.R- project.org/doc/Rnews/>.

Zhang, D. 2021. rsq: R-squared and related measures. – R package ver. 2.2, <https ://CRAN.R-project.org/package=rsq>.

Zuo, W. et al. 2012. A general model for effects of temperature on ectotherm ontogenetic growth and development. – Proc. R. Soc. B 279: 1840–1846.

1.7 SUPPORTING INFORMATION

Table 1.3. Median fish length in centimeters for each combination of group size and temperature

	Group size				
Temperature	1	2	4	8	16

29	4.0 ±0.1	3.4±0.3	3.6±0.2	3.7±0.1	3.9±0.2
25	3.9 ±0.2	3.3±0.1	3.4±0.2	3.5±0.2	3.5±0.2
21	4.0 ±0.3	3.4±0.2	3.5±0.3	3.6±0.1	3.6±0.1
17	4.2 ±0.4	3.5±0.2	3.4±0.3	3.5±0.3	3.3±0.1
13	4.0±0.2	3.3±0.2	3.4±0.1	3.6±0.1	3.6±0.1
9	4.1±0.2	3.6±0.1	3.5±0.2	3.6±0.1	3.7±0.1

1.7.1 *Sensitivity analysis*

In order to determine the sensitivity of our results to the startle threshold that we used to determine startles as well the speed and acceleration threshold to eliminate errors, we calculated the proportional change in our model output with a proportional change in the threshold (Equation 1).

$$\frac{\frac{x_2 - x_1}{x_1}}{\frac{\theta_2 - \theta_1}{\theta_1}} \qquad 1.5$$

For the latency and proportion of individuals startling, we examined the sensitivity of the model output to the startle threshold, speed threshold and acceleration threshold. For maximum speed and maximum acceleration models, we examined the sensitivity of model output to both the speed and acceleration thresholds. For all the models, we used the coefficient of temperature and temperature^2 as model outputs. We classified a model to be sensitive to a threshold if the value of the sensitivity term (equation 1) was > 1 or < -1. Of the ten combinations of models and thresholds, only three (Figures 1.5, 1.6 and 1.7) satisfied the above criteria of being ’sensitive’.

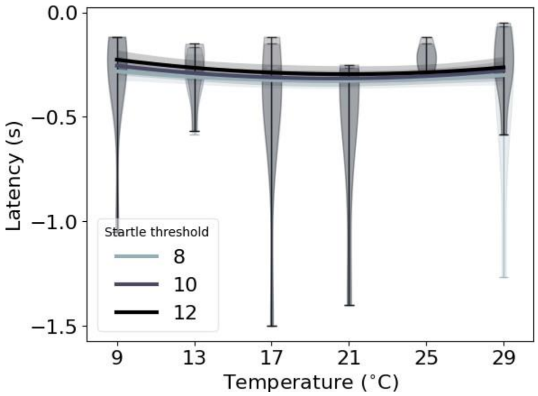

Figure 1.5. Latency is ’sensitive’ to startle threshold. The intercept of the curve decreases with decreasing threshold. This is as expected as the startle threshold decreasing would increase the number startles including ones that occurred earlier. There is minimal difference to the overall shape of the function.

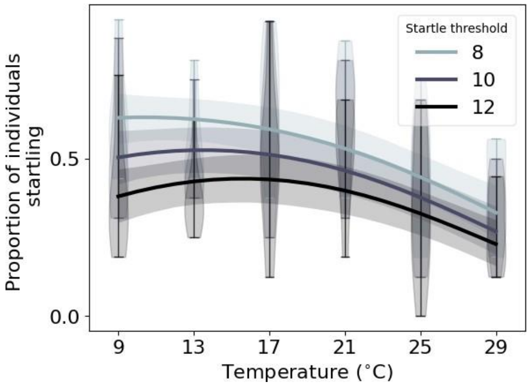

Figure 1.6. Proportion of individuals is ’sensitive’ to startle threshold. The intercept decreases with increasing thresholds because this excludes the number of startles considered. Additionally, the peak of the curve shifts to higher temperatures at higher startle thresholds. This could be a statistical anomaly as fewer data points are being considered because the maximum speed is below the startle threshold at higher temperatures (Figure 1.3a).

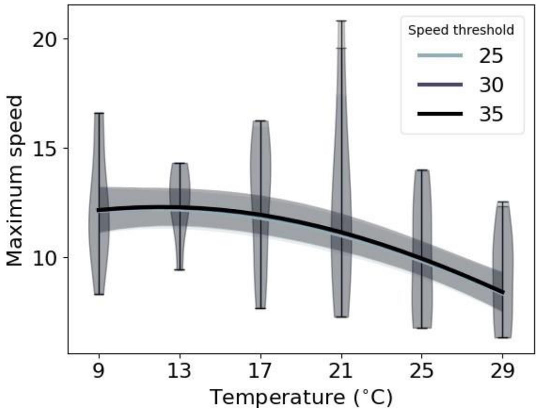

Figure 1.7. Maximum speed is ’sensitive’ to the speed threshold. The intercept of the curve decreases with decreasing threshold. This is because some data points are eliminated from analysis when the speed threshold decreases. There is minimal difference to the overall shape of the function.

1.7.2 *Average, median speed and acceleration*

In addition to the maximum speed and acceleration, we also examined the effect of temperature on the average and median.

For unperturbed swimming, we used equation 1.2 for average acceleration and equation 1 for everything else. For predation threat, we used equation 1.4 for average acceleration and equation 1.3 for everything else.

The summary of the model results for the average speed, median speed, average acceleration and median acceleration during both unperturbed swimming and predation threat are shown in Table 2.

Table 1.4. Model results for average, median speed and acceleration

Response Variable	Intercept	Temperature	Temperature^2	Group size	Loom	Group size x Temperature	R^2
			Unperturbed swimming				
Average speed	0.281	0.016	0	-0.004	-	-	0.052
Median speed	0.244	0.012	0	-0.05	-	-	0.029
Average acceleration	2.608	0.047	-0.001	-0.036	-	-0.002	0.244
Median acceleration	2.372	0.053	-0.001	-0.083	-	-	0.307
			Predation threat				
Average speed	0.732	0.012	0	0.037	-0.031	-	0.053
Median speed	0.487	0.012	0	-0.001	-0.026	-	0.035
Average acceleration	2.882	0.061	-0.002	0.075	-0.033	-0.003	0.088
Median acceleration	2.502	0.053	-0.001	-0.044	-0,018	-	0.080

1.7.2.1 Unperturbed swimming

Temperature did not have a significant effect on the average and median speed during unperturbed swimming (Table 1.2). On the other hand, average acceleration had a positive curvilinear relationship with temperature with the peak changing with group size. For group size 1, the peak was approximately 23 °C. Whereas, for group size 16, the peak was approximately 19 °C (Figure 1.6). While the maximum acceleration also had a positive curvilinear relationship with temperature (Figure 1.2b), the average acceleration peaks at a slightly lower temperature (Figure 1.6). Although, this optimal temperature was higher than the temperature at which acceleration was maximum during an escape response (Figure 1.3b). Similarly, the median acceleration during unperturbed swimming had a positive curvilinear relationship with temperature with a peak at approximately 21 °C. While the maximum acceleration also has a positive curvilinear relationship with temperature (Figure 1.2b), the median acceleration peaks at a slightly lower temperature (Figure 1.7). Although, this optimal temperature was higher than the temperature at which acceleration was maximum during an escape response (Figure 1.3b).

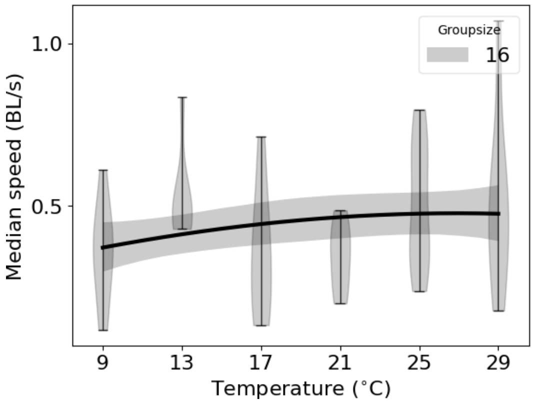

Figure 1.8. Median speed during unperturbed swimming

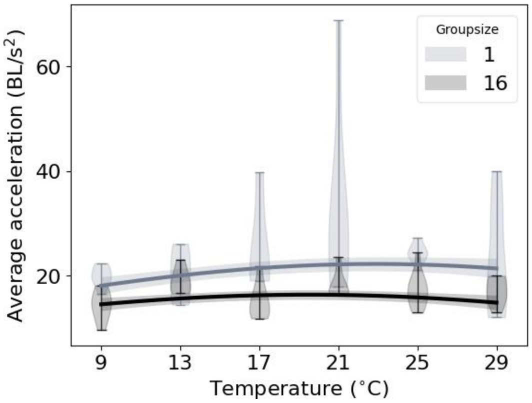

Figure 1.9. Average acceleration during unperturbed swimming

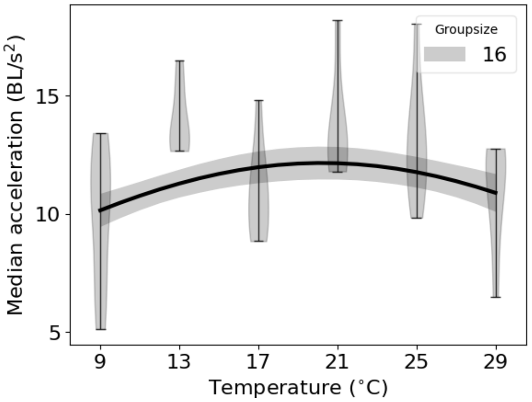

Figure 1.10. Median acceleration during unperturbed swimming

1.7.2.2 Predation threat

Temperature did not have a significant effect on the average and median speed during the predation threat (Table 1.2). On the other hand, the average acceleration during the predation threat had a positive curvilinear relationship with temperature with the peak changing with group size. For group size 1, the peak was approximately 19 °C. Whereas, for group size 16, the peak was approximately 15 °C (Figure 1.10). Median acceleration during the predation threat had a positive curvilinear relationship with temperature with a peak at approximately 20 °C. While the maximum acceleration also had a positive curvilinear relationship with temperature (Figure 1.2b), the median acceleration peaks at a higher temperature (Figure 1.11).

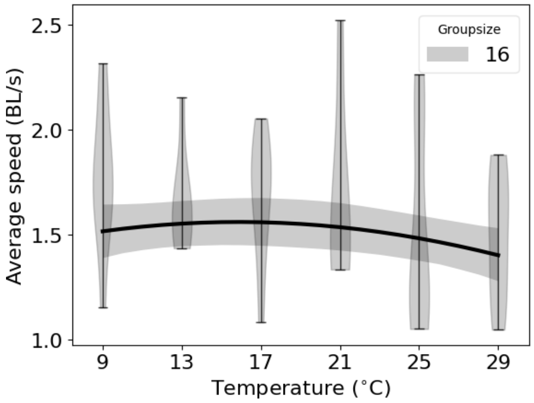

Figure 1.11. Average speed during the predation threat.

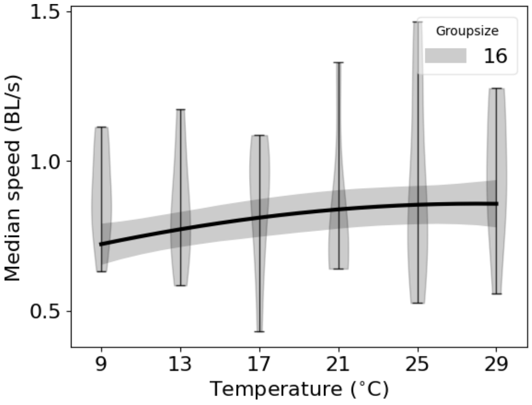

Figure 1.12. Median speed during the predation threat.

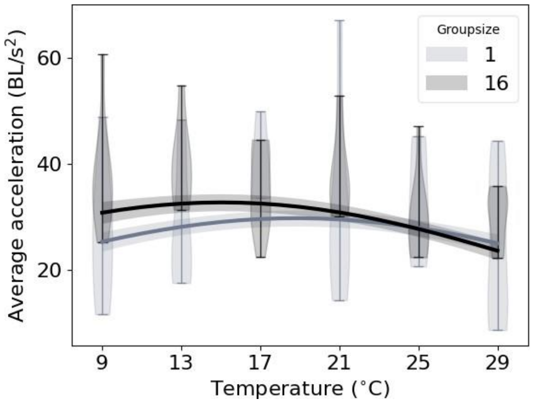

Figure 1.14. The average acceleration during the predation threat.

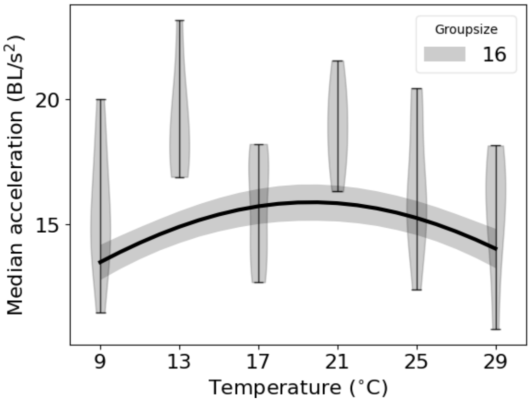

Figure 1.13. Median acceleration during the predation threat.

1.7.3 *Water temperature data*

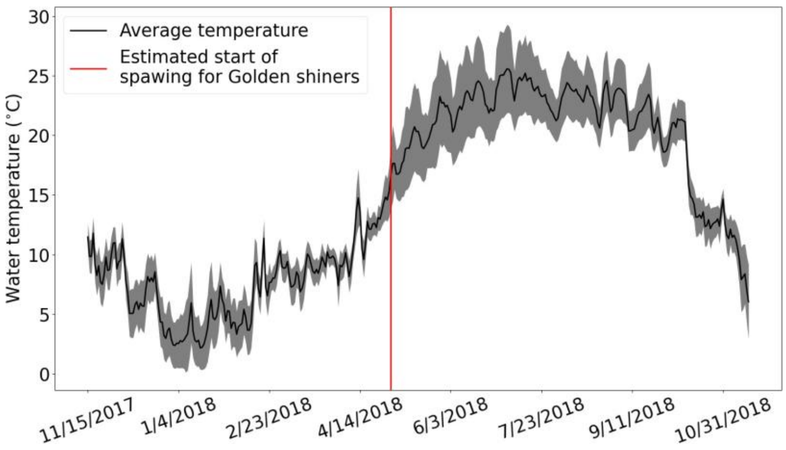

Figure 1.15. Water temperature of Meramec river watershed 2017 − 2018 (data from (Knouft et al., 2021)). Golden Shiners experience a large range of temperatures from 2 °C to 25 °C in the Missouri region.

1.7.4 *Correlation matrices*

To explore how the different results correlate with each other, we calculated the correlation matrix of the different behavioral metrics in the unperturbed swimming phase as well in the predation threat phase (R Core Team, 2013).

Table 1.5. Correlation between the different behavioral metrics related to unperturbed swimming

	Maximum speed	Maximum acceleration	ANND	Convex hull area	Polarization
Maximum speed	1.00	0.59	0.15	0.12	0.42
Maximum acceleration	0.59	1.00	0.15	0.31	0.21

ANND	0.15	0.15	1.00	-0.16	-0.20
Convex hull area	0.12	0.31	-0.16	1.00	-0.11
Polarization	0.42	0.21	-0.20	-0.11	1.00

Table 1.6. Correlation between the different behavioral metrics related to predation threat

	Proportion of startles	Latency	Maximum speed	Maximum acceleration	ANND	Convex hull area	Polarization
Proportion of startles	1.00	-0.15	0.85	0.78	0.07	-0.07	0.08
Latency	-0.15	1.00	-0.25	-0.28	0.07	-0.06	0.02
Maximum speed	0.85	-0.25	1.00	0.86	0.03	0.03	0.08
Maximum acceleration	0.78	-0.28	0.86	1.00	-0.03	0.03	0.08
ANND	0.07	0.07	0.03	-0.03	1.00	0.12	-0.12
Convex hull area	-0.07	-0.06	0.03	0.03	0.12	1.00	-0.08
Polarization	0.08	0.02	0.08	0.08	-0.12	-0.08	1.00

1.7.5 *References*

Knouft JH, Botero-Acosta A, Wu CL, Charry B, Chu ML, Dell AI, Hall DM, Herrington SJ. Forested Riparian Buffers as Climate Adaptation Tools for Management of Riverine Flow and Thermal Regimes: A Case Study in the Meramec River Basin. Sustainability. 2021; 13(4):1877.

R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria; 2013, http://www.R-project.org/, ISBN 3-900051-07-0.

Chapter 2. SOCIAL INFLUENCES COMPLEMENT ENVIRONMENTAL CUES TO STIMULATE MIGRATING JUVENILE SALMON

Publication history: This study was co-authored with Thomas P. Quinn, Joseph H. Anderson, Mark D. Scheuerell, Erika M. Miller, Andrew G. Berger, Connie Okasaki, John R. McMillan, George R. Pess, Peter A.H. Westley, and Andrew M. Berdahl. At the time this dissertation was published, this chapter was not in review with a journal.

2.1 ABSTRACT

Background: The large-scale seasonal migrations undertaken by many species require complex navigational and timing decisions. Animals migrating in groups might benefit from collective decision making, especially if the environment is noisy (i.e., has high degree of local variation rather than smooth gradients in, for example, salinity or temperature), unpredictable, or the migrants cannot rely on individually acquired information. We focus on juvenile salmon whose migration from fresh water to the ocean is timed to match suitable conditions for growth and survival. While the environmental and physiological factors that influence the timing of migration have been well studied, the influence of social interactions on migration timing is poorly understood.

Method: We compiled juvenile salmon data, collected over 19 years, at traps during their downstream seaward migration in three rivers in Washington state along with a suite of relevant environmental time series. We developed state space statistical models to estimate the influence of hatchery-produced salmon to stimulate the downstream migration of wild salmon, while also incorporating potential environmental stimuli.

Results: Our results are consistent with the “pied-piper” hypothesis that large numbers of migrating hatchery-origin salmon provide a social cue stimulating migration of co-occurring wild salmon. The number of hatchery salmon counted at the trap was a strong predictor of the number of wild sub-yearling Chinook salmon in the Dungeness and Puyallup rivers and on yearling coho salmon in the Puyallup and Skagit rivers. Migration timing was also influenced by a suite of physical factors related to temperature, river flow, photoperiod, and lunar phase.

Conclusions: Our findings highlight the potential for social cues to affect migration timing of downstream migrating salmon, in concert with environmental factors. Incorporating social information into timing decisions may allow animals to benefit from collective decision making strategies and better time their migrations. Moreover, understanding the effects of large-scale hatchery releases on wild salmon migration may provide valuable insights for planning the timing and duration of hatchery releases.

2.2 INTRODUCTION

From monarch butterflies (Danaus plexippus) to blue whales (Balaenoptera musculus), many species undertake large-scale seasonal migrations to take advantage of predictable changes in abiotic and biotic conditions (Dingle 2014). These migrations often involve challenging decisions regarding where and when to go. Such decisions must often be made based on noisy (i.e., locally variable) information that only weakly correlates with the conditions in distant locations the animals need to infer (Visser and Gienapp 2019; Wilson et al. 2021). For example, long-distance migrants like the East Atlantic light-bellied brent goose (Branta bernicla hrota) need to infer the timing of the onset of spring in the Arctic based on conditions in the temperate winter staging area (Clausen and Clausen 2013). Some animals can learn from previous experience (Baert et al. 2022) but first-time migrants may not be able to determine conditions in the destination until they arrive, and in some species cannot follow their parents or experienced migrants. Collective decision-making – where individuals synchronize movements and/or migrations partly based on the collective behaviors of the larger group – may improve the accuracy of decisions based on noisy information and migrating animals in groups potentially benefit from collective decision making (Berdahl et al. 2018; Larkin and Walton 1969). For example, the homing efficiency of homing pigeons (Columba livia) improved when flying in flocks (Biro et al. 2006; Kano, Sasaki, and Biro 2021). Even migrations that appear to be asocial – such as the highly dispersed migrations (Guttal and Couzin 2010) of monarch butterflies (Reppert, Guerra, and Merlin 2016) or blue whales (Oestreich et al. 2020) – can be influenced by social information, through indirect cues such as visual or olfactory cues or long-range communication (Couzin 2018; Aikens et al. 2022). While most of the research on collective decision making during migration has been focused on deciding where to go (i.e., collective navigation) interest is expanding to include another critical question migrants face: when to go (Oestreich et al. 2022; Kao et al., n.d.).

Pacific salmon and trout (Oncorhynchus species) migrate as juveniles from freshwater to the ocean and as adults return from the ocean back to their natal site to spawn (Quinn 2018). Species vary in social behavior as juveniles prior to seaward migration. Pink (O. gorbuscha) and chum (O. keta) salmon fry migrate immediately or almost immediately to sea after emerging from gravel nests but other species spend months or years feeding in freshwater habitats before migrating (Quinn 2018). Downstream migration is characteristically at night (Roberts et al. 2009) and schooling is difficult to observe directly, but experiments (Hoar 1958; McDonald 1960) and field observations (Munsch, Cordell, and Toft 2016) indicate strong schooling by pink and chum salmon fry. In contrast, juvenile coho salmon (O. kisutch), anadromous rainbow trout, known as steelhead (O. mykiss) and coastal cutthroat trout (O. clarkii clarkii) typically establish and defend feeding territories in streams (Taylor 1991; Sabo and Pauley 1997; Keeley 2001; Young 2004). However, the shift of this territorial behavior and upstream orientation to more aggregative behavior and downstream swimming is a key part of the transformation from stream-resident parr to seaward migrating, saltwater-tolerant smolts (Hoar 1976).

The smolt migration to sea is timed, on a broad level, to match arrival in salt water with optimal conditions for growth and survival in estuaries and at sea (Wilson et al. 2021; Cooney et al. 2001; Spence and Hall 2010). These conditions, including sea surface temperature and spring plankton bloom, vary from year to year (Trenberth and Hurrell 1994; Downton and Miller 1998). Consequently, the timing of arrival of juvenile salmon in marine waters affects their survival. For example, earlier migration is associated with higher survival in both hatchery and wild Chinook salmon, whereas later migration is associated with higher survival in hatchery coho salmon (James et al. 2023; Scheuerell, Zabel, and Sandford 2009). Photoperiod, combined with internal circannual rhythms, provides the primary cue for the complex changes in physiology and endocrine systems needed to prepare the fish for the radical change in osmotic environments and habitat (Björnsson, Stefansson, and McCormick 2011; McCormick 1994). The behavioral changes leading to the transformation from upstream-oriented territorial parr to downstream-migrating, more aggregative or schooling smolts (McDonald 1960) are much less well known than the physiological processes (Hoar 1976).

The importance of salmon in commerce, culture, and ecosystems in the northern Pacific Ocean (and Atlantic Ocean as well for Salmo salar, the Atlantic salmon) (Noakes 2014) has led to many long-term monitoring programs to assess the abundance of seaward migrating smolts and returning adults (Link and English 2000), and efforts to determine the environmental stimuli that trigger them (Roper and Scarnecchia 1999; Teichert et al. 2020; Simmons et al. 2021). Daily counts of migrating juvenile salmon from traps typically show a series of peaks and troughs rather than the smooth, more or less bell-shaped curve seen when data from many years are pooled. Efforts to model these day-to-day patterns have tended to focus on physical features of the rivers and especially aspects of water temperature and river flow, and lunar phase, typically with only modest success (Hvidsten et al. 1995). Considerable variation is left unexplained after various combinations of physical data are included in models. However, this ruggedness in count data from the spawning migrations of adult salmon have been replicated by models that include social behavior (Berdahl, Westley, and Quinn 2017). Therefore, social interactions may also be important in the timing of migrations of salmon smolts.

Hatcheries, used for many decades to bolster salmon populations, may incidentally provide a way to test for the use of social information in the migration timing decisions of juvenile salmon. Hatcheries rear young salmon in mortality-reduced conditions, before releasing them into rivers where they migrate to the ocean. Due to a combination of release strategies, physiological readiness to migrate and the abundance of hatchery-origin juveniles, these releases often greatly increase the number of fish in the rivers over a brief period of time. Data from traps reveal that hatchery-produced salmon often migrate rapidly, and en masse, to the ocean (Figure 2.1). Trap operators and biologists have hypothesized that these large numbers of hatchery-origin fish may provide a social cue to migrate for the wild conspecifics (personal communication with Peter Topping), which typically have a much more protracted migratory window (Hansen and Jonsson

1985; Kennedy et al. 1984). Efforts to test this so-called “pied-piper” hypothesis (referring to the folktale of the pied piper of Hamlin) have yielded supportive (Hvidsten et al. 1995) or equivocal results (Hillman and Mullan 1989).

With respect to migrating juvenile salmon, the pied piper hypothesis proposes that fish that are more or less physiologically ready, but have not yet begun to migrate may experience other conspecifics mighting downstream past them through visual, odor or lateral line cues. Due to social attraction, the former may be influenced to join the latter, increasing the social migration stimulus for downstream fish. Once this bolus of smolts has departed, there are fewer fish ready to migrate, and even ideal physical conditions do not result in large numbers of migrants, until the remaining fish increase in readiness and the process repeats itself until the population has all migrated. This conceptual model of migration in wild populations thus incorporates social with physical factors triggering migration, the result being a migration characterized by pulses of migrants even in the presence of smoothly varying potential environmental triggers for migration.

In this paper, we leverage a multidecadal dataset to test for the use of social information in the timing decisions of migrating salmon smolts of two different species. Specifically, we use a state space statistical model to estimate the influence of hatchery-produced coho and Chinook salmon (O. tshawytscha) smolts on the movement decisions of wild-origin smolts, relative to established physical factors affecting movement (Table 2.1). A state space model can allow us to estimate the effect of covariates (both environmental and social) on the number of wild salmon migrating after accounting for process errors, observation errors, and autocorrelation. Chinook and coho salmon are widely propagated in the region’s hatcheries (Naish et al. 2007), and transition from stream-resident to migratory behavior after several months to a year (Quinn 2018), and thus are suitable for testing our hypothesis. While augmenting our view of social decision making to include temporal aspects of migration, this work also contributes to our knowledge of salmon life history and our understanding of the unintended ecological impacts of hatcheries on wild salmon populations (Claussen and Philipp 2023; McMillan et al. 2023).

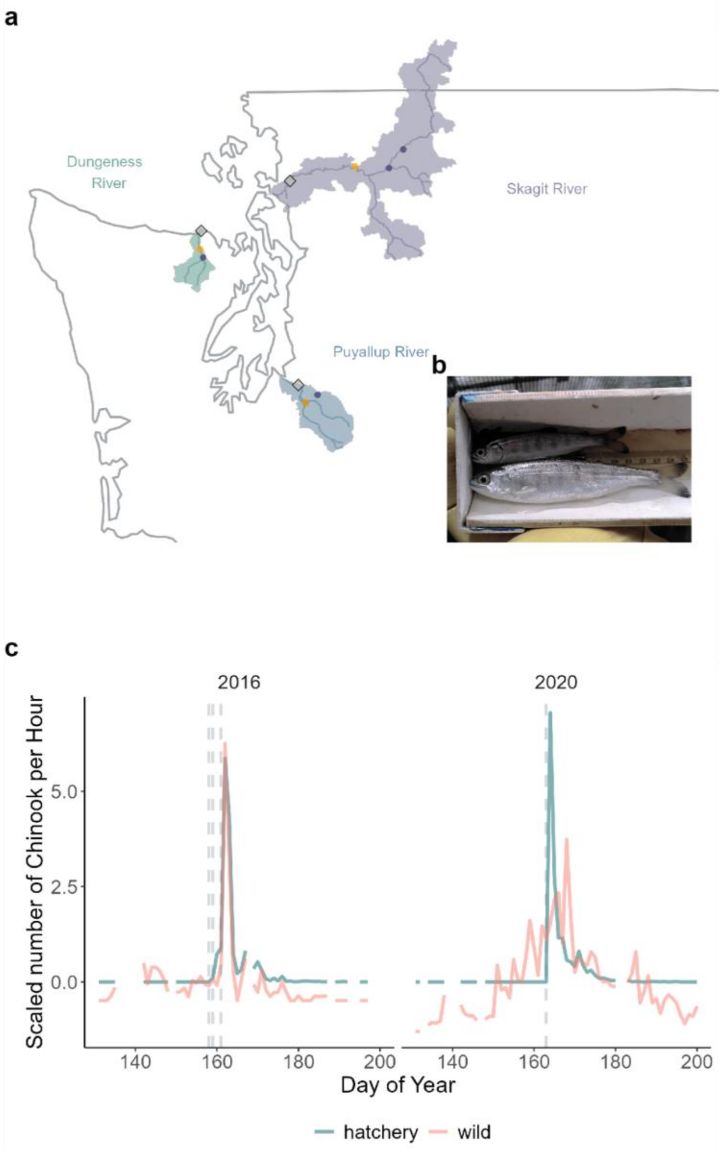

Figure 2.1. a) Map of the rivers (lines) included in this study, along with their watersheds (polygons) in Washington State, USA. Black diamonds indicate the location of the smolt traps. Purple and orange circles indicate common Chinook and coho salmon release sites respectively. b) Image of a wild (top), and a hatchery (bottom) yearling coho salmon caught in the Dungeness River trap. c) Scaled values of number of Chinook salmon per hour caught in the trap in the Dungeness River from 2016 and 2020. Gray vertical dashed lines indicate the date of hatchery release(s). In some years (e.g., 2016), many wild salmon migrate past the trap concurrent with the pulse of hatchery fish. In other years (e.g., 2020), this correlation is not clear.

2.3 METHODS

2.3.1 *Trap Data*

To estimate the influence of hatchery salmon on the migration of wild salmon, we focused on species in three rivers in Washington state with large hatchery programs propagating sub-yearling Chinook salmon (hereafter Chinook salmon) and yearling coho salmon (hereafter coho salmon) (Supplementary Information). We refer to hatchery-origin salmon as hatchery salmon and natural-origin salmon as wild salmon, acknowledging that fish termed “wild” may have recent hatchery ancestry (i.e., one or two hatchery-origin parents spawning in the river). Other life history variants such as yearling Chinook salmon and sub-yearling coho salmon are much less numerous and were excluded from our analyses. We used data from salmon traps deployed in the Dungeness (years 2005-2020), Puyallup (years 2004-2021), and Skagit (years 2010-2022) rivers to quantify juvenile salmon populations migrating to sea. These three rivers are representative of those in which coho and Chinook salmon naturally occur in the region, but are not replicates of each other. The Skagit is the largest in terms of watershed area, followed by the Puyallup, and the Dungeness is the smallest (Figure 2.1), and the extent of human habitat modification is greatest in the Puyallup River. We chose them primarily because they have long-term records of migrating hatchery and natural origin salmon. Average number of releases per year and average number of salmon released per year in each river is shown in Supplementary Information.

Migrating smolts are caught in a single floating screw trap (in the Dungeness and Puyallup rivers) or in both a floating scoop trap and a floating screw trap (in the Skagit River), counted and released (Volkhardt et al. 2007). The hatchery origin salmon were identified by trained staff operating the traps by the presence of an internal coded wire tag (detected magnetically), or a clipped adipose fin. While most hatcheries try to mark all the salmon that are released in the rivers, a small percentage (<5% of hatchery coho salmon in the Dungeness and Skagit rivers; <5% of hatchery Chinook salmon in the Skagit and Puyallup rivers; <12% of hatchery Chinook salmon in the Dungeness River; <5% of hatchery coho salmon in the Puyallup River except for two instances (2009 and 2021) with >50%) were unmarked (unclipped and untagged). The unmarked hatchery salmon are comparable in abundance to the wild salmon present in the Dungeness and Puyallup rivers. Because hatchery salmon are often bigger than wild salmon and have a different appearance (Figure 2.1), the trap operators sometimes distinguish between the hatchery salmon and wild salmon and such fish are recorded as ‘unmarked hatchery’; however, this categorization may not always be accurate. In the Puyallup River, the unmarked hatchery Chinook salmon were accounted for in the past seven years by subtracting the number of unmarked hatchery salmon estimated by Regional Mark Information System (RMIS) from the number of wild salmon caught. We addressed the issue of misidentification of unmarked hatchery salmon as wild salmon at the traps in all the rivers by using data from RMIS to get the proportion of unmarked hatchery salmon released by the hatcheries to look at the correlation between the number of unmarked hatchery salmon released and the number of wild salmon caught in the traps (Figure 2.4). A strong relationship would suggest wild catch totals were mostly driven by unmarked hatchery fish, potentially confounding our counts of wild salmon. We found no correlation between the number of unmarked hatchery salmon and the number of wild salmon for any river-species pair, except Skagit River coho salmon, which had a moderate correlation (0.36). Therefore, we use unmodified hatchery counts in our analysis. Because the proportion of unmarked hatchery coho salmon in the Puyallup River was unusually high in 2009 and 2021 (>50%), we reran our analysis without those years and found similar results (Figure 2.12).

In all three rivers, some Chinook salmon migrate shortly after emergence in January to March (fry migration) and others migrate later, from May to July, after feeding in the river for several months (parr migration), as is typical in the region [42,43]. This results in a strongly bimodal distribution of migration times. Since the hatchery smolt releases coincided with the later parr migration, we restricted our analysis to days of the year 130 - 200 in the Dungeness River and days of the year 130 - 218 in the Puyallup River (Figure 2.1). In the Skagit River, the proportions of fry migrants and parr migrants vary from year to year [44]. Most of the sub-yearlings migrated as fry in the years of data we had, leaving only a small proportion of the migrants remaining during hatchery releases. The Skagit River trap was only operated up to day 189 in some years. Therefore, we used only data from days 150 - 189 for Chinook salmon in the Skagit River. For coho salmon, we used data between days 120 and 160 in the Dungeness River, between days 90 and 160 in the Puyallup River, and between days 100 and 150 in the Skagit River.

In the Dungeness and Puyallup Rivers, salmon caught in the trap were counted roughly twice a day – at around 06:00 h and 18:00 h. ‘Night’ counts tended to be much higher than the ‘day’ counts (Figure 2.5) because the juvenile salmon tend to migrate at night. In the Skagit River, the trap operated only during the nights, except for every third day, when the trap operated all day, but was checked twice. Because two thirds of the ‘day’ counts were not enumerated, we only analyzed the ‘night’ counts in the Skagit River. The counts were separated by scoop trap counts and screw trap counts in the Skagit River. In all rivers, because the time at which the trap started and stopped operating varied slightly each deployment, we used the time deployed to calculate the catch per unit effort or catch rate for each day or night by dividing by the number of hours deployed.

We log-transformed the number of wild salmon (after adding 1 to each data point to avoid infinite values) because the data were log normally distributed. We scaled (divided by the standard deviation) and centered (subtracted the mean) the data for each year to account for large year-to-year variation in population size so that we could compare between the years. We scaled, but did not center, the catches of hatchery salmon counts so that the counts remained 0 when no hatchery fish were caught (for example, Figure 2.1c). Immediately after a hatchery release, the traps sometimes get inundated with hatchery salmon. To avoid this, trap operators sometimes suspend operations for a few days, resulting in missing data. We linearly interpolated the hatchery data for days when the trap was out since the analysis that we used does not allow missing values in the covariates. We interpolated around 16% (526 values) of the data from the Dungeness River, 37% (1148 values) of the data from the Puyallup River and 13% (267 values) of the data from the Skagit River. Most of the missing values in the Puyallup and Skagit rivers were towards the end of the season and during the Covid-19 lockdown in 2020. Because missing values are allowed in the response variable of our model, we did not interpolate missing values of the wild salmon counts.

2.3.2 *Environmental data*

We aimed to estimate the social effects on the migration of salmon smolts, while controlling for any environmental effects. Based on previous studies (Roper and Scarnecchia 1999; Sykes, Johnson, and Shrimpton 2009; Spence and Dick 2014; Melnychuk and Welch 2018), we selected ten environmental covariates (Table 2.1) that have been reported to influence Chinook (Roper and Scarnecchia 1999; Sykes, Johnson, and Shrimpton 2009; Melnychuk and Welch 2018) and coho salmon smolt migration (Spence and Dick 2014; Melnychuk and Welch 2018) in British Columbia (Sykes, Johnson, and Shrimpton 2009; Melnychuk and Welch 2018) and Oregon (Roper and Scarnecchia 1999; Spence and Dick 2014). Although this is not a comprehensive review of the literature on environmental effects on salmon smolt migration, and there may be differences in the results due to geographic variations (Spence and Dick 2014), we hypothesized that these covariates would affect salmon smolt migration downstream included in our study. All the environmental data that we used were collected in the same river basin as the migrating salmon. While these data do not capture the full range of environmental conditions that the fish experience throughout the spatial extent of juvenile rearing habitats, we assumed that measured water/air temperature and discharge downstream were correlated to the water temperature and discharge experienced by the fish.

For the Dungeness River, we used flow data from the Washington Department of Ecology (Dungeness River mouth, Station ID 18A050). For the Skagit River, we used flow data from USGS (Newhalem, Site no 1217800). For the Puyallup River, we used flow data measured by the Puyallup Tribe of Indians near the trap.

For the Skagit River, we obtained water temperature data from USGS (Site no. - 12178000). Water temperature data was not available for the Puyallup River so we supplemented this with air temperature data from USDA Natural Resources Conservation Service (Mowich, 941), a site within the Puyallup drainage. For the Dungeness River, we obtained water temperature data from the Washington Department of Ecology (2004-2014, Station ID 18A050) and from the Washington Department of Fish and Wildlife (2016-2020) and calculated the accumulated temperature units (ATU) as the cumulative sum of the daily mean water temperature from the earliest date that was sampled every year (April 1st). In the Skagit/Puyallup rivers, we calculated ATU as the cumulative sum of the daily mean water/air temperature from the Winter Solstice of the previous year (December 21st). Even though no catch data were used prior to May 10, temperatures prior to this date affect growth and hence migration decisions after May 10.

We scaled, and for some variables centered, the environmental data for each year to compare the effects of all the covariates (Table 2.1). Since our analysis did not allow missing variables in the covariates, we linearly interpolated the data for the days in which the data were missing. Before using the environmental data as covariates in the model, we calculated the correlation between every pair of covariates (Figure 2.7, Figure 2.10, and Figure 2.14). If the correlation of any pair was > 0.5, we did not use those covariates in the model at the same time. Instead, we determined the covariate in each pair that had more support from the data (with lower AICc value) and then used those covariates for subsequent analysis.

2.3.3 *Analysis*

We used multivariate autoregressive state-space (MARSS) models to estimate the influence of the number of hatchery salmon migrating downstream as determined by the number of hatchery salmon caught in the trap, and of the different environmental variables, on the number of wild juvenile salmon out-migrating (Hinrichsen and Holmes 2009; Holmes, Ward, and Wills 2012). MARSS models allowed us to separate the underlying process from the observed data. In the MARSS framework, y_t is the $n \times 1$ vector of the log of the observations of wild salmon per hour on the tth day of the year for n years and x_t represents the $n \times 1$ vector of the log of the true, but unknown number of wild salmon per hour on the tth day of the year.

They are related by the following equations:

$$\text{Observation model - } y_t = x_t + Dd_t + v_t, v_t \sim MVN(R) \qquad 2.1$$

$$\text{Process model - } x_t = x_{t-1} + Bc_t + w_t, w_t \sim MVN(Q) \qquad 2.2$$

where c_t are the $p \times 1$ vector of covariates affecting the states or the average number of salmon per hour migrating past the trap, p is the number of covariates multiplied by the number of years, B is the $n \times p$ matrix of coefficients relating the effects of the covariates c_t to the states x_t, d_t is the vector of covariates affecting the observations, D is the $n \times p$ matrix of the effects of the covariates on the observation. w_t and v_t are the $n \times 1$ vectors of normally distributed errors. R is the $n \times n$ variance-covariance matrix of the observation errors and Q is the $n \times n$ variance-covariance matrix of the process errors. We assumed that the observations and states were independent between years and that the observation and process variances were the same for all

Table 2.1. List of environmental covariates, source of data, description, data transformation, predicted effect on number of wild salmon migrating (positive or negative) of the covariates used in MARSS analysis for each river. The reference column provides an example of a paper that has used the given covariate in a model of juvenile migration timing of Chinook, and coho salmon in various rivers. (–) indicates no reference but we hypothesize that the covariate would have an effect on migration timing of juvenile salmon.

Covariate	**Data Source**	**Description**	**Transformation**	**Predicted effect (+/-)**	**Reference**
Temperature	WA Department of Ecology, WDFW, USGS, USDA Natural Resources Conservation Service	Daily mean of water temperature (Skagit River) or water temperature measured at a time point closest to the midpoint of the daily trapping duration (Dungeness River) or daily mean of air temperature (Puyallup River)	Scaled and centered	+	(Roper and Scarnecchia 1999; Spence and Dick 2014)
Temperature difference	Calculated	Change in water/air temperature between that day and previous day $x_t - x_{t-1}$	Scaled	+	(Spence and Dick 2014)
ATU (accumulated thermal units)	Calculated	Cumulative sum of water/air temperature starting on the winter solstice of the previous year (Skagit and Puyallup rivers) or April 1st (Dungeness River)	Scaled and centered	+	(Sykes, Johnson, and Shrimpton 2009)
Temperature residuals	Calculated	Residual effect of temperature after controlling for photoperiod in a linear model	Scaled	+	–
Photoperiod	sunrise-sunset.org	Number of daylight hours for a latitude, longitude near the trap	Scaled and centered	+	(Roper and Scarnecchia 1999; Spence and Dick 2014)
Photoperiod difference	Calculated	Change in photoperiod between that day and previous day $x_t - x_{t-1}$	Scaled	+	–
Flow	WA department of Ecology, USGS, Puyallup Tribe of Indians	Daily mean of water flow (Skagit River), or daily flow measured at a time point closest to the midpoint of the trapping duration (Dungeness River), or daily flow measured when the trapping started (Puyallup River)	Scaled and centered	-	(Sykes, Johnson, and Shrimpton 2009)
Flow difference	Calculated	Change in water flow between that day and previous day $x_t - x_{t-1}$	Scaled	+	(Spence and Dick 2014)
Lunar phase	Ephem package, python	Percentage of the moon illuminated	Scaled and centered	-	(Roper and Scarnecchia 1999; Spence and Dick 2014)
Secchi depth	Puyallup Tribe of Indians	Water clarity measured with a Secchi disk when the trapping started (only available for Puyallup River)	Scaled and centered	-	(Melnychuk and Welch 2018)

and that the observation and process variances were the same for all years. Therefore, R and Q are diagonal matrices.

We separated the data into day and night for the analysis and then fit two models: one with equal process variances and the other with unequal process variances for day and night. The effect of the environmental covariates was assumed to be equal for all years and for day and night, whereas the effect of hatchery was equal for all years but allowed to be different for day and night. We did this to test the hypothesis that the effect of hatchery salmon would be higher during the day because the wild salmon might have stronger visual cues from the presence of hatchery salmon during the day (Simmons et al. 2021).

To ensure that the errors met the model assumptions, we plotted the residuals of the predicted values against the fitted values, the autocorrelation function of the residuals, as well as quantile-quantile plots. We assumed that both the process errors and observation errors are identical, independent, and normally distributed within years.

The MARSS framework allowed us to address an alternate hypothesis to the pied piper: that hatchery and wild salmon are *independently* responding to the same environmental stimuli. For example, if both hatchery and wild smolts independently respond to the river flow, peaks in their respective migration timing distributions would coincide. However, in this scenario, a high number of wild smolts would be correlated with high flow when there are no hatchery smolts migrating downstream as well as when there are many hatchery smolts migrating. Therefore this model would estimate the coefficient of flow to be positive and the coefficient of the hatchery (catch rate of hatchery smolts) covariate to be zero and not falsely support the pied piper hypothesis.

2.3.3.1 Model selection and relative importance of variables

Akaike Information Criterion (AIC) is often used to select the best model among models with different combinations of covariates. However, with autocorrelated data, the sample size is much lower than the number of data points we have. Thus, we used AICc, which is AIC with a correction factor for small sample size, to compare models.

We first compared the model with equal process variance for day and night with the model with unequal process variance for day and night and used AICc to select the most appropriate variance structure in all six cases.

Among the models with each of the correlated covariates, the model with photoperiod difference had the lowest AICc for Chinook salmon in the Dungeness and Puyallup rivers (Supplementary Information). In the Skagit river, the model with temperature residuals had the lowest AICc for Chinook salmon (Supplementary Information). For coho salmon in the Dungeness River, the model with photoperiod had the lowest AICc among all the correlated covariates (Supplementary Information). On the other hand, the model with ATU had the lowest AICc among the correlated covariates for coho salmon in the Puyallup River and the Skagit River (Supplementary Information). We then fit each model for each river-species combination with every combination of uncorrelated covariates (including the hatchery covariate) and chose the model with the lowest AICc to get the estimates of the effects (B) and model diagnostics.

In addition to estimating the best model from model selection, we calculated the relative variable importance as the probability that the given variable is in the best model. We estimated the probability by calculating the Akaike weight of each model and then summing the weights of all the models for which that variable was present. We consider a variable ‘important’ if it has at least 90% probability of being in the best model. While this method does not describe the significance of the variable or the size of the effect that the variable has on the response variable, it describes the relative importance of the covariate in the set of candidate models.

2.4 RESULTS

2.4.1 *Social effects*

To test the pied piper hypothesis, we looked at the following three criteria. One, whether the hatchery covariate was in the top model(s) (i.e., the model with the lowest AICc contained the hatchery covariate). The hatchery covariate being included in this top model indicates that considering the number of hatchery fish out migrating allows for better predation of smolt outmigration than considering only environmental variables (discussed in following section). Two, the effect size and significance of the hatchery covariate. A positive effect means that more wild fish migrated when the hatchery fish migrated, even accounting for environmental cues that could cause them both to migrate independently. The significance means that the estimated range of effect sizes did not include zero. Three, the relative importance of the hatchery covariate – described in the Methods section. The importance measures the role of a variable across all potential model fits and we used a threshold of ≥0.9 to indicate high relative variable importance.

2.4.1.1 Chinook in the Dungeness and Puyallup rivers

The hatchery covariate was included in the top AICc scoring model in the Dungeness and Puyallup rivers. The effect of hatchery salmon on wild salmon had a positive effect in both day and night in both rivers (Figure 2.2a, 2.2b). The estimated effect size was equal for both day and night, meaning we found no difference between the social effect during day and during night. The hatchery covariate was an important variable in both rivers compared to all other variables we tested in model selection (Supplementary Information), as it is in all the top models.

2.4.1.2 Chinook in the Skagit River

While the best model for Chinook salmon in the Skagit River did not have the hatchery covariate, a model with equal support ($\Delta AICc < 2$, Supplementary Information) did. The effect was positive, but the confidence intervals overlapped with 0 (Figure 2.2c). The hatchery covariate was not an 'important' variable in the Skagit River compared to all other variables we evaluated in model selection (Supplementary Information).

2.4.1.3 Coho in the Dungeness River

In the Dungeness River, while the hatchery covariate was not in the best model, the model with this covariate had equal support ($\Delta AICc < 2$, Supplementary Information). The effect of the hatchery covariate was positive during the day and negative during the night and the confidence intervals for both estimates overlapped with 0 (Figure 2.3a). The hatchery covariate was not an 'important' variable in the Dungeness River compared to all other variables we tested in model selection (Supplementary Information).

2.4.1.4 Coho in the Puyallup and Skagit rivers

In both the Puyallup and Skagit rivers the hatchery covariate was included in the top scoring model (Figure 2.3b,c). In both rivers, we found a strong positive effect of the hatchery covariate on the number of wild salmon migrating (Figure 2.3b,c). Further, the hatchery covariate was an important variable in the both rivers compared to all other variables we tested in model selection (Supplementary Information).

2.4.1.5 Social summary

For both species, we found that increases in the number of wild salmon migrating coincided with increases in the number of hatchery salmon migrating in two out three rivers. For Chinook salmon in the Skagit river, the estimate of the effect was also positive, but did overlap zero. This consistency is on par with the consistency of 'known' environmental effects explored in the following section. In summary, although our results are correlative, the positive effect of hatchery smolts on the migration of wild smolts is consistent with the results we would expect under the pied piper hypothesis – wild smolts being influenced to migrate when they observe many hatchery smolts outmigrating.

2.4.2 *Environmental effects, Chinook salmon*

2.4.2.1 Flow & Δ flow

Among all the covariates, flow difference or increase in the river's flow had the strongest positive effect on the number of Chinook salmon migrating in the Dungeness and Puyallup rivers (Figure 2.2a, 2.2b). However, absolute flow had a small negative effect in the Puyallup River (Figure 2.2b). This suggests that when the flows are low, an increase in flow of the river from the previous day was correlated with more salmon migrating downstream. Flow was not a covariate in the top models in the Skagit River.

2.4.2.2 Photoperiod & Δ photoperiod

Photoperiod difference, or increase in day-length, also had a positive effect on the number of Chinook salmon migrating in the Dungeness and Puyallup rivers (Figure 2.2a,b). Photoperiod had a negative effect on Chinook salmon in the Skagit River (Figure 2.2c), indicating that as the season progressed and day length increased, the number of salmon migrating increased in two rivers but declined in the third.

2.4.2.3 Temperature, Δ temperature, & temperature residuals

Temperature difference, or change in water temperature from the previous day, had the strongest negative effect on the number of Chinook salmon migrating in the Dungeness and Skagit rivers (Figure 2.2a, c). The residuals of the model with temperature also had a negative effect on Chinook salmon in the Skagit River. This suggests that a drop in water temperature or unseasonably cooler water was correlated with more Chinook salmon migrating. Air temperature had a strong positive effect on Chinook salmon in the Puyallup river (Figure 2.2b), suggesting that more Chinook salmon migrated when the air was warmer, though warm air can lead to cool water through snow melt.

2.4.2.4 Lunar phase

Lunar phase had a small positive effect (Figure 2.2b) on Chinook salmon in the Puyallup River, suggesting that Chinook salmon were more likely to migrate during the full moon.

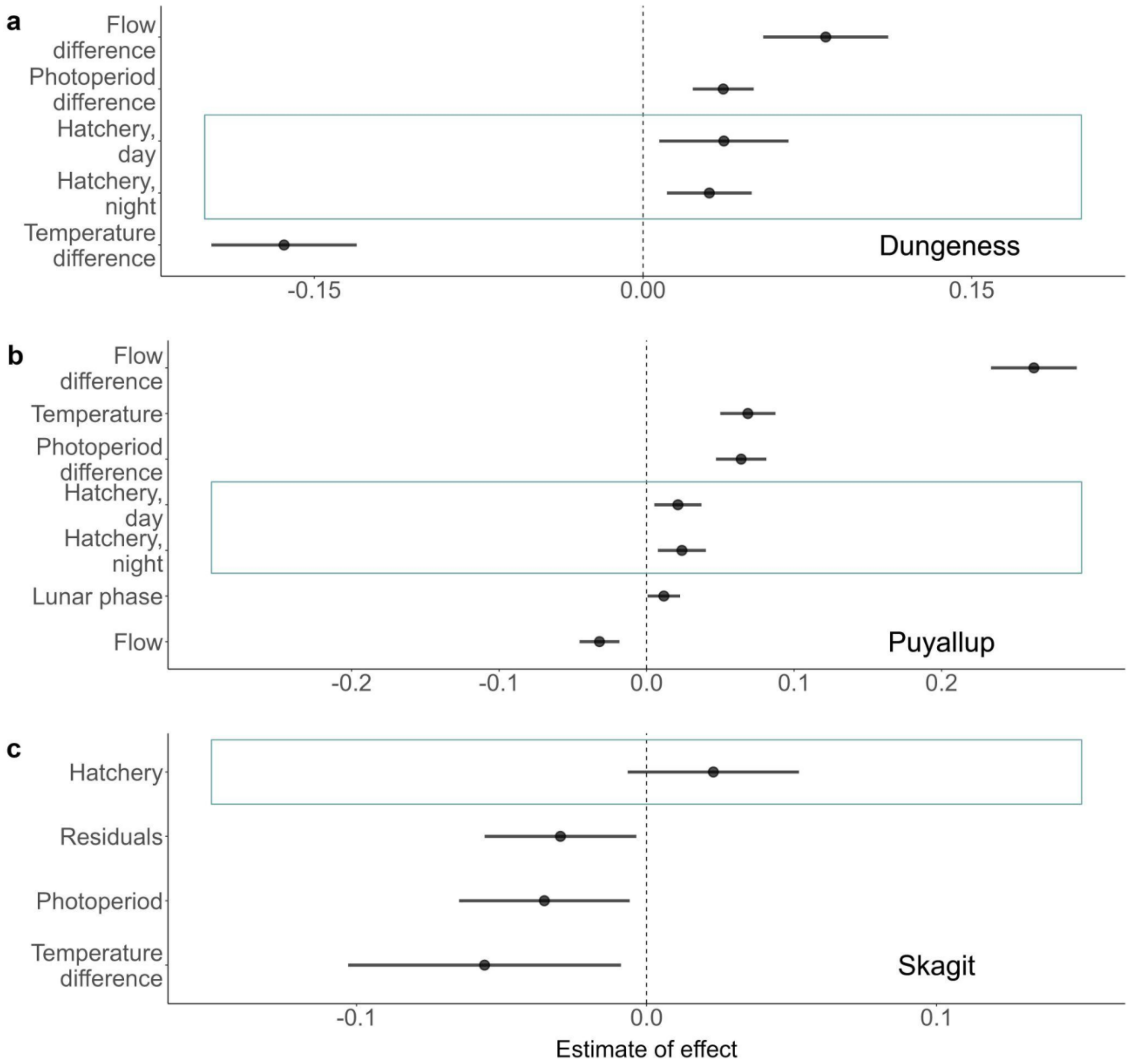

Figure 2.2. Estimates of the effect of different covariates in the best MARSS model or MARSS model with equal support for the number of wild Chinook salmon in the a) Dungeness, b) Puyallup, and c) Skagit rivers. Blue boxes indicate social variables associated with the pied piper hypothesis.

2.4.3 *Environmental effects, coho salmon*

2.4.3.1 Flow & Δ flow

Among all the covariates, flow difference or increase in the river’s flow had the strongest positive effect on the number of Chinook salmon migrating in the Dungeness and Puyallup rivers (Figure 2.3a, 2.3b). However, absolute flow had a small negative effect in the Puyallup River (Figure 2.3b). This suggests that when the flows are low, an increase in flow of the river from the previous day was correlated with more salmon migrating downstream. Flow was not a covariate in the top models in the Skagit River.

2.4.3.2 Photoperiod & Δ photoperiod

Photoperiod difference, or increase in day-length, also had a positive effect on the number of Chinook salmon migrating in the Dungeness and Puyallup rivers (Figure 2.3a,b). Photoperiod had a negative effect on Chinook salmon in the Skagit River (Figure 2.3c), indicating that as the season progressed and day length increased, the number of salmon migrating increased in two rivers but declined in the third.

2.4.3.3 Temperature, Δ temperature, & temperature residuals

Temperature difference, or change in water temperature from the previous day, had the strongest negative effect on the number of Chinook salmon migrating in the Dungeness and Skagit rivers (Figure 2.3a, c). The residuals of the model with temperature also had a negative effect on Chinook salmon in the Skagit River. This suggests that a drop in water temperature or unseasonably cooler water was correlated with more Chinook salmon migrating. Air temperature had a strong positive effect on Chinook salmon in the Puyallup river (Figure 2.3b), suggesting that more Chinook salmon migrated when the air was warmer, though warm air can lead to cool water through snow melt.

2.4.3.4 Lunar phase

Lunar phase had a small positive effect (Figure 2.3b) on Chinook salmon in the Puyallup River, suggesting that Chinook salmon were more likely to migrate during the full moon.

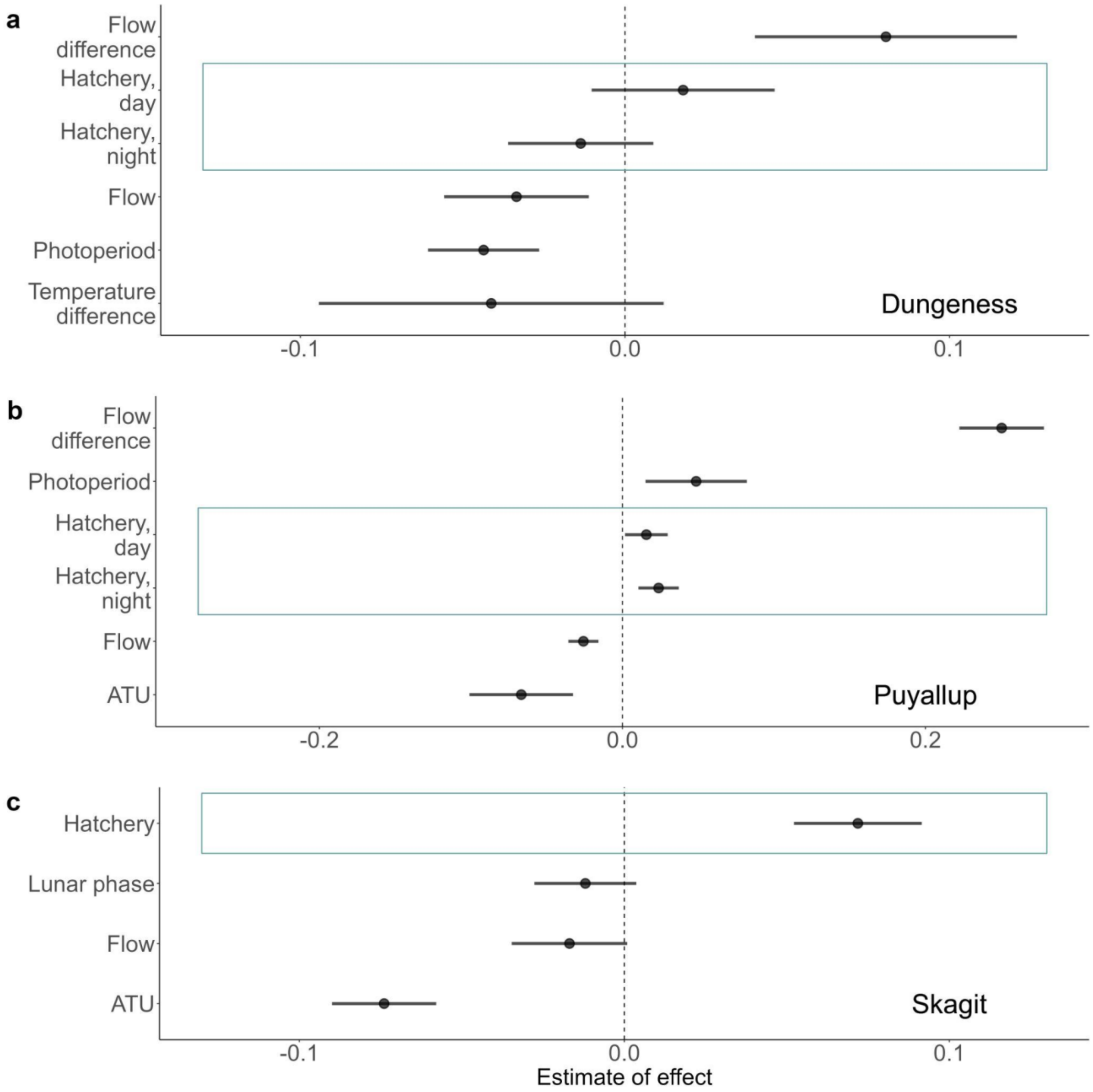

Figure 2.3. Estimates of the effect of different covariates in the best MARSS model or MARSS model with equal support for the number of wild coho salmon in the a) Dungeness, b) Puyallup, and c) Skagit rivers. Blue boxes indicate social variables associated with the pied piper hypothesis. Puyallup River coho results were similar when we excluded years with anomalously high proportions of unmarked hatchery smolts (Figure 2.12).

2.5 DISCUSSION

Our main objective was to determine if social information was important in the timing decisions of wild Chinook and coho salmon smolts during their seaward migration within the context of the many physical variables previously linked to migration of these species (Table 2.1). We hypothesized migrating hatchery smolts would stimulate wild smolts to join, therefore increasing the number of wild smolts migrating above that expected based on the contemporary environmental effects. In four of our six river-species combinations - Chinook salmon in the Dungeness and Puyallup rivers and coho salmon in the Puyallup and Skagit rivers - the number of hatchery smolts was an important variable with a positive statistical relationship with the number of wild salmon smolts, consistent with the pied piper hypothesis. Our results are supported by the visual observation that following hatchery releases of Chinook salmon in the Wenatchee River: wild Chinook smolts moved downstream along with the hatchery smolts unless they could not see the hatchery smolts (Hillman and Mullan 1989). Thus the weight of the evidence indicated an effect of social interactions with hatchery fish, though its magnitude varied among species and rivers, and the relative effects of different physical factors also varied among species and rivers.

For the Chinook salmon in the Dungeness and Puyallup rivers, and the coho salmon in the Puyallup and Skagit rivers, the results were consistent with the pied piper hypothesis that the numerous hatchery salmon smolts migrating downstream trigger the migration of wild salmon smolts. These social influences, however, are best understood in the context of the river’s environmental conditions (aspects of flow and temperature), time of year including photoperiod change, and lunar phase. In some cases (coho salmon in the Skagit River) the effect size of the hypothesized social influence was comparable to the environmental factors, whereas in other cases (Chinook salmon in the Dungeness and Puyallup rivers, and coho salmon in the Puyallup River) the effect of the social influence was smaller than the effect of the largest environmental factors, but as important. We did not find an effect of social influence in the coho salmon in the Dungeness River and the Chinook salmon in the Skagit rivers. Several factors may have contributed to the absence of detectable social cues. A large portion of the wild salmon smolts may have migrated before the hatchery fish were released. Alternatively, wild salmon may have relied more heavily on tributaries and were thus spatially isolated from the locations of hatchery releases, thereby diminishing the potential for interaction. Furthermore, some of the wild salmon may have been upstream of the hatchery release sites, and thus not exposed to the hatchery salmon.

We saw a markedly greater correlation between hatchery and wild Chinook salmon movements in the Dungeness and Puyallup rivers than in the Skagit River. Several factors might have influenced this difference. First, the temporal separation between fry and parr migration is clearer in the Dungeness and Puyallup rivers than in the Skagit river (Figure 2.4). This means that when subyearling Chinook salmon were released from the hatcheries on the Skagit River, fewer salmon remained to migrate, therefore reducing the pied piper effect. Second, when both hatchery and wild Chinook were present, the hatchery fish were much more numerous than the wild fish in the Dungeness and Puyallup rivers (Supplementary Information). In contrast, hatchery and wild Chinook salmon were similar in abundance in the Skagit River. Third, the Skagit River is much larger than the other two rivers (Figure 2.1) (e.g., Skagit River flows in May, when many smolts migrate, are ca. 4-5 times those in the Puyallup River and ca. 50 times those in the Dungeness River, based on USGS data), including many spawning and rearing areas that are not on the direct migration route from the hatchery to the trap. Furthermore, the Skagit River encompasses six independent populations of Chinook salmon monitored at the trap, whereas the Dungeness and Puyallup rivers each hold a single population (Ruckelshaus et al. 2006). We expect that all of these factors contribute to the greater influence of hatchery origin Chinook salmon in the Dungeness and Puyallup rivers than in the Skagit River.

We found a stronger statistical effect size of the number of hatchery coho salmon in the Skagit and Puyallup rivers than in the Dungeness River. The Dungeness and Puyallup rivers had similarly high ratios of hatchery to wild coho salmon so that attribute does not explain the result. As noted above, the Skagit River is much larger than the Dungeness and Puyallup rivers but it is not obvious why that might matter in this case. Some aspect of the distribution of breeding and fry emergence (primarily in the tributaries of the Skagit River rather than the river itself (Austin, Torgersen, and Quinn 2023)), and their subsequent rearing and movements, presumably contributes to these patterns.

Previous studies reported that temperature experience (Sykes, Johnson, and Shrimpton 2009), stream temperatures (Roper and Scarnecchia 1999), and temperature residuals (Scheuerell, Zabel, and Sandford 2009) strongly influenced the migration of Chinook salmon. Temperature difference and temperature residuals had the strongest (negative) effect on the number of wild Chinook salmon in the Dungeness and Skagit rivers, respectively. Thus a drop in water temperature or unseasonably cooler water seemed to cause Chinook salmon parr to migrate, as can occur when rivers rise with melting snow after an increase in air temperatures or rain on snow events (Leach and Moore 2014). In line with this expectation, in the Puyallup River, air temperature had a strong positive effect on the number of Chinook salmon migrating. The correlation between a drop in water temperature and the increase in the number of salmon smolts migrating has previously been shown (Hvidsten et al. 1995; Spence and Dick 2014). This was contrary to our expectation since warmer temperatures resulted in earlier migration in Chinook salmon (Sykes, Johnson, and Shrimpton 2009). Similarly, we found that ATU had a negative effect on the number of wild coho salmon migrating in the Puyallup and Skagit rivers. Similar patterns of negative effect of degree days were shown in coho salmon in Deer Creek, Oregon (Spence and Dick 2014). We found that flow difference had the strongest effect on both Chinook and coho salmon, in the Dungeness and Puyallup rivers. However, flow difference was not a covariate in the best model for Chinook or coho salmon in the Skagit River. This might be because the Skagit River has several dams that affect flows, whereas the Dungeness River does not currently have any dams. The Puyallup River has one dam and its floodplain habitat is more degraded than the other rivers. Its flow varies widely, and so an increase in the flow can provide a cue for migration.

Although the data from salmon traps are highly appropriate for the purposes of our study, and collected “blind” with respect to our hypotheses, there remain some limitations to our data that warrant consideration. First, analyses assume that all unmarked individuals are ‘wild’, which we explored by looking at the correlation between the number of unmarked hatchery salmon released and the number of wild salmon caught in the traps (Figure 2.4). We found only a low-to-moderate correlation between the two, implying that the increase in the number of wild salmon was not because of the unmarked hatchery salmon. Second, the time scale at which data is collected by the traps might not be the time scale of the social influence we tried to study. If wild salmon respond to the hatchery salmon immediately or within a few hours, the effect of this social influence would be diluted by recording data only every 12 hours. Third, we could not distinguish between wild smolts being led by hatchery fish (pied piper hypothesis) or those wild smolts being displaced – wild smolts leaving their in-river holding areas due to an influx of hatchery fish entering those holding areas – downstream by hatchery smolts. Fourth, although we attempted to account for common environmental cues, we cannot exclude the possibility that both hatchery and wild fish responded to stimuli external to our model, rather than hatchery fish causing wild fish to migrate. Finally, the suspension of trap operations following a hatchery release resulted in the loss of valuable data – in particular data most likely to add support for the pied piper hypothesis – so our results may reflect a lower bound on the effect.

Despite the limitations of the dataset and the potential dilution of the effect caused by missing data and the time resolution of the data, our results suggest that along with environmental covariates, social information appears to provide additional cues for salmon seaward migration. This suggests that future studies, in addition to considering environmental cues, should consider social cues from both hatchery and wild conspecifics while studying migration timing of salmon smolts. If large hatchery releases motivate the wild salmon smolts to migrate with them, this can have fundamental ecological consequences. Wild salmon smolts that are being influenced by hatchery salmon smolts might migrate earlier than they normally would, encounter less than optimal foraging conditions and could encounter more predators, thereby experiencing higher mortality at sea (Scheuerell, Zabel, and Sandford 2009). On the other hand, wild salmon out migrating with the hatchery salmon might benefit from predator swamping (Furey, Martins, and Hinch 2021).

Showing that salmon smolts use social information, especially that from hatchery conspecifics, can have implications for conservation and management of these species that are commercially and culturally important. Salmon hatcheries were set up in response to overfishing, the continued loss of habitat, and other factors decreasing salmon runs and they provide many sociocultural and economic benefits. While the goals of the hatcheries were to either increase abundance for fishing or, later, to promote conservation of imperiled populations, they can have unintended ecological consequences on the wild populations (Naish et al. 2007; Maynard and Trial 2014; Bottom 1997). Therefore, reforming hatcheries to maximize the benefit and minimize the risk on wild populations is crucial (Anderson et al. 2020). Our study highlights another avenue by which hatcheries could indirectly impact wild salmon populations. To reduce the impact of hatchery releases on the migration timing of wild salmon, hatcheries could experiment with different release strategies. For example, hatcheries can consider timing their releases towards the end of the migration period of the wild salmon or consider releasing the hatchery salmon more downstream of the wild salmon habitat. Some hatcheries are moving to volitional releases, which may spread the migration of hatchery smolts over a longer period of time (Johnson, Murdoch, and Moran 2015). This practice may reduce the pied piper effect, if the wild smolts respond to a large threshold number of hatchery smolts, or may increase the pied piper effect, by providing a longer social cue to influence the wild smolts. Our results suggest that managers should monitor changes in wild smolt migration timing patterns as they experiment with release practices.

Our findings, consistent with Pacific salmon smolts using social information when timing migrations, fit two nascent patterns in the field of collective behavior, with possible population-level implications. First, our results support an increasing recognition of the importance of sociality in salmon, from navigation (Berdahl, Westley, et al. 2016; Okasaki et al. 2020) to trophic interactions (Polyakov et al. 2022). Second, and more generally, our results expand a growing body of literature documenting the importance of social information on timing decisions in a wide range of taxa (Oestreich et al. 2022; Berdahl, Westley, and Quinn 2017; Dibnah et al. 2022; Gall et al. 2017; Helm, Piersma, and van der Jeugd 2006; Sandlund et al. 2017). It remains to be seen if, and how, collective timing decisions may improve the accuracy of those decisions (Kao et al., n.d.). If salmon, and other species, do improve decision making by using social information, especially during fitness-critical events such as migration, reductions in population size are expected to decrease decision making ability and thereby feedback on further population decline, possibly contributing to population crashes (Berdahl, Van Leeuwen, et al. 2016; Fagan et al. 2012; Granger and Johnsen 2022). We hope our results encourage more studies exploring social influence on timing decisions and the potential population-level implications.

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2.7 REFERENCES

Aikens, Ellen O., Iris D. Bontekoe, Lara Blumenstiel, Anna Schlicksupp, and Andrea Flack. 2022. “Viewing Animal Migration through a Social Lens.” *Trends in Ecology & Evolution* 37 (11): 985–96. https://doi.org/10.1016/j.tree.2022.06.008.

Anderson, Joseph H, Kenneth I Warheit, Bethany E Craig, Todd R Seamons, and Alf H Haukenes. 2020. “A Review of Hatchery Reform Science in Washington State.” *Washington Department of Fish and Wildlife*, Final report to the Washington Fish and Wildlife Commission, , January.

Austin, Catherine S., Christian E. Torgersen, and Thomas P. Quinn. 2023. “Who Spawns Where? Temperature, Elevation, and Discharge Differentially Affect the Distribution of Breeding by Six Pacific Salmonids within a Large River Basin.” *Canadian Journal of Fisheries and Aquatic Sciences* 80 (8): 1365–84. https://doi.org/10.1139/cjfas-2022-0252.

Baert, Jan M, Eric W M Stienen, Frederick Verbruggen, Nico Van De Weghe, Luc Lens, and Wendt Müller. 2022. “Resource Predictability Drives Interannual Variation in Migratory Behavior in a Long-Lived Bird.” Edited by Leigh W Simmons. *Behavioral Ecology* 33 (1): 263–70. https://doi.org/10.1093/beheco/arab132.

Berdahl, Andrew, Albert B. Kao, Andrea Flack, Peter A. H. Westley, Edward A. Codling, Iain D. Couzin, Anthony I. Dell, and Dora Biro. 2018. “Collective Animal Navigation and Migratory Culture: From Theoretical Models to Empirical Evidence.” *Philosophical Transactions: Biological Sciences* 373 (1746): 1–16.

Berdahl, Andrew, Anieke Van Leeuwen, Simon A. Levin, and Colin J. Torney. 2016. “Collective Behavior as a Driver of Critical Transitions in Migratory Populations.” *Movement Ecology* 4 (1): 18. https://doi.org/10.1186/s40462-016-0083-8.

Berdahl, Andrew, Peter A H Westley, Simon A Levin, Iain D Couzin, and Thomas P. Quinn. 2016. “A Collective Navigation Hypothesis for Homeward Migration in Anadromous Salmonids.” *Fish and Fisheries* 17 (2): 525–42. https://doi.org/10.1111/faf.12084.

Berdahl, Andrew, Peter A. H. Westley, and Thomas P. Quinn. 2017. “Social Interactions Shape the Timing of Spawning Migrations in an Anadromous Fish.” *Animal Behaviour* 126 (April):221–29. https://doi.org/10.1016/j.anbehav.2017.01.020.

Biro, Dora, David J. T. Sumpter, Jessica Meade, and Tim Guilford. 2006. “From Compromise to Leadership in Pigeon Homing.” *Current Biology* 16 (21): 2123–28. https://doi.org/10.1016/j.cub.2006.08.087.

Björnsson, Björn Thrandur, Sigurd O. Stefansson, and Stephen D. McCormick. 2011. “Environmental Endocrinology of Salmon Smoltification.” *General and Comparative Endocrinology* 170 (2): 290–98. https://doi.org/10.1016/j.ygcen.2010.07.003.

Bottom, Daniel L. 1997. “To till the Water—a History of Ideas in Fisheries Conservation.” In *Pacific Salmon & Their Ecosystems: Status and Future Options*, edited by Deanna J. Stouder, Peter A. Bisson, and Robert J. Naiman, 569–97. New York: Chapman and Hall. https://doi.org/10.1007/978-1-4615-6375-4_31.

Clausen, Kevin Kuhlmann, and Preben Clausen. 2013. “Earlier Arctic Springs Cause Phenological Mismatch in Long-Distance Migrants.” *Oecologia* 173 (3): 1101–12. https://doi.org/10.1007/s00442-013-2681-0.

Claussen, Julie E., and David P. Philipp. 2023. “Assessing the Role of Supplementation

Stocking: A Perspective.” *Fisheries Management and Ecology* 30 (6): 583–91. https://doi.org/10.1111/fme.12573.

Cooney, Robert T., J. R. Allen, M. A. Bishop, D. L. Eslinger, T. Kline, B. L. Norcross, C. P. Mcroy, et al. 2001. “Ecosystem Controls of Juvenile Pink Salmon (*Oncorhynchus Gorbuscha*) and Pacific Herring (*Clupea Pallasi*) Populations in Prince William Sound, Alaska.” *Fisheries Oceanography* 10 (s1): 1–13. https://doi.org/10.1046/j.1054-6006.2001.00039.x.

Couzin, Iain D. 2018. “Collective Animal Migration.” *Current Biology* 28 (17): R976–80. https://doi.org/10.1016/j.cub.2018.04.044.

Dibnah, Alex J., James E. Herbert-Read, Neeltje J. Boogert, Guillam E. McIvor, Jolle W. Jolles, and Alex Thornton. 2022. “Vocally Mediated Consensus Decisions Govern Mass Departures from Jackdaw Roosts.” *Current Biology* 32 (10): R455–56. https://doi.org/10.1016/j.cub.2022.04.032.

Dingle, Hugh. 2014. *Migration: The Biology of Life on the Move*. Oxford University Press.

Downton, Mary W, and Kathleen A Miller. 1998. “Relationships between Alaskan Salmon Catch and North Pacific Climate on Interannual and Interdecadal Time Scales.” *Canadian Journal of Fisheries and Aquatic Sciences* 55 (10): 2255–65. https://doi.org/10.1139/f98-106.

Fagan, William F., Robert Stephen Cantrell, Chris Cosner, Thomas Mueller, and Andrew E. Noble. 2012. “Leadership, Social Learning, and the Maintenance (or Collapse) of Migratory Populations.” *Theoretical Ecology* 5 (2): 253–64. https://doi.org/10.1007/s12080-011-0124-2.

Furey, Nathan B., Eduardo G. Martins, and Scott G. Hinch. 2021. “Migratory Salmon Smolts Exhibit Consistent Interannual Depensatory Predator Swamping: Effects on Telemetry-Based Survival Estimates.” *Ecology of Freshwater Fish* 30 (1): 18–30. https://doi.org/10.1111/eff.12556.

Gall, Gabriella E. C., Ariana Strandburg-Peshkin, Tim Clutton-Brock, and Marta B. Manser. 2017. “As Dusk Falls: Collective Decisions about the Return to Sleeping Sites in Meerkats.” *Animal Behaviour* 132 (October):91–99. https://doi.org/10.1016/j.anbehav.2017.08.001.

Granger, Jesse, and Sönke Johnsen. 2022. “Collective Movement as a Solution to Noisy Navigation and Its Vulnerability to Population Loss.” *Proceedings of the Royal Society B: Biological Sciences* 289 (1987): 20221910. https://doi.org/10.1098/rspb.2022.1910.

Guttal, Vishwesha, and Iain D. Couzin. 2010. “Social Interactions, Information Use, and the Evolution of Collective Migration.” *Proceedings of the National Academy of Sciences* 107 (37): 16172–77. https://doi.org/10.1073/pnas.1006874107.

Hansen, Lars P., and Bror Jonsson. 1985. “Downstream Migration of Hatchery-Reared Smolts of Atlantic Salmon (*Salmo Salar* L.) in the River Imsa, Norway.” *Aquaculture*, Salmonid Smoltification II, 45 (1): 237–48. https://doi.org/10.1016/0044-8486(85)90273-X.

Helm, Barbara, Theunis Piersma, and Henk van der Jeugd. 2006. “Sociable Schedules: Interplay between Avian Seasonal and Social Behaviour.” *Animal Behaviour* 72 (2): 245–62. https://doi.org/10.1016/j.anbehav.2005.12.007.

Hillman, T. W., and J. W. Mullan. 1989. “Effect of Hatchery Releases on the Abundance and Behavior of Wild Juvenile Salmonids.” Final Report to Chelan County Public Utility District. Summer and Winter Ecology of Juvenile Chinook Salmon and Steelhead Trout in the Wenatchee River, Washington. McCall, Idaho: Don Chapman Consultants.

Hinrichsen, Richard, and Elizabeth Holmes. 2009. “Using Multivariate State-Space Models to Study Spatial Structure and Dynamics.” *Spatial Ecology*, August, 145–66. https://doi.org/10.1201/9781420059861.ch8.

Hoar, William S. 1958. “The Evolution of Migratory Behaviour among Juvenile Salmon of the Genus *Oncorhynchus*.” *Journal of the Fisheries Research Board of Canada* 15 (3): 391–428. https://doi.org/10.1139/f58-020.

———. 1976. “Smolt Transformation: Evolution, Behavior, and Physiology.” *Journal of the Fisheries Research Board of Canada* 33 (5): 1233–52. https://doi.org/10.1139/f76-158.

Holmes, Elizabeth, E., Eric Ward J., and Kellie Wills. 2012. “MARSS: Multivariate Autoregressive State-Space Models for Analyzing Time-Series Data.” *The R Journal* 4 (1): 11. https://doi.org/10.32614/RJ-2012-002.

Hvidsten, Nils Arne, Arne J. Jensen, Helga Vivas, Bakke Oyvind, and Tor G. Heggberget. 1995. “Downstream Migration of Atlantic Salmon Smolts in Relation to Water Flow, Water Temperature, Moon Phase and Social Interaction.” *Nordic Journal of Freshwater Research*, no. 70, 38–48.

James, Samantha E., Beau Doherty, Sean P. Cox, Isobel A. Pearsall, and Brian Riddell. 2023. “Size and Timing of Hatchery Releases Influence Juvenile-to-Adult Survival Rates of British Columbia Chinook (*Oncorhynchus Tshawytscha*) and Coho (*Oncorhynchus Kisutch*) Salmon.” *Canadian Journal of Fisheries and Aquatic Sciences* 80 (4): 700–718. https://doi.org/10.1139/cjfas-2022-0121.

Johnson, McLain S., Andrew R. Murdoch, and Christopher P. H. Moran. 2015. “Adult Survival of Hatchery Spring Chinook Salmon Released Volitionally or Forcibly as Juveniles.” *North American Journal of Aquaculture* 77 (4): 547–50. https://doi.org/10.1080/15222055.2015.1069429.

Kano, Fumihiro, Takao Sasaki, and Dora Biro. 2021. “Collective Attention in Navigating Homing Pigeons: Group Size Effect and Individual Differences.” *Animal Behaviour* 180 (October):63–80. https://doi.org/10.1016/j.anbehav.2021.08.004.

Kao, Albert B., Shoubhik Banerjee, Fritz Francisco, and Andrew Berdahl. n.d. “Timing Decisions as the next Frontier for Collective Intelligence.” https://doi.org/10.48550/arXiv.2312.02187.

Keeley, Ernest R. 2001. “Demographic Responses to Food and Space Competition by Juvenile Steelhead Trout.” *Ecology* 82 (5): 1247–59. https://doi.org/10.1890/0012-9658(2001)082[1247:DRTFAS]2.0.CO;2.

Kennedy, G. J. A., C. D. Strange, R. J. D. Anderson, and P. M. Johnston. 1984. “Experiments on the Descent and Feeding of Hatchery-Reared Salmon Smolts (*Salmo Salar* L.) in the River Bush.” *Aquaculture Research* 15 (1): 15–25. https://doi.org/10.1111/j.1365-2109.1984.tb00578.x.

Larkin, P. A., and A. Walton. 1969. “Fish School Size and Migration.” *Journal of the Fisheries Research Board of Canada* 26 (5): 1372–74. https://doi.org/10.1139/f69-121.

Leach, J. A., and R. D. Moore. 2014. “Winter Stream Temperature in the Rain-on-Snow Zone of the Pacific Northwest: Influences of Hillslope Runoff and Transient Snow Cover.” *Hydrology and Earth System Sciences* 18 (2): 819–38. https://doi.org/10.5194/hess-18-819-2014.

Link, Michael R., and Karl K. English. 2000. “Long-Term, Sustainable Monitoring of Pacific Salmon Populations Using Fishwheels to Integrate Harvesting, Management, and Research.” In *Sustainable Fisheries Management*, edited by E. Eric Knudsen and Donald

McDonald, 667–74. CRC Press.

Maynard, Desmond J., and Joan G. Trial. 2014. “The Use of Hatchery Technology for the Conservation of Pacific and Atlantic Salmon.” *Reviews in Fish Biology and Fisheries* 24 (3): 803–17. https://doi.org/10.1007/s11160-013-9341-7.

McCormick, Stephen D. 1994. “Ontogeny and Evolution of Salinity Tolerance in Anadromous Salmonids: Hormones and Heterochrony.” *Estuaries* 17 (1): 26. https://doi.org/10.2307/1352332.

McDonald, J. 1960. “The Behaviour of Pacific Salmon Fry during Their Downstream Migration to Freshwater and Saltwater Nursery Areas.” *Journal of the Fisheries Research Board of Canada* 17 (5): 655–76. https://doi.org/10.1139/f60-051.

McMillan, John R., Brian Morrison, Nick Chambers, Greg Ruggerone, Louis Bernatchez, Jack Stanford, and Helen Neville. 2023. “A Global Synthesis of Peer-Reviewed Research on the Effects of Hatchery Salmonids on Wild Salmonids.” *Fisheries Management and Ecology* 30 (5): 446–63. https://doi.org/10.1111/fme.12643.

Melnychuk, Michael C, and David W Welch. 2018. “Habitat-Mediated Effects of Diurnal and Seasonal Migration Strategies on Juvenile Salmon Survival.” *Behavioral Ecology* 29 (6): 1340–50. https://doi.org/10.1093/beheco/ary119.

Munsch, Sh, Jr Cordell, and Jd Toft. 2016. “Fine-Scale Habitat Use and Behavior of a Nearshore Fish Community: Nursery Functions, Predation Avoidance, and Spatiotemporal Habitat Partitioning.” *Marine Ecology Progress Series* 557 (September):1–15. https://doi.org/10.3354/meps11862.

Naish, Kerry A., Joseph E. Taylor, Phillip S. Levin, Thomas P. Quinn, James R. Winton, Daniel Huppert, and Ray Hilborn. 2007. “An Evaluation of the Effects of Conservation and Fishery Enhancement Hatcheries on Wild Populations of Salmon.” In *Advances in Marine Biology*, 53:61–194. Academic Press. https://doi.org/10.1016/S0065-2881(07)53002-6.

Noakes, Donald J. 2014. “Overview of Salmon and Their Ecological and Economic Importance.” In *Salmon. Biology, Ecological Impacts and Economic Importance*, edited by Patrick T. K. Woo and Donald J. Noakes, 1–10. Nova Science Publishers.

Oestreich, William K., Kanoe M. Aiu, Larry B. Crowder, Megan F. McKenna, Andrew Berdahl, and Briana Abrahms. 2022. “The Influence of Social Cues on Timing of Animal Migrations.” *Nature Ecology & Evolution* 6 (11): 1617–25. https://doi.org/10.1038/s41559-022-01866-0.

Oestreich, William K., James A. Fahlbusch, David E. Cade, John Calambokidis, Tetyana Margolina, John Joseph, Ari S. Friedlaender, et al. 2020. “Animal-Borne Metrics Enable Acoustic Detection of Blue Whale Migration.” *Current Biology* 30 (23): 4773-4779.e3. https://doi.org/10.1016/j.cub.2020.08.105.

Okasaki, Connie, Matthew L. Keefer, Peter A. H. Westley, and Andrew Berdahl. 2020. “Collective Navigation Can Facilitate Passage through Human-Made Barriers by Homeward Migrating Pacific Salmon.” *Proceedings of the Royal Society B: Biological Sciences* 287 (1937): 20202137. https://doi.org/10.1098/rspb.2020.2137.

Polyakov, Anne Y., Thomas P. Quinn, Katherine W. Myers, and Andrew Berdahl. 2022. “Group Size Affects Predation Risk and Foraging Success in Pacific Salmon at Sea.” *Science Advances* 8 (26): eabm7548. https://doi.org/10.1126/sciadv.abm7548.

Quinn, Thomas P. 2018. *The Behavior and Ecology of Pacific Salmon and Trout*. 2nd ed. Seattle: University of Washington Press.

Reppert, Steven M., Patrick A. Guerra, and Christine Merlin. 2016. “Neurobiology of Monarch Butterfly Migration.” *Annual Review of Entomology* 61 (1): 25–42. https://doi.org/10.1146/annurev-ento-010814-020855.

Roberts, L. J., J. Taylor, P. J. Gough, D. W. Forman, and C. Garcia De LEANIZ. 2009. “Night Stocking Facilitates Nocturnal Migration of Hatchery-Reared Atlantic Salmon, Salmo Salar, Smolts.” *Fisheries Management and Ecology* 16 (1): 10–13. https://doi.org/10.1111/j.1365-2400.2008.00611.x.

Roper, Brett B, and Dennis L Scarnecchia. 1999. “Emigration of Age-0 Chinook Salmon (*Oncorhynchus Tshawytscha*) Smolts from the Upper South Umpqua River Basin, Oregon, U.S.A.” *Canadian Journal of Fisheries and Aquatic Sciences* 56 (6): 939–46. https://doi.org/10.1139/f99-023.

Ruckelshaus, Mary, Ken Currens, William Graeber, Robert Fuerstenberg, Kit Rawson, Norma Sands, and Jim Scott. 2006. “Independent Populations of Chinook Salmon in Puget Sound.” *NOAA Technical Memorandum NMFS-NWFSC-78.*

Sabo, J L, and G B Pauley. 1997. “Competition between Stream-Dwelling Cutthroat Trout (*Oncorhynchus Clarki*) and Coho Salmon (*Oncorhynchus Kisutch*): Effects of Relative Size and Population Origin” 54.

Sandlund, Odd Terje, Ola H. Diserud, Russell Poole, Knut Bergesen, Mary Dillane, Gerard Rogan, Caroline Durif, Eva B. Thorstad, and Leif Asbjørn Vøllestad. 2017. “Timing and Pattern of Annual Silver Eel Migration in Two European Watersheds Are Determined by Similar Cues.” *Ecology and Evolution* 7 (15): 5956–66. https://doi.org/10.1002/ece3.3099.

Scheuerell, Mark D., Richard W. Zabel, and Benjamin P. Sandford. 2009. “Relating Juvenile Migration Timing and Survival to Adulthood in Two Species of Threatened Pacific Salmon (*Oncorhynchus* Spp.).” *Journal of Applied Ecology* 46 (5): 983–90. https://doi.org/10.1111/j.1365-2664.2009.01693.x.

Simmons, Olivia M., Stephen D. Gregory, Phillipa K. Gillingham, William D. Riley, Luke J. Scott, and J. Robert Britton. 2021. “Biological and Environmental Influences on the Migration Phenology of Atlantic Salmon *Salmo Salar* Smolts in a Chalk Stream in Southern England.” *Freshwater Biology* 66 (8): 1581–94. https://doi.org/10.1111/fwb.13776.

Spence, Brian C., and E.J. Dick. 2014. “Geographic Variation in Environmental Factors Regulating Outmigration Timing of Coho Salmon (*Oncorhynchus Kisutch*) Smolts.” *Canadian Journal of Fisheries and Aquatic Sciences* 71 (1): 56–69. https://doi.org/10.1139/cjfas-2012-0479.

Spence, Brian C., and James D. Hall. 2010. “Spatiotemporal Patterns in Migration Timing of Coho Salmon (*Oncorhynchus Kisutch*) Smolts in North America.” Edited by Ian Fleming. *Canadian Journal of Fisheries and Aquatic Sciences* 67 (8): 1316–34. https://doi.org/10.1139/F10-060.

Sykes, Gregory E., Chris J. Johnson, and J. Mark Shrimpton. 2009. “Temperature and Flow Effects on Migration Timing of Chinook Salmon Smolts.” *Transactions of the American Fisheries Society* 138 (6): 1252–65. https://doi.org/10.1577/T08-180.1.

Taylor, Eric B. 1991. “Behavioural Interaction and Habitat Use in Juvenile Chinook, *Oncorhynchus Tshawytscha*, and Coho, *O. Kisutch*, Salmon.” *Animal Behaviour* 42 (5): 729–44. https://doi.org/10.1016/S0003-3472(05)80119-8.

Teichert, Nils, Jean-Philippe Benitez, Arnaud Dierckx, Stéphane Tétard, Eric Oliveira, Thomas

Trancart, Eric Feunteun, and Michaël Ovidio. 2020. “Development of an Accurate Model to Predict the Phenology of Atlantic Salmon Smolt Spring Migration.” *Aquatic Conservation: Marine and Freshwater Ecosystems* 30 (8): 1552–65. https://doi.org/10.1002/aqc.3382.

Trenberth, Kevin E., and James W. Hurrell. 1994. “Decadal Atmosphere-Ocean Variations in the Pacific.” *Climate Dynamics* 9 (6): 303–19. https://doi.org/10.1007/BF00204745.

Visser, Marcel E., and Phillip Gienapp. 2019. “Evolutionary and Demographic Consequences of Phenological Mismatches.” *Nature Ecology & Evolution* 3 (6): 879–85. https://doi.org/10.1038/s41559-019-0880-8.

Volkhardt, Gregory C., Steven L. Johnson, Bruce A. Miller, Thomas E. Nickelson, and David E. Seiler. 2007. “Rotary Screw Traps and Inclined Plane Screen Traps.” In *Salmonid Field Protocols Handbook: Techniques for Assessing Status and Trends in Salmon and Trout Populations*, by David H. Johnson, Brianna M. Shrier, Jennifer S. O’Neal, John A. Knutzen, Xanthippe Augerot, Thomas A. O’Neil, and Todd N. Pearsons, 235–66. Bethesda, MD : Portland, Or: American Fisheries Society ; State of the Salmon.

Wilson, Samantha M., Thomas W. Buehrens, Jennifer L. Fisher, Kyle L. Wilson, and Jonathan W. Moore. 2021. “Phenological Mismatch, Carryover Effects, and Marine Survival in a Wild Steelhead Trout *Oncorhynchus Mykiss* Population.” *Progress in Oceanography* 193 (April):102533. https://doi.org/10.1016/j.pocean.2021.102533.

Young, Kyle A. 2004. “Asymmetric Competition, Habitat Selection, and Niche Overlap in Juvenile Salmonids.” *Ecology* 85 (1): 134–49. https://doi.org/10.1890/02-0402.

2.8 SUPPLEMENTARY INFORMATION

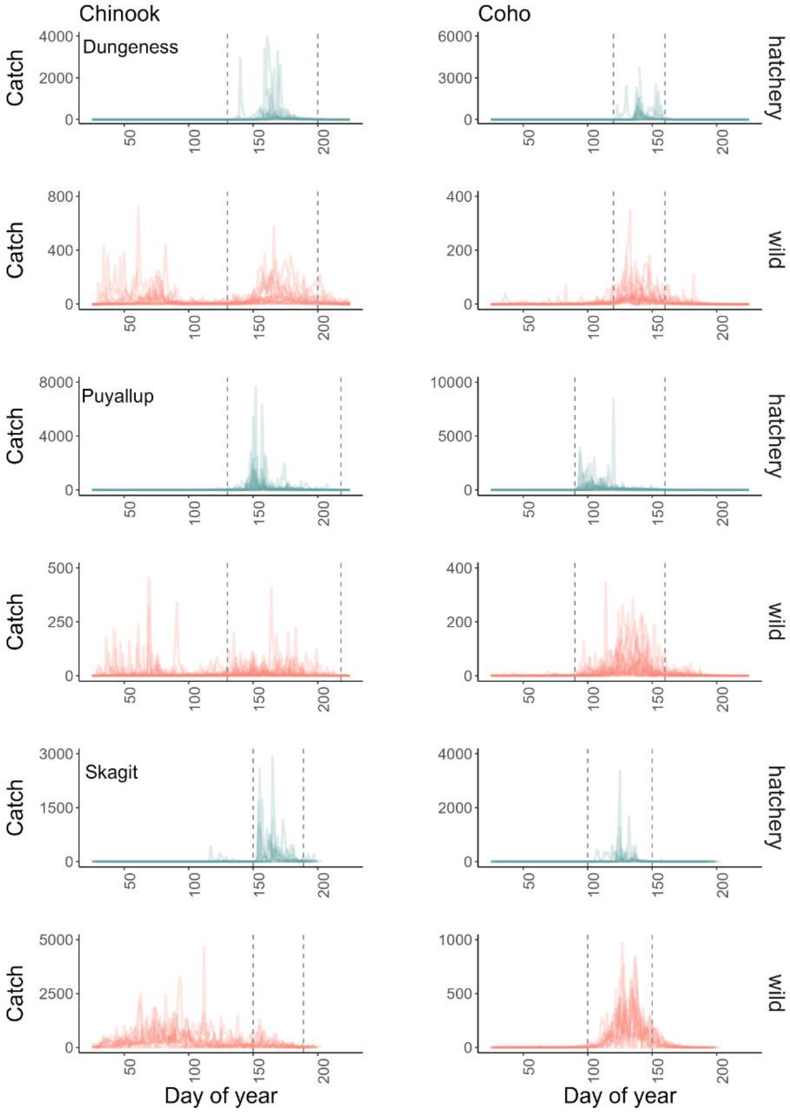


Figure 2.4. Daily catches for hatchery and wild sub-yearling Chinook salmon, hatchery and wild yearling coho salmon in the Dungeness (years 2005-2020), Puyallup (years 2004-2021), and Skagit rivers (years 2010-2022). Raw data without interpolation from every year available is overlaid. The vertical dashed lines bracket the period when both hatchery and wild salmon were caught in the trap, which was the portion of data we used for the analysis.

Table 2.2. Total and maximum number of fish caught in the trap during the days and years used in our analysis.

River	Species	Origin	Total number caught	Max number caught
Dungeness	Chinook	hatchery	62146	3274
Dungeness	Chinook	wild	42836	355
Dungeness	Coho	hatchery	60173	1983
Dungeness	Coho	wild	17653	348
Puyallup	Chinook	hatchery	153030	7429
Puyallup	Chinook	wild	15360	342
Puyallup	Coho	hatchery	81903	3921
Puyallup	Coho	wild	1975	126
Skagit	Chinook	hatchery	51332	2912
Skagit	Chinook	wild	47285	982
Skagit	Coho	hatchery	29207	3364
Skagit	Coho	wild	83347	976

2.8.1 *Unmarked hatchery salmon*

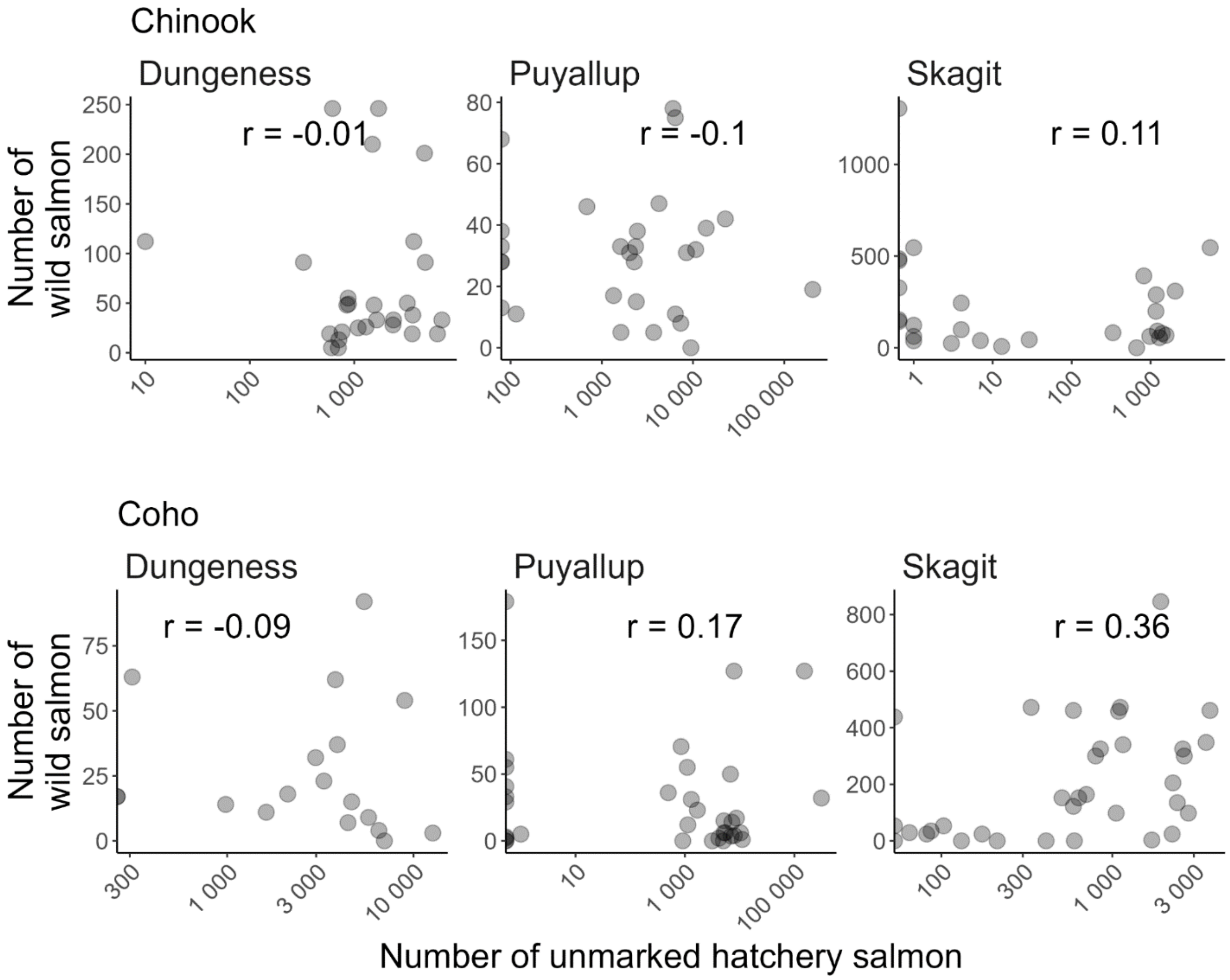


Figure 2.5. Correlation between unmarked hatchery salmon and wild salmon for Chinook and coho salmon in the Dungeness, Puyallup, and Skagit rivers. Each data point represents a day with the maximum number of hatchery salmon caught in the trap within ten days of a hatchery release. Note log scale on the x-axis.

2.8.2 *Proportion of day vs. night migrants*

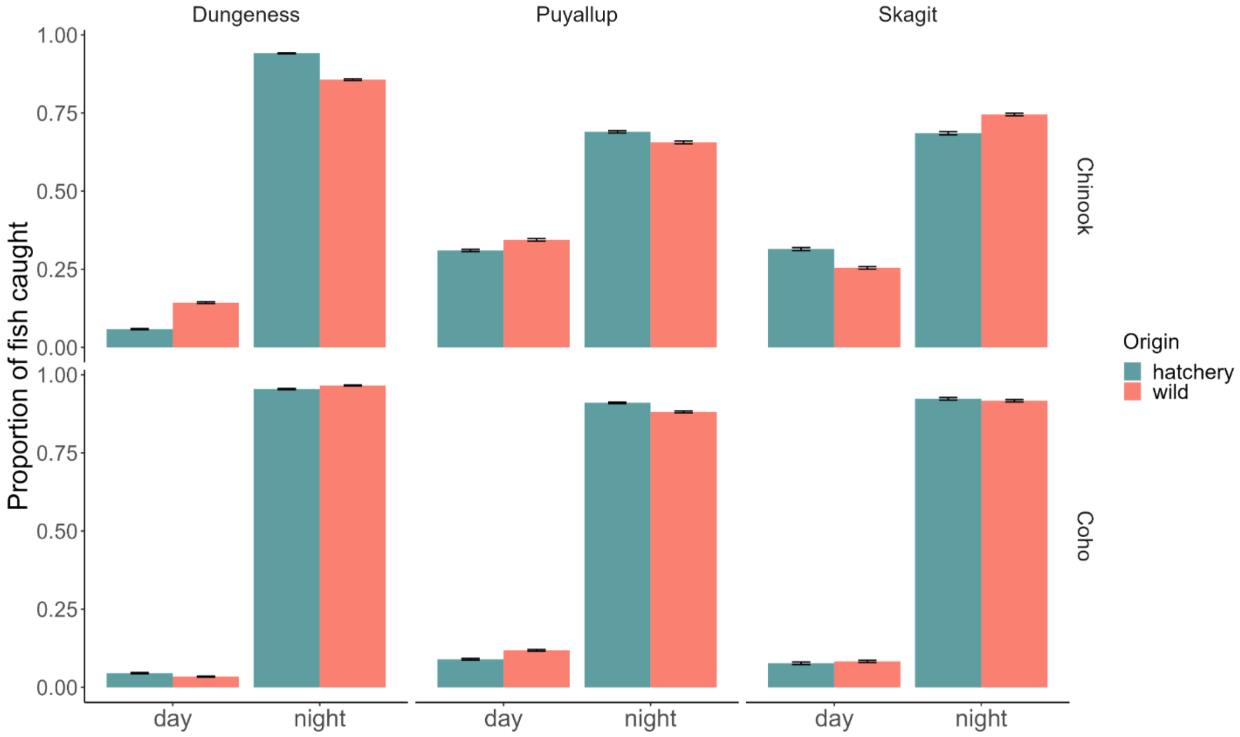


Figure 2.6. Average proportion of Chinook salmon and coho salmon caught in the trap at night vs. day in all three rivers.

2.8.3 *Dungeness River*

The Dungeness River is a 45-km river in the northwest part of Washington State. It originates in the Olympic Mountains and drains into the Strait of Juan de Fuca. The Dungeness River is fed through melting snowpack from the Olympic Mountains and by rain. The lowest flows are in August-September whereas the highest temperature is around 15° C in July-August. The Dungeness River supports seven species of salmonids - Chinook, coho, chum and pink salmon, steelhead, cutthroat and bull trout. There are multiple hatcheries that release Chinook and coho salmon and steelhead into the river at various stages. The Dungeness River hatchery, Gray Wolf, Hurd Creek, and Upper Dungeness Hatchery are the main hatcheries on the Dungeness River. A rotary screw trap is used to monitor juvenile salmon that migrate from their natal site to the ocean. The trap, operated by the Washington Department of Fish and Wildlife (WDFW), is located about 1.6 km upstream of the Strait of Juan De Fuca (48.1441, -123.1283).

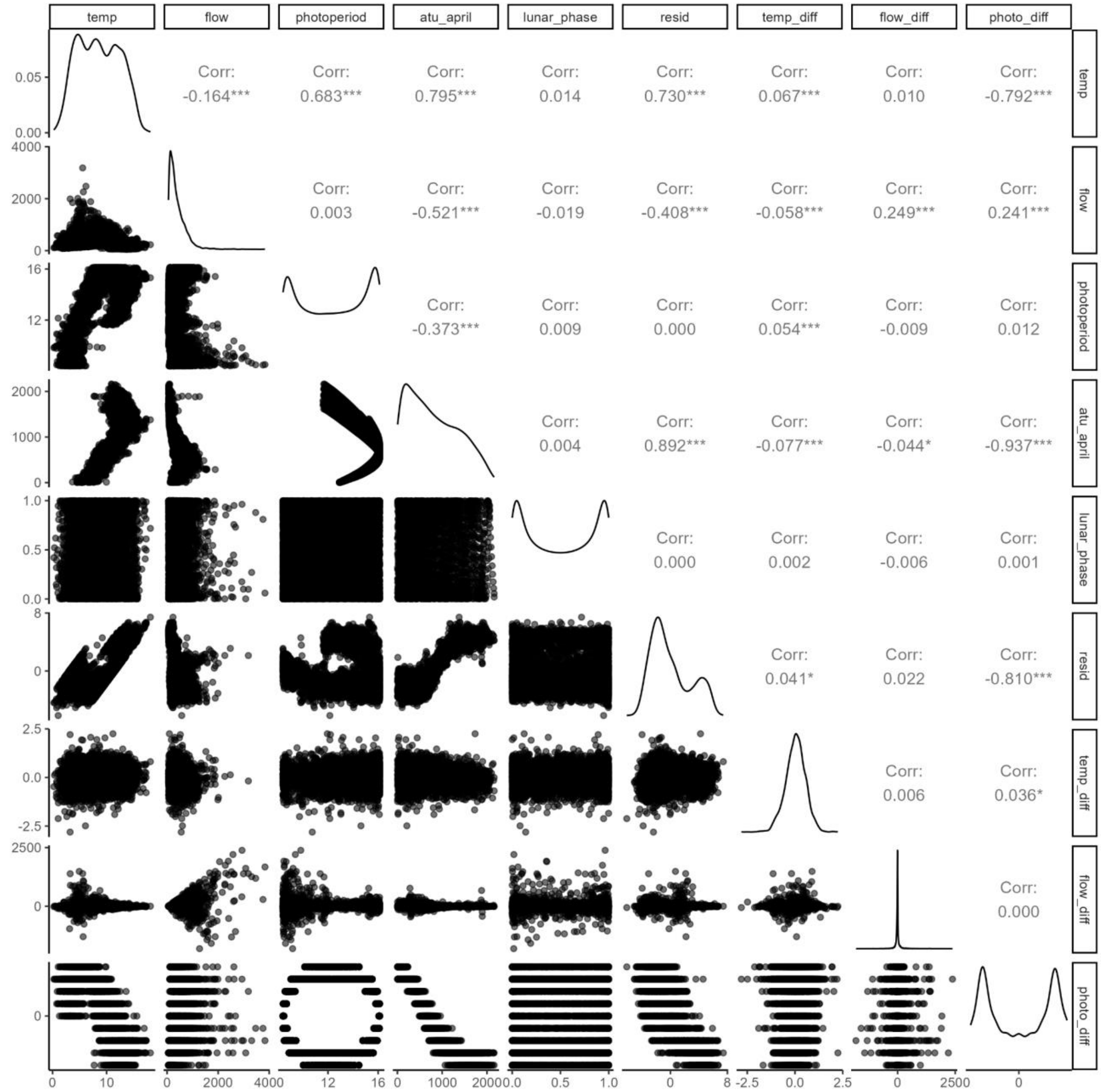


Figure 2.7. Correlation between all the environmental covariates in the Dungeness River.

Table 2.3. Model selection for Chinook salmon and coho salmon in the Dungeness with each of the correlated covariates.

Chinook		**Coho**	
Covariate	$\Delta AICc$	**Covariate**	$\Delta AICc$
Photoperiod difference	0	Photoperiod	0
Flow	3.73	ATU	3.03
ATU	5.50	Flow	27.9
Temperature	8.37	Temperature	30.01
Residuals	12.56	Photoperiod difference	43.12
Photoperiod	25.09	Residuals	44.16

Table 2.4. Relative variable importance for all variables used in the model selection process for sub-yearling Chinook salmon and yearling coho salmon in the Dungeness River.

Chinook		**Coho**	
Variable	**Relative Importance**	**Variable**	**Relative Importance**
Temperature difference	1	Photoperiod	1
Flow difference	1	Flow difference	1
Photoperiod difference	1	Flow	0.9
Hatchery	1	Temperature difference	0.5
Lunar Phase	0.4	Hatchery	0.4
Photoperiod	0.4	Photoperiod difference	0.3
Flow	0.3	Lunar phase	0.3

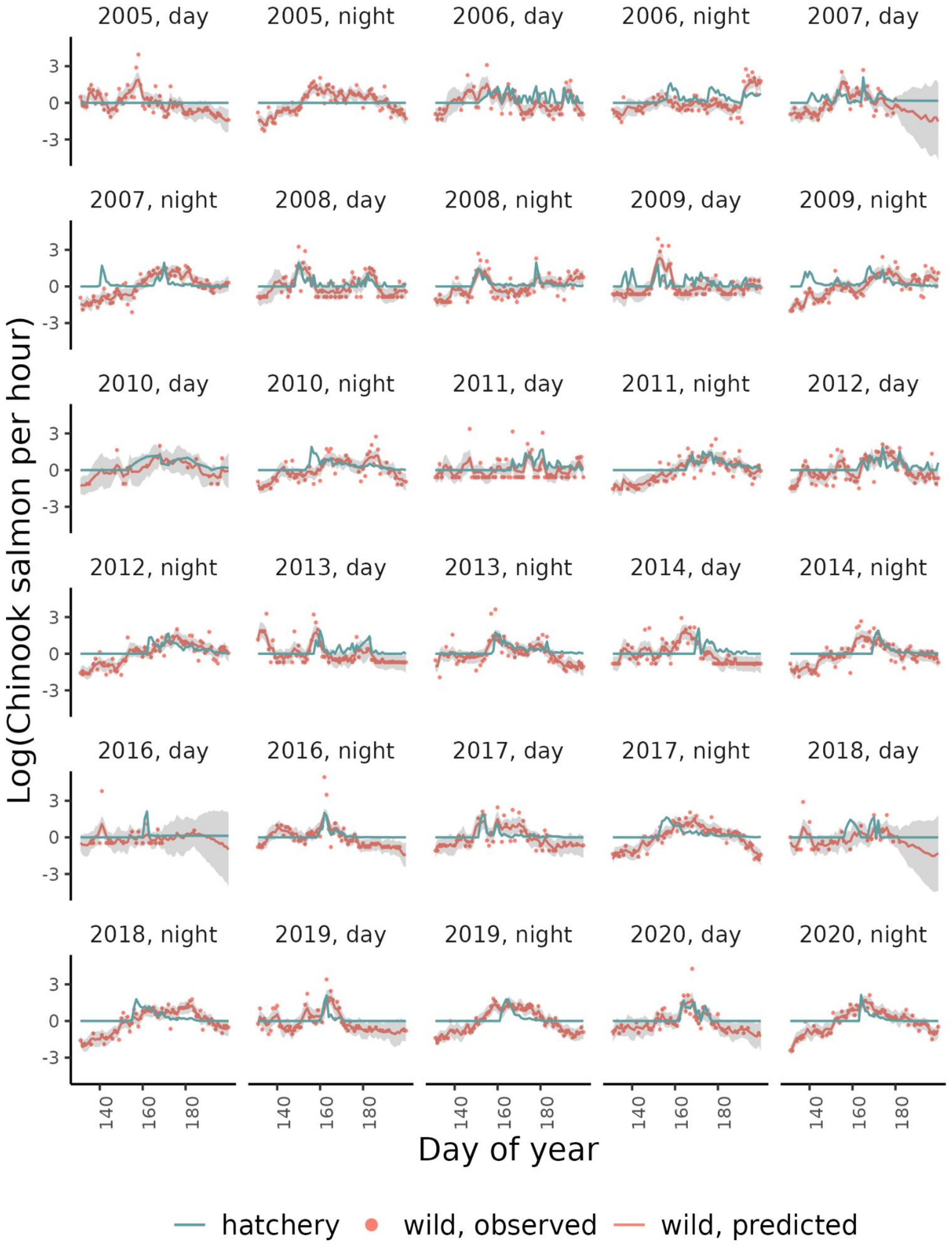


Figure 2.8. Model estimates and observations of wild Chinook salmon and observations of hatchery Chinook salmon in the Dungeness River.

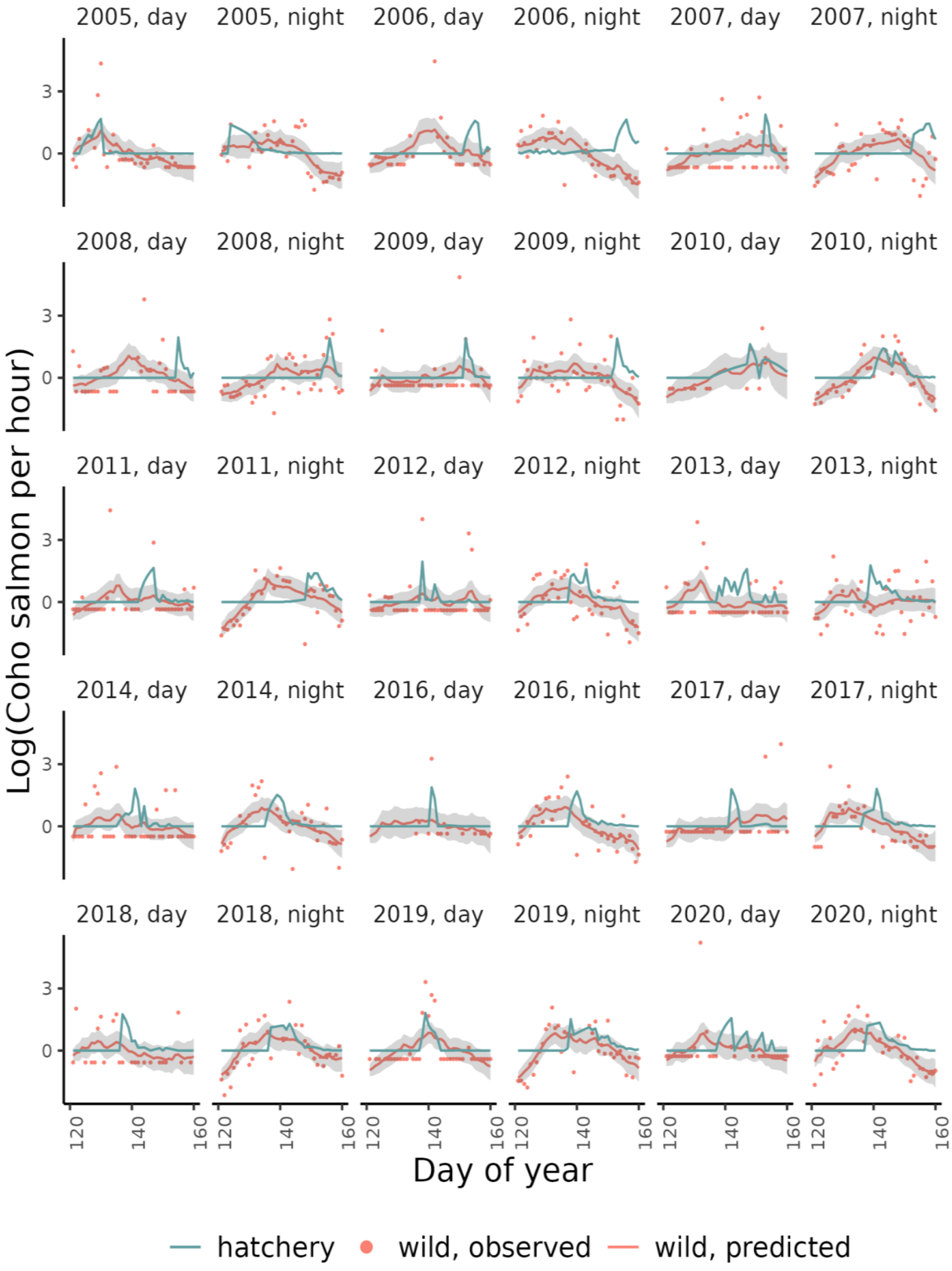


Figure 2.9. Model estimates and observations of wild coho salmon and observations of hatchery coho salmon in the Dungeness River

2.8.4 *Puyallup River*

The Puyallup River is a 72-km river that originates in the glaciers on Mount Rainier and drains into Puget Sound. In the summer, the river is fed by melting glaciers which increases the turbidity. Since the Puyallup River is not dammed, the flow and turbidity of the river varies widely. The highest water temperatures are around July-August and the lowest flows are in September-October. The Puyallup River supports Chinook, coho, and chum salmon, and steelhead and cutthroat trout. The Puyallup River trap, operated by the Puyallup Tribe of Indians, is located just upstream of the confluence of the White River and Puyallup River (47.1971, -122.2523). The trap catches hatchery salmon from the Voights Creek hatchery, and Rushingwater, Cowskull, and Wilkeson Creek acclimation ponds and Lake Kapowsin net pen.

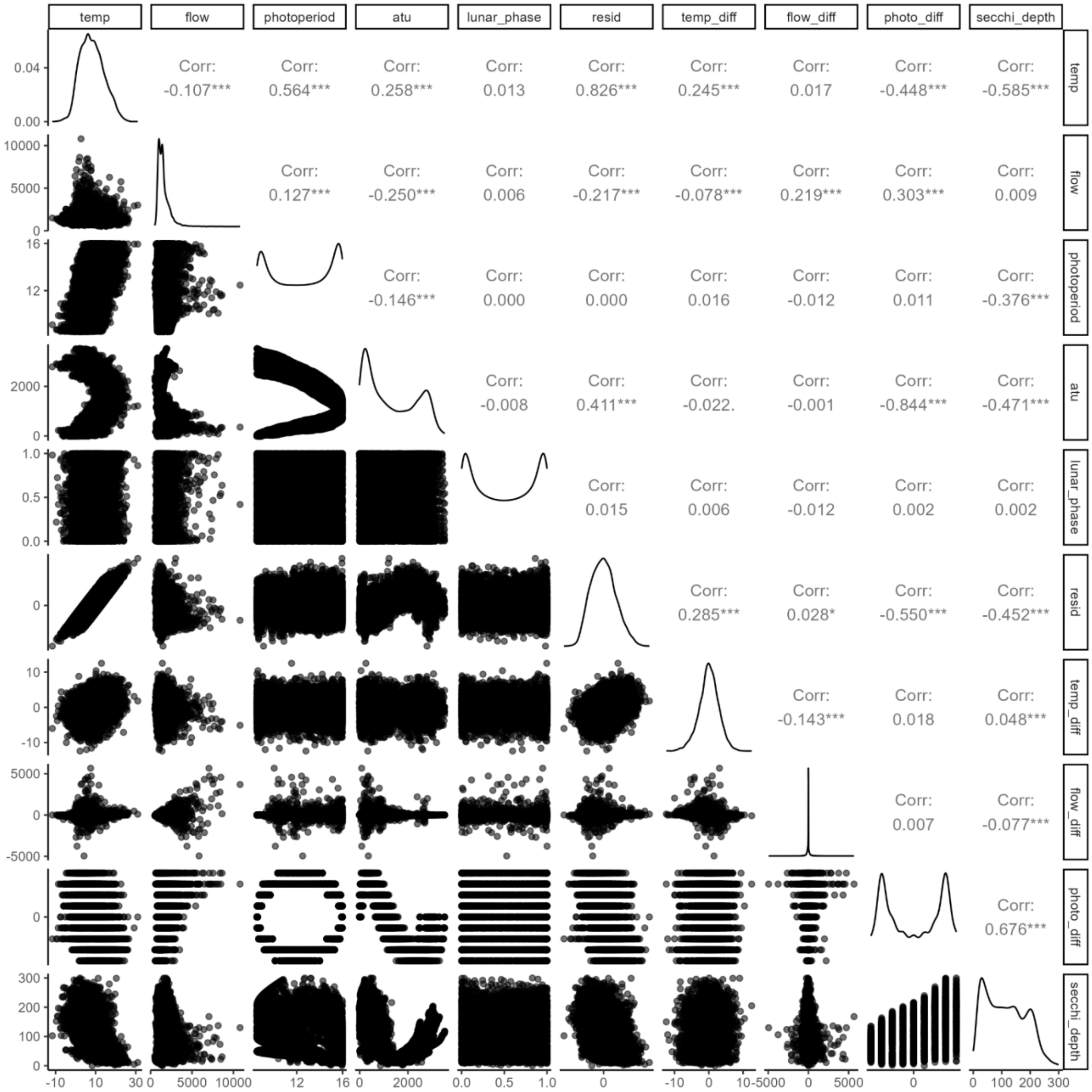


Figure 2.10. Correlation between all the environmental variables in the Puyallup River.

Table 2.5. Model selection for Chinook and coho salmon in the Puyallup River with each of the correlated covariate.

Chinook		**Coho**	
Covariate	$\Delta AICc$	**Covariate**	$\Delta AICc$

Photoperiod difference	0	ATU	0
ATU	1.26	Photoperiod	12.51
Residuals	6.76	Photoperiod difference	25.58
Temperature	8.33	Secchi depth	31.18
Secchi depth	10.36	Temperature	36.51
Photoperiod	12.22	Residuals	36.55

Table 2.6. Relative variable importance for all variables used in the model selection process for Chinook and coho salmon in the Puyallup River.

Chinook		Coho	
Variable	**Relative Importance**	**Variable**	**Relative Importance**
Flow difference	1	Flow difference	1
Temperature	1	Flow	1
Flow	1	Hatchery	1
Hatchery	1	ATU	1
Photoperiod difference	1	Photoperiod	0.9
Lunar Phase	0.4	Lunar phase	0.5
Temperature difference	0.3	Temperature difference	0.3

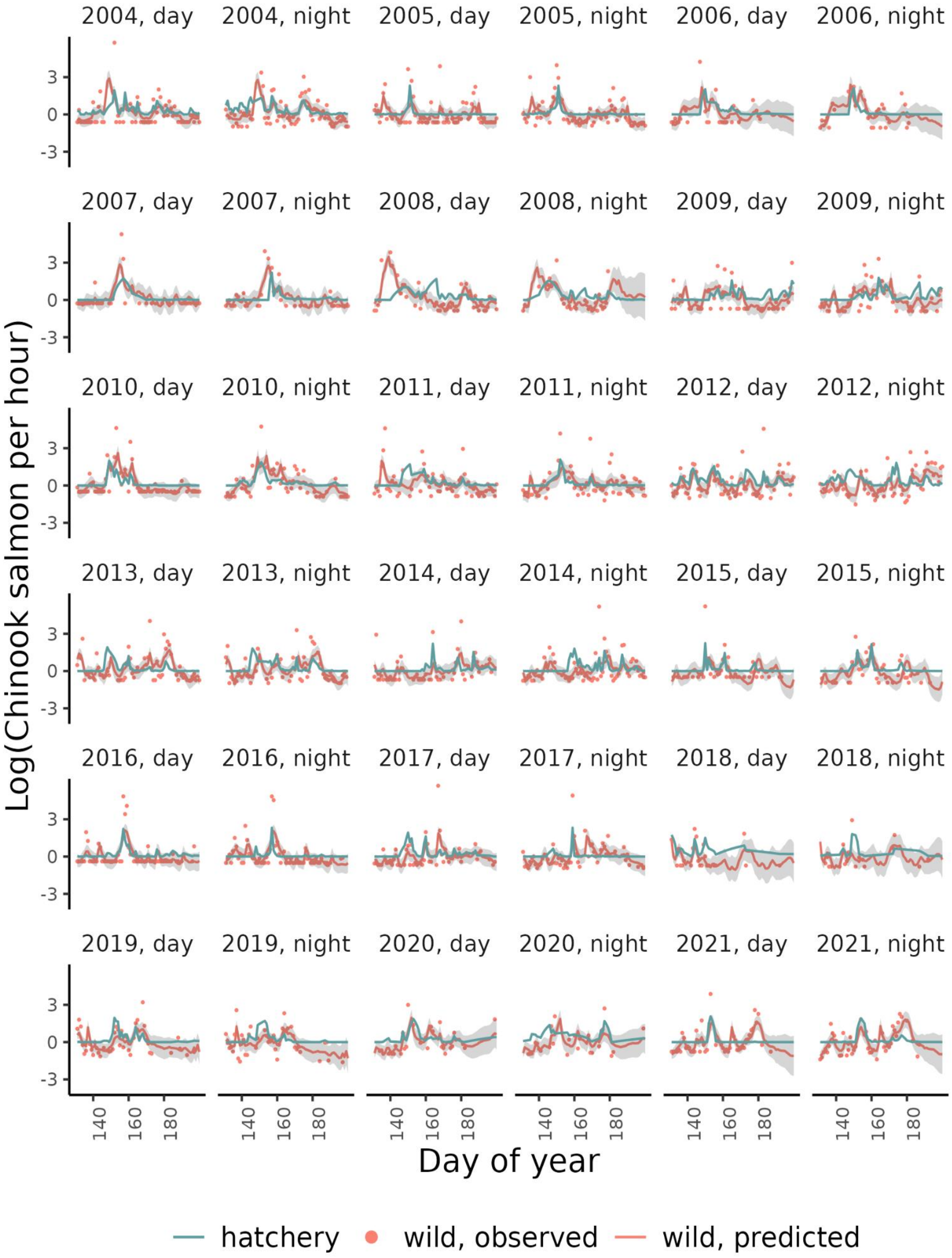


Figure 2.11. Model estimates and observations of wild Chinook salmon and observations of hatchery Chinook salmon in the Puyallup River.

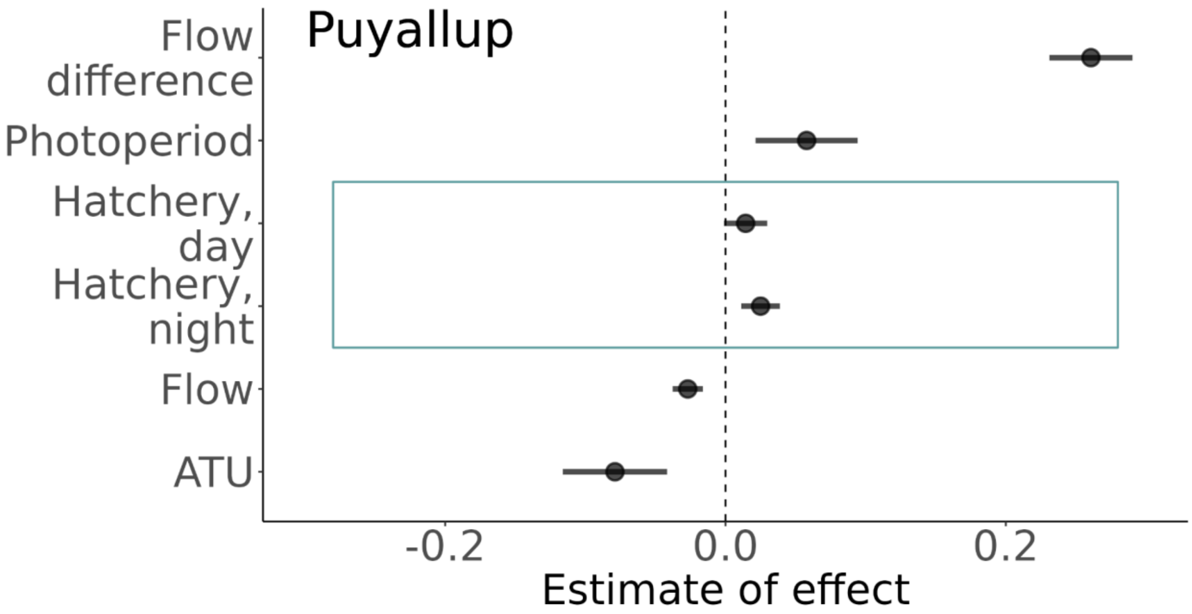


Figure 2.12. Estimates of the effect of different covariates in the best MARSS model for coho salmon in the Puyallup River without 2009 and 2021 data (years with high proportions of unmarked hatchery fish). Blue boxes indicate social variables associated with the pied piper hypothesis.

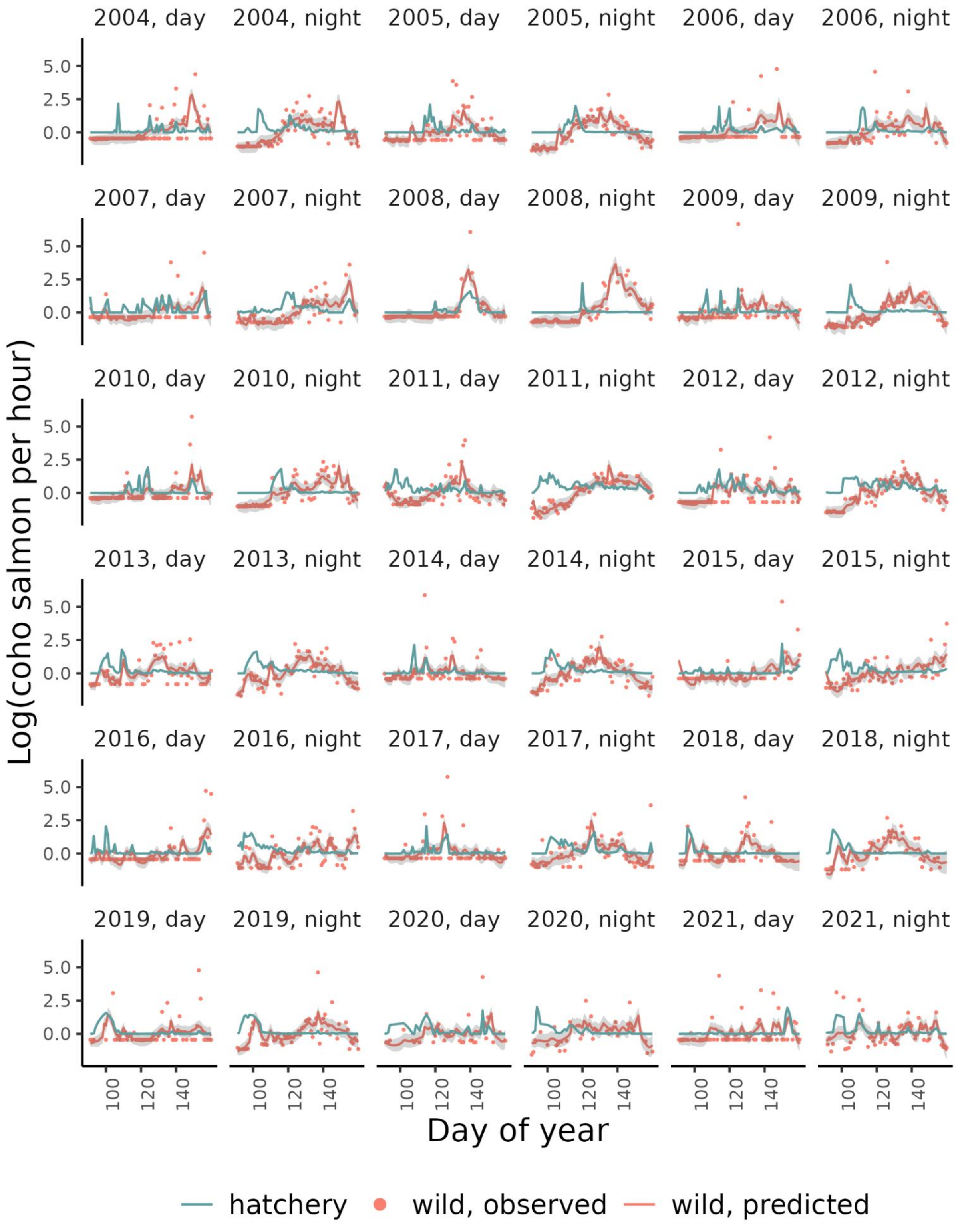


Figure 2.13. Model estimates and observations of wild coho salmon and observations of hatchery coho salmon in the Puyallup River.

2.8.5 *Skagit River*

The Skagit River is a 240-km river that originates in the Canadian Cascades and drains into the Puget Sound. Several dams regulate the flow of the river. The Skagit River supports all five species of Pacific Salmon as well as Steelhead and Cutthroat. WDFW operates a screw trap and a scoop trap on the mainstem of the Skagit River (48.4451, -122.3251), 27 km upstream of the river mouth. The traps catch hatchery salmon released from Countyline Ponds, Baker Lake Hatchery, and Marblemount Hatchery.

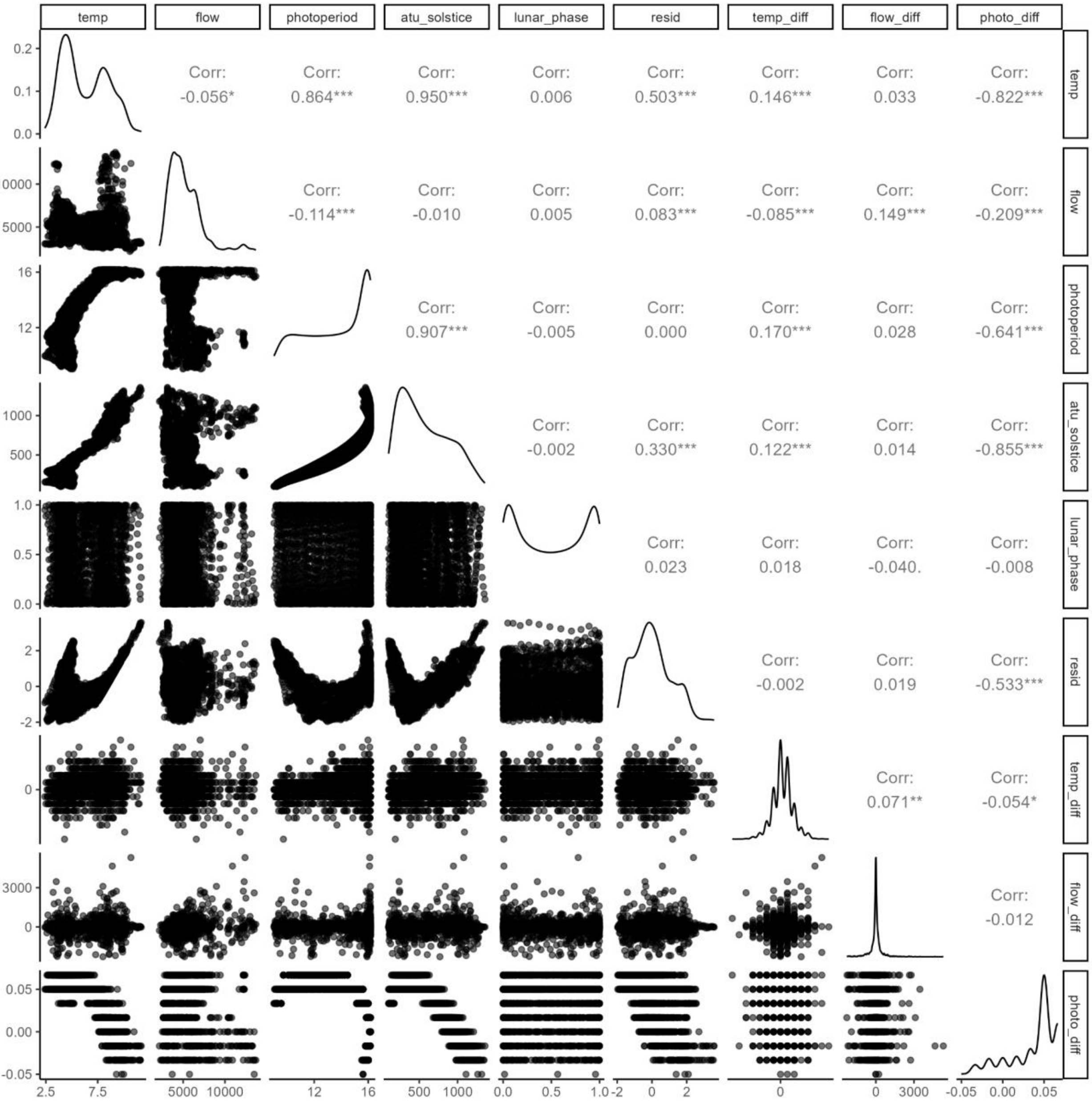


Figure 2.14. Correlation between all the environmental covariates in the Skagit River.

Table 2.7. Model selection for Chinook salmon and coho salmon in the Skagit River with each of the correlated covariates.

Chinook		**Coho**	
Covariate	$\Delta AICc$	**Covariate**	$\Delta AICc$
Residuals	0	ATU	0
Photoperiod	4.37	Photoperiod	6.61
Temperature	6.76	Residuals	7.33
ATU	8.03	Temperature	7.46
Photo difference	11.54	Photo difference	24.75

Table 2.8. Relative variable importance for all variables used in the model selection process for Chinook salmon and coho salmon in the Skagit.

Chinook		**Coho**	
Variable	**Relative Importance**	**Variable**	**Relative Importance**
Temperature difference	1	ATU	1
Residuals	0.9	Hatchery	1
Photoperiod	0.8	Flow	0.9
Hatchery	0.4	Lunar phase	0.5
Flow difference	0.3	Temperature difference	0.4

Lunar phase 0.3

Flow difference 0.3

Flow 0.3

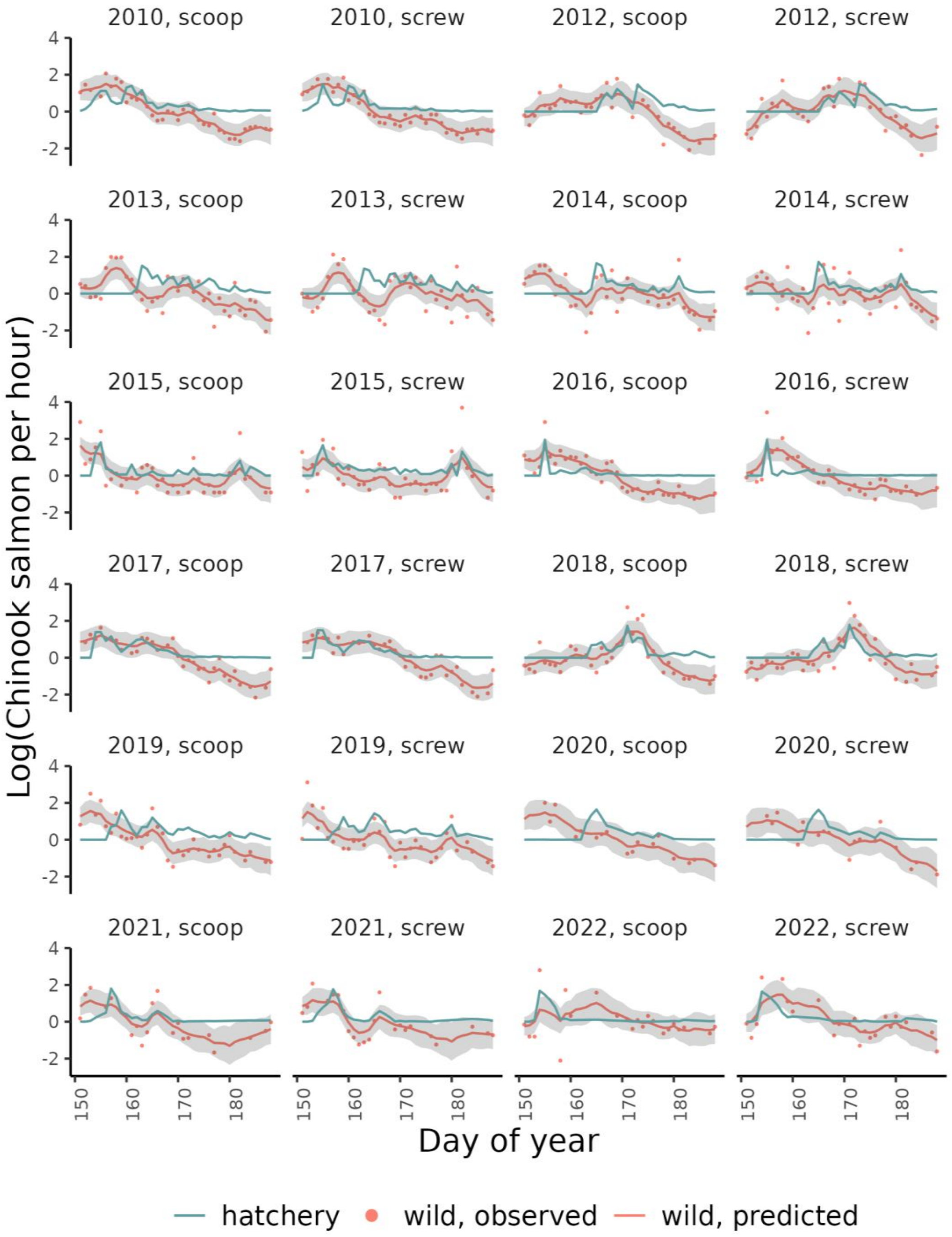


Figure 2.15. Model estimates and observations of wild Chinook salmon and observations of hatchery Chinook salmon in the Skagit River.

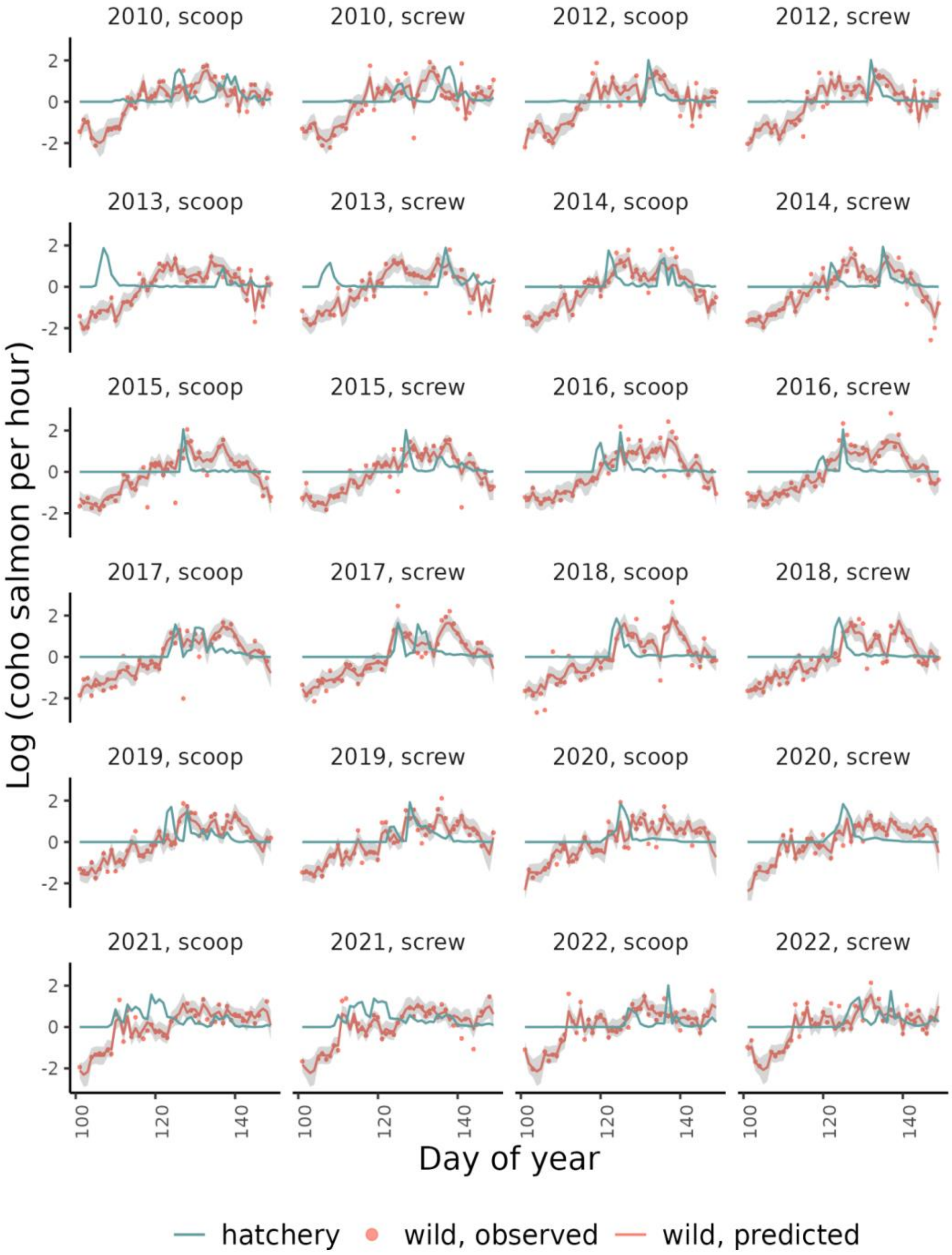


Figure 2.16. Model estimates and observations of wild coho salmon and observations of hatchery coho salmon in the Skagit River.

Table 2.9. Average number of hatchery salmon released, hatchery location names, and average number of hatchery releases for each river-species combination as reported in RMIS.

Species	River	Average releases	Average total released	Hatcheries
Chinook	Dungeness	2	147731	GRAY WOLF R ACCL PD, DUNGENESS HATCHERY, UPR DUNGENESS ACC PD, HURD CR HATCHERY
Chinook	Puyallup	2	1279570	VOIGHTS CR HATCHERY , GREENWATER ACCLIMATION PD, COWSKULL ACCLIM POND, PUYALLUP TRIBAL HATCHERY
Chinook	Skagit	2	848206	MARBLEMOUNT HATCHERY
Coho	Dungeness	1	548141	DUNGENESS HATCHERY
Coho	Puyallup	2	844170	VOIGHTS CR HATCHERY , GREENWATER ACCLIMATION PD, COWSKULL ACCLIM POND, PUYALLUP TRIBAL HATCHERY
Coho	Skagit	3	421403	MARBLEMOUNT HATCHERY, BAKER LK HATCHERY

Chapter 3. EFFECT OF TEMPERATURE, FLOW, AND HATCHERY RELEASES ON JUVENILE SALMON MIGRATION PATTERNS

Publication history: At the time this dissertation was published, this chapter was not in review with a journal.

3.1 ABSTRACT

Pacific salmon migrate from freshwater to the ocean as juveniles without parental guidance or prior experience. Different species of Pacific salmon have different migration strategies and a combination of internal factors, environmental and social cues determine the timing of their migration. We explored the effect of environmental and social factors on the migration timing of juvenile Chinook, coho, and chum salmon in three rivers in Washington state spanning the years 2004-2022. We used hierarchical modeling to fit distributions to the migration date with the mean and the variance of the distribution as function of different covariates. We estimated the effect of accumulated thermal units (ATU) – temperature experience – and cumulative flow on the peak of the migration, and the number of cumulative hatchery salmon released on the duration of migration of Pacific salmon in the Dungeness, Skagit, and Puyallup rivers. Our findings indicate that sub-yearling Chinook salmon migrate earlier with increasing ATU in the Dungeness and Skagit rivers. Yearling coho salmon display earlier peak migration with increasing cumulative flow across all rivers. Additionally, we observed a negative relationship between the cumulative number of hatchery salmon released and the duration of migration for wild coho salmon in the Puyallup and Skagit rivers. Finally, we found that Chum salmon in the Dungeness River migrated earlier with increasing ATU. Climate change predictions indicate an increase in stream temperatures and advancement of streamflows in Washington state. Therefore, these findings can help us understand how migration phenology may shift under various anthropogenic stressors, providing valuable insights for future management strategies for salmon populations and their habitats.

3.2 INTRODUCTION

Animals migrate seasonally to capitalize on the abundant resources that are only available in distant locations at certain times of the year (Dingle and Drake 2007; Dingle 2014). Maximizing the time spent at the destination when the food is plenty can compensate for the risks associated with the migration. However, early arrival is associated with costs because body condition upon arrival can significantly influence subsequent survival or reproductive success (Rotics et al. 2018). Typically, only larger individuals or those in optimal body conditions can afford to migrate early (Bearhop et al. 2004; Heim et al. 2016). On the other hand, late arrivals may face increased competition and less overlap with the availability of resources such as site or food (Brooke 1979). Consequently, there exists an optimal arrival time to maximize the benefits of migration. Animals must time their migration based on local cues, which may or may not align with the environmental conditions at their destination (Clausen and Clausen 2013). For some species, prior experience (Baert et al. 2022) or social cues from conspecifics (Berdahl, Westley, and Quinn 2017) or older individuals can help with the decision of timing. The timing of animal migration is a complex process influenced by various factors, including body condition (Heim et al. 2016), competition (Sirot and Touzalin 2014), resource availability (Bridge et al. 2010), social (Oestreich et al. 2022) and environmental cues (Rickbeil et al. 2019).

Anadromous fish, as juveniles, undertake a migration from freshwater to the ocean, in the absence of prior experience and parental guidance (Quinn 2018). This migration necessitates a shift to an unfamiliar environment and demands a physiological transformation (Hoar 1976). This phase of migration represents a pivotal period in their life history, since the first year in the ocean is characterized by high mortality rates (Parker 1962). Body size on arrival is a predictor of survival, making the timing of migration critical (Moss et al. 2005). Opting to stay in freshwater offers the advantage of encountering fewer predators, but it also limits opportunities for feeding and growth (Quinn 2018). Larger fish are more likely to survive in the marine environment (Duffy and Beauchamp 2011). Larger fish also tend to migrate earlier than their smaller counterparts (Beckman et al. 1998).

In this paper, we focus on Chinook, coho, and chum salmon. These species coexist in the rivers of Washington state, each exhibiting unique life histories and migration strategies (Quinn 2018). Chum salmon, for instance, migrate as fry shortly after emergence, predominantly occupying the lower stretches of the stream. Chinook salmon display the most diverse life history strategies, with some migrating soon after emergence in late winter, others in the spring and summer, and yet others migrating the following summer as yearlings. Notably, the ocean-type Chinook salmon, which migrate to the ocean within their first year are found in the lower reaches of the Skagit River (Austin, Torgersen, and Quinn 2023). Conversely, Coho salmon typically migrate as yearlings after spending a year in freshwater, usually occupying the smaller streams in the river's higher reaches. The variety in life histories and migration strategies among different species indicates that the environmental and social signals influencing their migration could differ significantly.

The timing of migration is influenced by a combination of internal rhythms, such as hormonal changes (Hoar 1976), external environmental cues (Sykes, Johnson, and Shrimpton 2009), and social cues (Chapter 2). Several environmental factors control the physiological transformations, as well as the behavioral changes involved in migration. For example, photoperiod affects the internal rhythms of hormones that regulate the parr-to-smolt transformation process in coho salmon (Hoar 1958). Temperature increases the rate of development of eggs and fry (Beacham and Murray 1990). An increase in water temperatures can motivate salmon to swim downstream (Keenleyside and Hoar 1954).

Several studies have tried to estimate the effects of environmental factors on the number of smolts migrating downstream and the timing of the out-migration using statistical models (Scheuerell, Zabel, and Sandford 2009). Chinook salmon migrate earlier after a warmer spring in Oregon (Roper and Scarnecchia 1999). The interannual variation in the timing of migration of coho smolts and chum fry is explained by water temperature in Carnation Creek, BC (Holtby, McMahon, and Scrivener 1989). We hypothesize that temperature has a negative effect on the peak out-migration timing of Chinook, chum and coho salmon, with salmon migrating earlier as the accumulated thermal units (or temperature experience) increase. Increasing median daily run-off in spring advances the out-migration start date in coho salmon smolts in California (Kastl et al. 2022). We also hypothesize that cumulative flow would have a negative influence on the peak migration timing of coho smolts.

In addition to environmental cues, social cues also play a role in the out-migration of Chinook and coho salmon, as well as Atlantic salmon. For example, Atlantic salmon smolts arrive in schools towards the end of the migration. Visual observations show that wild Chinook salmon in the Wenatchee river move along with more abundant hatchery Chinook salmon following hatchery releases (Hillman and Mullan 1989). The number of wild Chinook and coho salmon out-migrating is positively correlated with the number of hatchery salmon out-migrating, suggesting that the downstream migration of hatchery salmon following a hatchery release might serve as a catalyst, motivating the wild salmon to out-migrate (Chapter 2). Based on these observations, we hypothesize that an increase in the cumulative number of hatchery salmon out-migrating could potentially shorten the duration of migration of wild salmon.

The environmental and social cues mediating the timing of out-migration in salmon are likely to change in the future. The environmental cues can be affected by various anthropogenic factors and may not change at the same rate (Allen and Wolfe 2013). These factors, like climate change, can affect ocean conditions and freshwater conditions differently which can cause mismatch in the timing of ocean entry and timing of food availability (Wilson et al. 2023). This mismatch can have important survival consequences for salmon populations (Cushing 1990). Large-scale studies with multiple populations of Pacific salmon show that phenological shifts are often population specific with local adaptations (Wilson et al. 2023). Therefore, it is important to understand the various cues at the local scale to manage watersheds efficiently and to predict how migration phenology may shift under various anthropogenic stressors.

In this paper, we used a dataset spanning roughly 19 years (2004-2022) and fit distributions to run timing data and modeled the mean (peak of migration) and variance (duration of migration) of the distribution as a function of the different covariates. We estimated the effect of accumulated thermal units and cumulative flow on the peak out-migration timing of Chinook, coho and chum salmon in three rivers in Washington state. Additionally, we estimated the effect of the cumulative number of hatchery salmon released on the duration of migration of Chinook salmon and coho salmon. This paper provides information that resource managers can use to anticipate the effects of climate change as well as change the timing of hatchery releases on the out-migration timing of salmon in Washington state. Finally, our findings emphasize the importance of considering both environmental and social factors in predicting the timing of juvenile salmon migration.

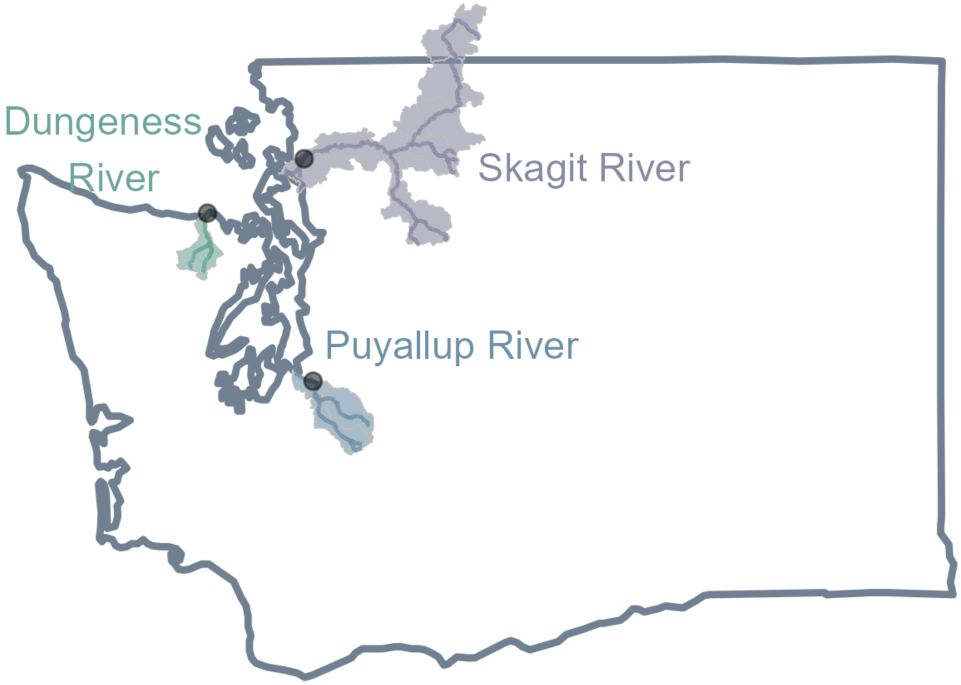


Figure 3.1. Map of the rivers and the watersheds included in the study. Black dots represent locations of the traps.

3.3 METHODS

For this study, we restricted our analysis to the migration of salmon populations based on abundance in the river (at least 1000 fish caught on average in the trap over each season), and the availability of data (at least 10 years of data). We analyzed the migration data for sub-yearling Chinook salmon, yearling coho salmon, and sub-yearling chum salmon. These three species have different life histories and migration patterns. Therefore, different environmental factors might have different effects on the migration patterns of these different species.

Study Locations

We chose three rivers in Washington state supporting multiple species of salmon that represent variability in terms of watershed area, thermal regimes, presence of dams, flood plain degradation, and impact of forest harvesting on stream temperatures (Figure 3.1).

Originating in the Olympic Mountains, fed through melting snowpack, and draining into the Strait of Juan de Fuca, the Dungeness River is a 45-km waterway in northwest Washington State. Historically, clear cutting prevailed until 1994 (Hall et al. 2019), but current practices involve thinning, maintaining the river's riparian buffer. The Dungeness River supports seven species of salmonids - Chinook, coho, chum and pink salmon, steelhead, cutthroat and bull trout. We chose sub-yearling Chinook salmon that migrate as parr in early spring, yearling coho salmon and sub-yearling chum salmon from years 2005 - 2020 for our analysis. Pink salmon, abundant in even years, couldn't be included due to insufficient data.

Flowing from Mount Rainier glaciers into Puget Sound, the 72-km Puyallup River experiences increased turbidity from summer glacier melting. Unregulated flow and turbidity vary widely due to lack of dams. Intensive logging since the 1940s has severely degraded riparian and floodplain habitats. Many streams have elevated water temperatures which are linked to the riparian habitat being severely compromised (Kerwin 1999). The Puyallup River supports Chinook, coho, and chum salmon, and steelhead and cutthroat trout. We analyzed coho salmon data from years 2004 - 2021.

The Skagit River is the largest of the three rivers in this study - 240 km - that originates in the Canadian Cascades and drains into the Puget Sound. Several dams regulate the flow of the river. Altered by logging and agriculture, riparian forests have regrown since the 1980s peak in logging activity (Maher and Veldhuisen 2023). The Skagit River supports all five species of Pacific Salmon as well as Steelhead and Cutthroat. We analyzed sub-yearling Chinook salmon, yearling coho salmon, and sub-yearling chum salmon data from years 2010 - 2022.

3.3.1 *Trap Data*

Salmon smolt traps are deployed in rivers to monitor juvenile salmon populations as they out-migrate to the ocean. Situated near the river mouths, traps are submerged in the water one to two times in 24 hours for around 12 hours, catching on average 11%, 4%, and 3% of the migrating smolts in the Dungeness, Puyallup and Skagit rivers respectively. A trained trap operator counts and identifies the species, age, and origin (natural or hatchery) of the salmon.

In the Dungeness and Puyallup rivers, the traps are submerged twice every 24 hours, once during the day for 12 hours and once during the night for 12 hours. In order to determine the number of smolts migrating every 24 hours, we aggregated the data so that we have one data point per day in the Dungeness and Puyallup rivers. In the Skagit River, since the smolts are counted every night for 12 hours and every third day for 12 hours, we only used the night counts as daily counts.

Large scale hatchery programs for subyearling Chinook and yearling coho salmon in the Dungeness, Puyallup, and Skagit rivers release a large number of hatchery salmon into the rivers each year. We calculated the cumulative sum of hatchery salmon released into the river for each species. The hatcheries report released fish numbers, accessible via the RMIS website. However, there are multiple releases (1 to 3) each season at different locations and the reported release locations are not always accurate. Thus, trap catch calculations provide the most reliable estimate of upstream releases.

3.3.2 *Environmental Data*

Our objective was to identify environmental factors that affect the peak and duration of migration for natural-origin juvenile salmon in the Dungeness, Puyallup and Skagit rivers. Roper and Scarnecchia, 1999 has shown that stream temperature negatively affects the timing of emigration of sub-yearling Chinook salmon in the South Umpqua River basin, Oregon, USA.. Similarly, Holtby, McMahon, and Scrivener, 1989 has shown that average stream temperatures affect the migration timing of coho smolts migrate negatively in the Carnation Creek, BC, Canada. Apart from stream temperatures, flow has also been shown to affect salmon out-migration timing. Kastl et al. 2022 has shown that median daily flow negatively affects the start date of migration in coho smolts in the Russian River basin, California, USA.

For the Dungeness River, daily water temperature was not available in the winter for all years of our study. Therefore, we obtained daily air temperature data from the Washington Department of

Ecology for years 2005-2020 (Station ID 18A050), a site near the Dungeness River mouth. Average air temperature does not differ greatly from average water temperature in small streams (Macan 1958). We dropped the data for 2019 because we observed anomalies (higher than 50 °C) in the temperature data in that year. For the Puyallup River, we did not have access to any water temperature data. Therefore, we used air temperature data from USDA Natural Resources Conservation Service measured at Mowich (site 941), which is a site within the Puyallup drainage. For the Skagit River we used water temperature data collected by USGS (Marblemount, Site no. - 12181000) for the entire time period.

We calculated accumulated thermal units (ATU) as the cumulative sum of water temperature (Skagit) or air temperature (Dungeness, and Puyallup rivers) starting from the winter solstice (December 21) of the previous year and subtracted the mean ATU from the data. We then subtracted the mean of the ATU for each river from the data. Therefore, ATU can take negative values in our study. While ATU is traditionally calculated as the water temperature experienced since spawning, we did not have access to spawning data and chose to select a date that is consistent to start cumulatively summing the temperature. We only had water temperature from the winter for all years for the Skagit River. Therefore, we chose to use air temperature in the Puyallup and Dungeness rivers. However, the analysis for each river is separate and does not depend on having the same methods for calculating ATU.

We obtained daily flow data for every year for each of the rivers. For the Dungeness River, we used flow data from the Washington Department of Ecology (Station ID 18A050). For the Puyallup River, we used flow data measured by the Puyallup Tribe of Indians near the trap. For the Skagit River, we used flow data collected by USGS (Site no. - 12181000). We calculated cumulative flow as the cumulative sum of the daily flow starting from the earliest day that was sampled every year (day of year 83, 22, and 1 for the Dungeness, Puyallup, and Skagit rivers respectively) to have comparable values of cumulative flow between years.

3.3.3 *Analysis*

In order to extract the peak date of migration and the duration of migration (operationally defined as the time between the first and third quartiles), we used package ‘phenomix’ to fit a distribution to the observation data using hierarchical models (Wilson, Anderson, and Ward 2023). This method is not sensitive to the period of data collection, which is fixed by agencies and trap operators, which might start after salmon have already started migrating and is disrupted by global events (e.g., Covid-19).

We compared model fits with 3 different error distributions (gaussian, lognormal, negative binomial) and 2 different tail distributions (gaussian and student-t) and chose the model with lowest Akaike Information Criterion (AIC). All models had random effects in the mean (peak of the migration) and the variance, allowing the mean and variance to vary with year. All models were allowed to be asymmetric, meaning the standard deviation of the distribution before the mean can be different from the standard deviation after the mean. We modeled the mean of the distribution (peak of migration) as a function of ATU and cumulative flow in the Puyallup and Skagit rivers. In the Dungeness River, ATU and cumulative flow were correlated (correlation > 0.5). Therefore, we fit models with ATU and cumulative flow separately and chose the model with the lowest AIC. We modeled the variance before and after the mean as a function of the cumulative number of hatchery salmon released.

3.3.3.1 Covariates

ATU and cumulative flow were added as covariates in the model of the peak migration, whereas cumulative hatchery was added as a covariate in the model of the duration of migration. To choose a value for ATU and cumulative flow for every year we first calculated the day of year that 50% of the run for the year had passed. We then calculated the minimum day of year of the 50% run for all the years, and used the ATU and cumulative flow associated with that day of year. We calculated the day of year that 90% of the wild run had passed for each year. We then calculated the minimum day of year among all years and calculated the cumulative sum of hatchery salmon released until that day for all the years. This allowed us to choose a date that is consistent across all years.

Table 3.1. List of response variables and predictor variables for every River and species included in the study. ATU refers to accumulated thermal units or the temperature experienced by the salmon from Dec 21st of the previous year, cumulative flow is the cumulative sum of the flow, and cumulative hatchery refers to the cumulative sum of hatchery salmon caught in the trap. Dark green represents p value < 0.05.

Chinook						
Dungeness			**Skagit**			
Peak Migration	ATU	Cumulative Flow	ATU	Cumulative Flow		
Duration of migration	Cumulative Hatchery					
Coho						
Dungeness			**Skagit**			**Puyallup**
Peak Migration	ATU	Cumulative Flow	ATU	Cumulative Flow	ATU	Cumulative Flow
Duration of migration	Cumulative Hatchery		Cumulative Hatchery			Cumulative Hatchery
Chum						
Dungeness			**Skagit**			
Peak Migration	ATU	Cumulative Flow	ATU	Cumulative Flow		

3.4 RESULTS

3.4.1 *Chinook salmon*

In the Dungeness and Skagit rivers, we observed a negative effect of accumulated thermal units (ATU) on the peak migration of Chinook salmon smolts (p = 0.01 and p < 0.01, respectively), indicating earlier migration following warmer winters (Figure 3.2, Figure 3.3). On the contrary, we did not detect any influence of flow on the peak migration of Chinook salmon smolts in these rivers (Supplementary Information). Furthermore, our analysis revealed no effect of cumulative hatchery salmon releases on the migration duration of Chinook salmon in the Dungeness River. In the Skagit River, where hatcheries release Chinook salmon smolts towards the tail end of the migration period for wild Chinook salmon smolts, the cumulative number of hatchery salmon released by the 90th percentile of the run was consistently zero across all years.

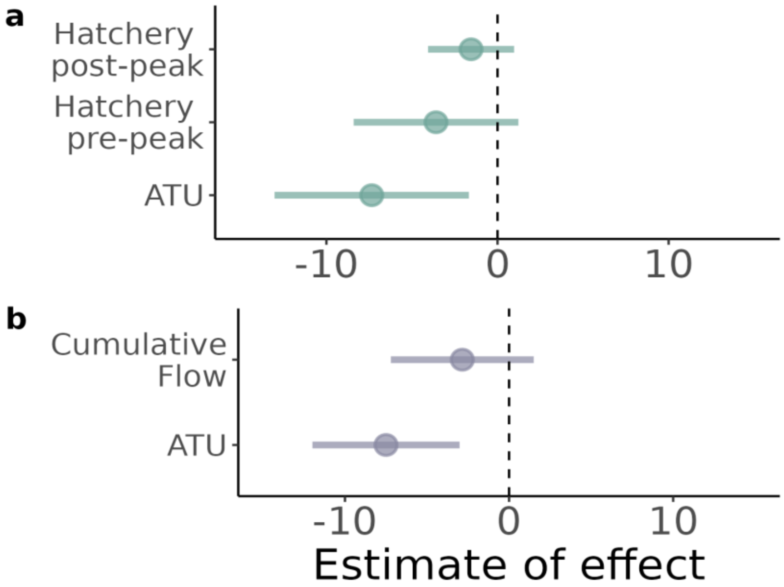


Figure 3.2. Estimates of the effect of environmental covariates on the peak migration day and hatchery covariate on the duration of migration of Chinook salmon smolts in the a) Dungeness River and the b) Skagit River.

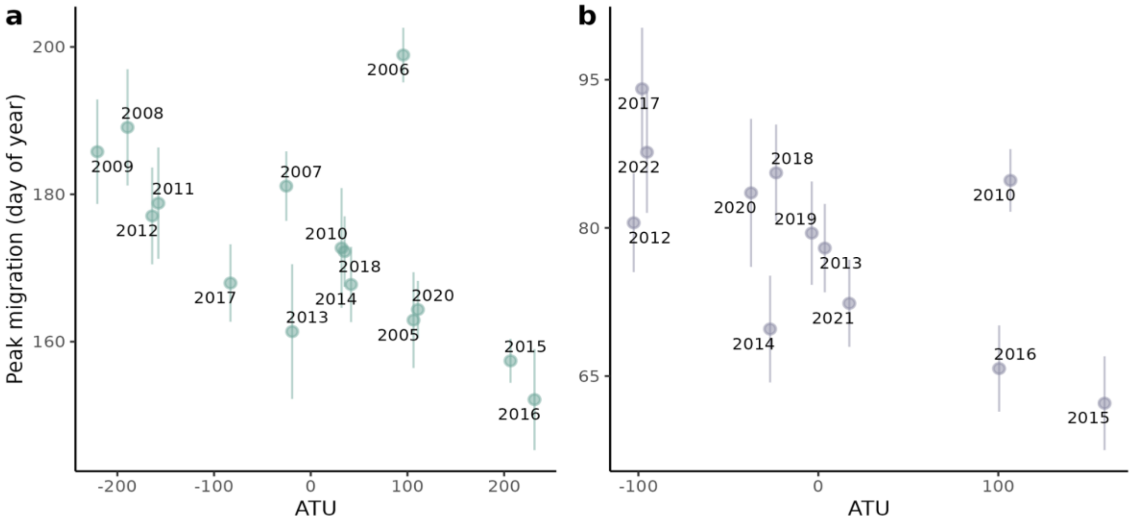


Figure 3.3. Effect of ATU on the peak migration day of Chinook salmon smolts in the a) Dungeness River and the b) Skagit River.

3.4.2 *Coho salmon*

In our analysis across the Dungeness, Puyallup, and Skagit rivers, we observed no significant effect of accumulated thermal units (ATU) on the peak migration of coho salmon smolts (Figure 3.4). Conversely, we identified a negative correlation between cumulative flow and the peak migration day of coho salmon smolts in all three rivers ($p = 0.02$ for Dungeness, $p = 0.05$ for Puyallup, $p = 0.04$ for Skagit) (Figure 3.4, 3.5). Additionally, our findings indicated a negative impact of cumulative hatchery salmon releases on the duration of migration post-peak for coho salmon in the Puyallup ($p = 0.02$) and pre-peak for coho salmon in the Skagit rivers ($p < 0.01$) (Figure 3.6).

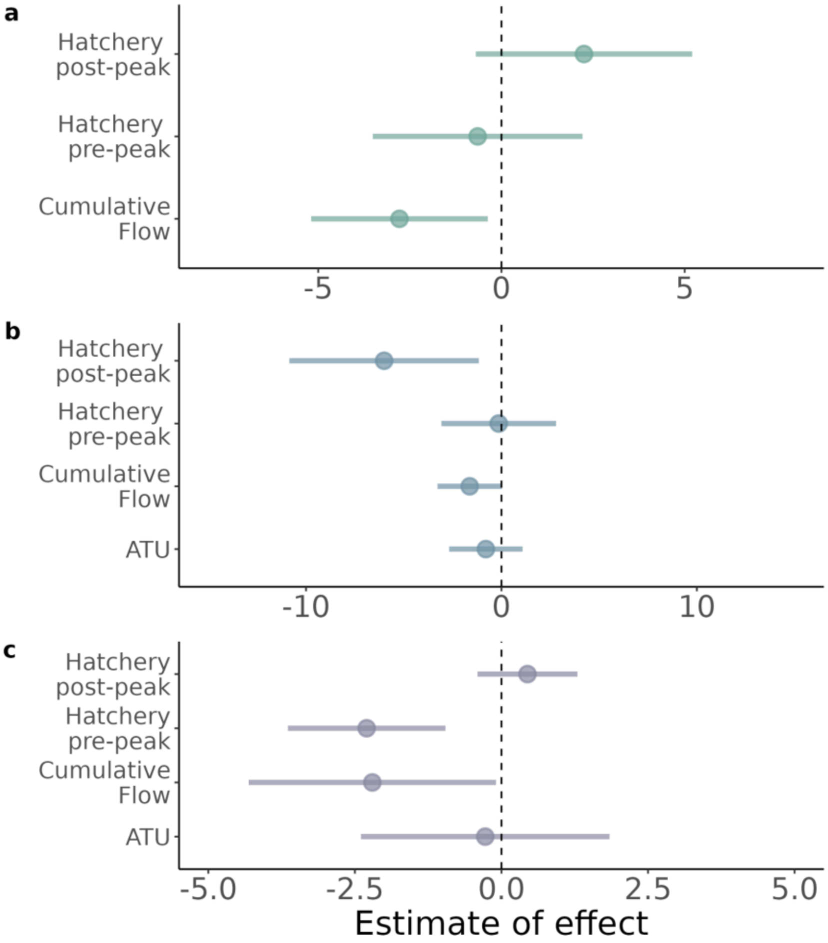


Figure 3.4. Estimates of the effect of environmental covariates on the peak migration day and hatchery covariate on the duration of migration of coho salmon smolts in the a) Dungeness River, b) Puyallup River and the c) Skagit River.

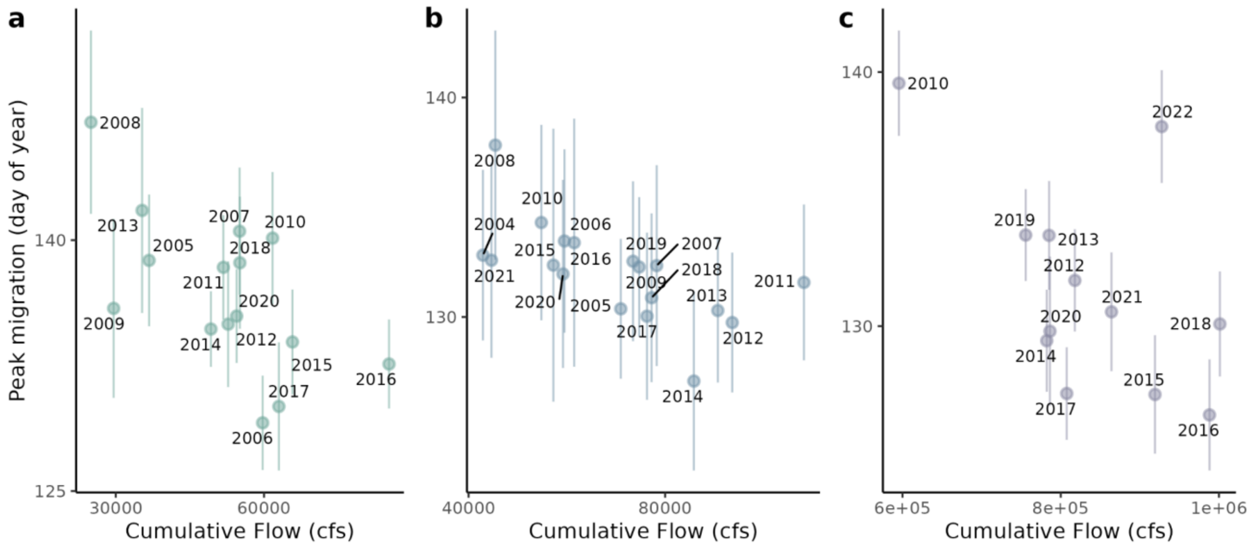


Figure 3.5. Effect of cumulative flow on the peak migration day of coho salmon smolts in the a) Dungeness River, b) Puyallup River, and the c) Skagit River.

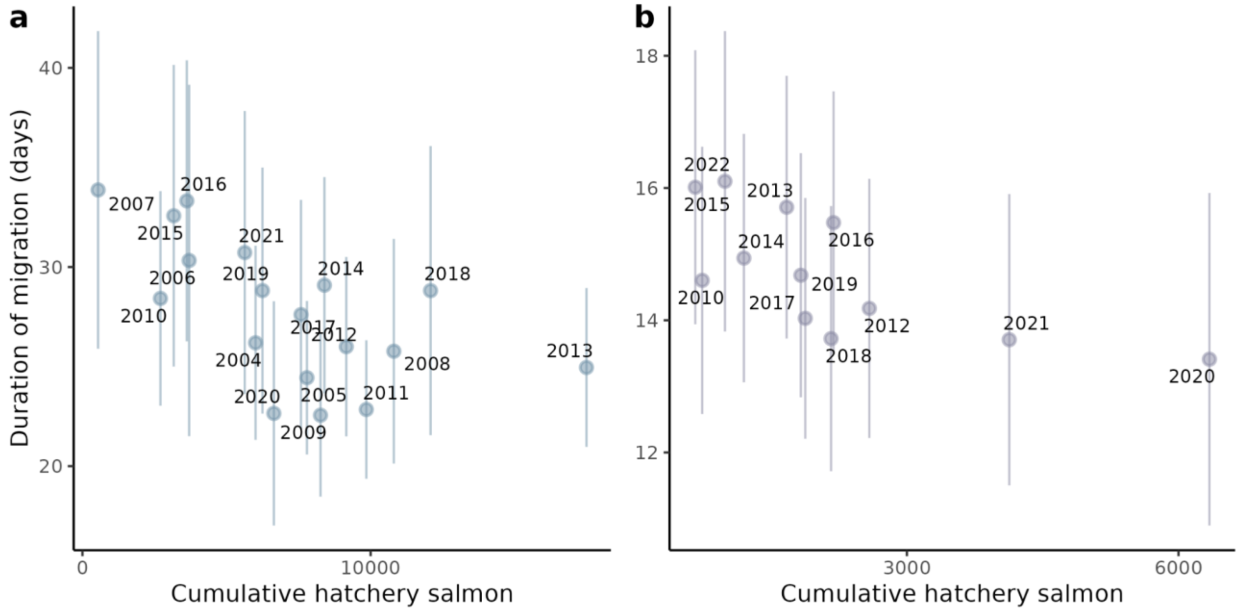


Figure 3.6. Effect of cumulative number of hatchery coho salmon released on the duration of migration (difference between the 75th percentile and 25th percentile) of coho salmon smolts in the a) Puyallup River and the c) Skagit River.

3.4.3 *Chum salmon*

We observed a significant negative effect of ATU on the peak migration timing of Chum salmon fry in the Dungeness River (p= 0.01). However, we did not find any such effect of ATU on the peak migration timing of chum salmon fry in the Skagit River (Figure 3.7). Furthermore, we did not find any effect of cumulative flow on the peak of migration of chum salmon fry in the Dungeness and Skagit rivers (Figure 3.7).

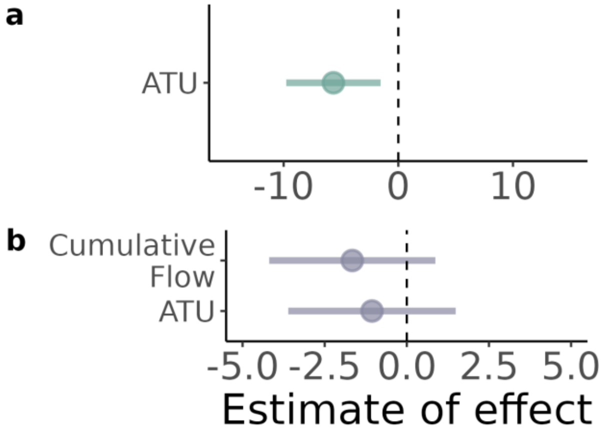


Figure 3.7. Estimates of the effect of environmental covariates on the peak migration day of chum salmon in the a) Dungeness River and the b) Skagit River.

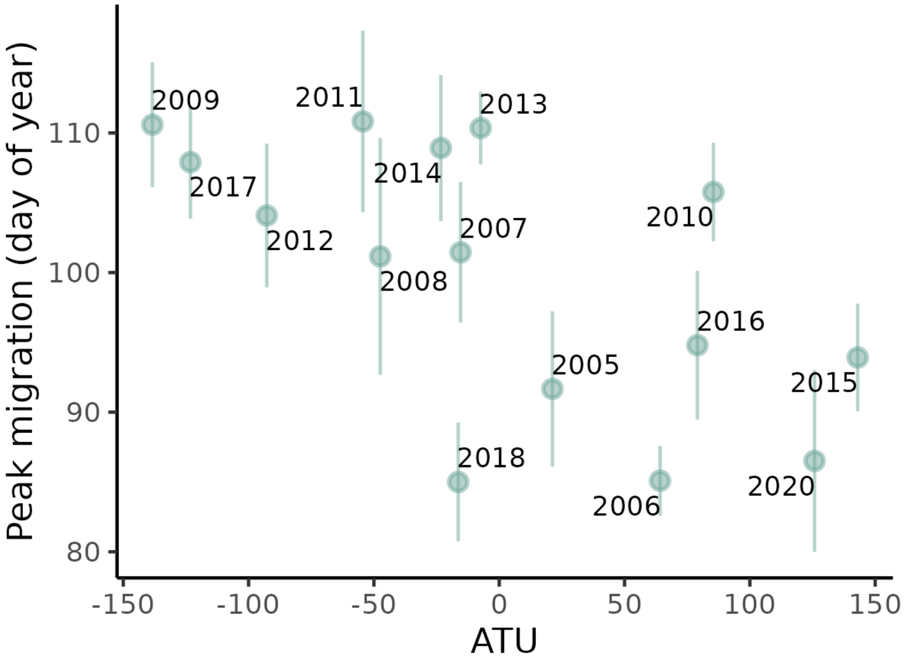


Figure 3.8. Effect of ATU on the peak migration day of chum salmon smolts in the Dungeness River.

3.5 DISCUSSION

Through our study we aimed to determine the effects of environmental factors and social cues on the timing of migration in sub-yearling Chinook salmon, yearling coho salmon, and sub-yearling chum salmon. We hypothesized that increasing temperature and flow would influence the peak migration timing of these juvenile salmon, anticipating an earlier migration with higher accumulated thermal units and higher cumulative flow. We also hypothesized that social cues would influence the migration of juvenile salmon and that a large number of hatchery salmon migrating downstream over a short period of time would motivate the wild salmon to join, thereby reducing the duration of migration of wild salmon. We found that Chinook salmon in the Dungeness and Skagit rivers as well as chum salmon in the Dungeness River migrate earlier in years with higher accumulated thermal units. We also found that coho salmon in all three rivers migrate earlier in years with higher cumulative flows. Finally, we found the duration of migration in coho salmon in the Puyallup and Skagit rivers is shorter when larger numbers of hatchery salmon are released earlier in the season.

Other studies have examined the influence of temperature on the migration timing of Chinook salmon smolts, demonstrating that higher stream temperatures advance the median migration date in Oregon (Roper and Scarnecchia 1999) and that increased accumulated thermal units (ATU) positively impact the number of Chinook salmon smolts migrating in British Columbia (Sykes, Johnson, and Shrimpton 2009), and our findings corroborates this relationship. Similarly, research focusing on the effects of stream temperatures on chum fry migration timing has indicated that migration occurs earlier in warmer years in both Washington (Weinheimer et al. 2017) and British Columbia (Holtby, McMahon, and Scrivener 1989), a pattern that aligns with our observations in the Dungeness River. Previous studies in California have also shown that an increase in median daily run-off advances the start of migration (Kastl et al., 2022), a result consistent with our finding of a negative effect of cumulative flow on the peak migration timing of coho salmon.

Numerous studies have demonstrated the influence of social behavior on the decision to initiate migration and subsequently on migration timing (Oestreich et al. 2022; Aikens et al. 2022). In salmon, research suggests social behavior in other life stages (Polyakov et al. 2022) as well as during the adult migration (Berdahl, Westley, and Quinn 2017; Okasaki et al. 2020). However, the influence of social cues on juvenile salmon migration is less well understood. Environmental factors alone do not account for all the variation in migration patterns, leading to speculation about the impact of social interactions on migration timing (Hvidsten et al. 1995). Previous work has shown that the large number of hatchery salmon migrating downstream is associated with a large number of wild salmon migrating downstream (Chapter 2). Our results are consistent with this hypothesis that the large number of hatchery salmon migrating downstream over a short period of time motivates the wild salmon to join, consequently shortening the duration of migration of the wild salmon. Having temporal variation in migration timing can increase the probability that some individuals will survive to adulthood (Schroeder et al. 2016). Therefore, factors that can lead to the contraction of the migration period can be detrimental for the population.

Some of our results diverge from expectations based on prior studies. We did not see an effect of ATU on the migration timing of chum fry in the Skagit River, despite temperature being closely linked to their emergence timing. However, chum salmon emergence and out-migration is closely linked to the timing of the adult spawning. Therefore, ATU calculated immediately after spawning may serve as a more accurate predictor of chum salmon out-migration timing in the Skagit River. Additionally, it's plausible that the temperature data we used, collected at Marblemount, lies upstream of chum salmon habitat. Nonetheless, chum salmon surveys are conducted in Marblemount, and we also reanalyzed the data using water temperature data from Mount Vernon (situated downstream of Marblemount and near the trap location), yielding consistent results. This discrepancy could arise from multiple chum salmon populations in the rivers experiencing different temperatures from those used in our analysis.

Similarly, we did not observe an effect of ATU on the migration timing of coho salmon, despite evidence indicating temperature's impact on their migration timing in British Columbia (Holtby, McMahon, and Scrivener 1989). This discrepancy might be attributed to a correlation between cumulative flow and ATU in the Dungeness River; however, the model incorporating cumulative flow exhibited a lower AIC. Nonetheless, this does not explain why we did not see an effect of temperature on the migration timing of coho salmon in the Puyallup and Skagit rivers. Considering that juvenile coho salmon spend a year in freshwater before migrating to the ocean, temperature fluctuations in the preceding year may also influence their emergence timing and growth.

Climate change is predicted to transition most of the watersheds included in this study from a mixed rain and snow watershed to rain dominant watersheds (Mantua, Tohver, and Hamlet 2010; Lee, Hamlet, and Grossman 2016) except for the upper Skagit watersheds that are higher in elevation (Mauger et al. 2015). Winter temperatures are projected to increase and will result in a longer growing season (Mauger et al. 2015) for juvenile salmon. Based on the results of our analysis, increasing winter temperatures are likely to advance the migration timing of sub-yearling Chinook salmon and sub-yearling Chum salmon. In addition to winter temperatures, spring precipitation is projected to increase with spring flows occurring earlier in the season (Mauger et al. 2015). The peak timing of spring flows are projected to advance by 18 days on average in the Puyallup River and by 15 days on average in the Dungeness River by the 2080’s (Mauger et al. 2015). On the other hand, peak flows in the Skagit River are predicted to shift from spring to fall or winter due to increases in temperatures and winter precipitation (Lee, Hamlet, and Grossman 2016). Advancing peak spring flows are likely to advance the migration timing of yearling coho salmon. Climate change will likely impact freshwater temperatures differently than marine water conditions. If the timing of migration is desynchronized with the timing of optimal conditions in the ocean, juvenile salmon migrating earlier might encounter suboptimal ocean conditions upon arrival which can negatively impact their survival. As we anticipate future shifts in climate patterns, characterized by increasing winter temperatures and altered precipitation regimes, our findings suggest potential advancements in the migration timing of various salmon species.

3.6 REFERENCES

Aikens, Ellen O., Iris D. Bontekoe, Lara Blumenstiel, Anna Schlicksupp, and Andrea Flack. 2022. “Viewing Animal Migration through a Social Lens.” *Trends in Ecology & Evolution* 37 (11): 985–96. https://doi.org/10.1016/j.tree.2022.06.008.

Allen, S. E., and M. A. Wolfe. 2013. “Hindcast of the Timing of the Spring Phytoplankton Bloom in the Strait of Georgia, 1968–2010.” *Progress in Oceanography*, Strait of Georgia Ecosystem Research Initiative (ERI), 115 (August):6–13. https://doi.org/10.1016/j.pocean.2013.05.026.

Austin, Catherine S., Christian E. Torgersen, and Thomas P. Quinn. 2023. “Who Spawns Where? Temperature, Elevation, and Discharge Differentially Affect the Distribution of Breeding by Six Pacific Salmonids within a Large River Basin.” *Canadian Journal of Fisheries and Aquatic Sciences* 80 (8): 1365–84. https://doi.org/10.1139/cjfas-2022-0252.

Baert, Jan M, Eric W M Stienen, Frederick Verbruggen, Nico Van De Weghe, Luc Lens, and Wendt Müller. 2022. “Resource Predictability Drives Interannual Variation in Migratory Behavior in a Long-Lived Bird.” Edited by Leigh W Simmons. *Behavioral Ecology* 33 (1): 263–70. https://doi.org/10.1093/beheco/arab132.

Beacham, Terry D., and Clyde B. Murray. 1990. “Temperature, Egg Size, and Development of Embryos and Alevins of Five Species of Pacific Salmon: A Comparative Analysis.” *Transactions of the American Fisheries Society* 119 (6): 927–45. https://doi.org/10.1577/1548-8659(1990)119<0927:TESADO>2.3.CO;2.

Bearhop, Stuart, Geoff M. Hilton, Stephen C. Votier, and Susan Waldron. 2004. “Stable Isotope Ratios Indicate That Body Condition in Migrating Passerines Is Influenced by Winter Habitat.” *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271 (suppl_4): S215–18. https://doi.org/10.1098/rsbl.2003.0129.

Beckman, Brian R., Donald A. Larsen, Beeda Lee-Pawlak, and Walton W. Dickhoff. 1998. “Relation of Fish Size and Growth Rate to Migration of Spring Chinook Salmon Smolts.” *North American Journal of Fisheries Management* 18 (3): 537–46. https://doi.org/10.1577/1548-8675(1998)018<0537:ROFSAG>2.0.CO;2.

Berdahl, Andrew, Peter A. H. Westley, and Thomas P. Quinn. 2017. “Social Interactions Shape the Timing of Spawning Migrations in an Anadromous Fish.” *Animal Behaviour* 126 (April):221–29. https://doi.org/10.1016/j.anbehav.2017.01.020.

Bridge, Eli S., Jeffrey F. Kelly, Paul E. Bjornen, Claire M. Curry, Priscilla H. C. Crawford, and Jacqueline M. Paritte. 2010. “Effects of Nutritional Condition on Spring Migration: Do Migrants Use Resource Availability to Keep Pace with a Changing World?” *Journal of Experimental Biology* 213 (14): 2424–29. https://doi.org/10.1242/jeb.041277.

Brooke, M. De L. 1979. “Differences in the Quality of Territories Held by Wheatears (Oenanthe Oenanthe).” *Journal of Animal Ecology* 48 (1): 21–32. https://doi.org/10.2307/4097.

Clausen, Kevin Kuhlmann, and Preben Clausen. 2013. “Earlier Arctic Springs Cause Phenological Mismatch in Long-Distance Migrants.” *Oecologia* 173 (3): 1101–12. https://doi.org/10.1007/s00442-013-2681-0.

Cushing, D. H. 1990. “Plankton Production and Year-Class Strength in Fish Populations: An Update of the Match/Mismatch Hypothesis.” In *Advances in Marine Biology*, edited by J. H. S. Blaxter and A. J. Southward, 26:249–93. Academic Press. https://doi.org/10.1016/S0065-2881(08)60202-3.

Dingle, Hugh. 2014. *Migration: The Biology of Life on the Move*. Oxford University Press.

Dingle, Hugh, and V. Alistair Drake. 2007. “What Is Migration?” *BioScience* 57 (2): 113–21. https://doi.org/10.1641/B570206.

Duffy, Elisabeth J, and David A Beauchamp. 2011. “Rapid Growth in the Early Marine Period Improves the Marine Survival of Chinook Salmon (Oncorhynchus Tshawytscha) in Puget Sound, Washington.” *Canadian Journal of Fisheries and Aquatic Sciences* 68 (2): 232–40. https://doi.org/10.1139/F10-144.

Hall, Eric S., Robert K. Hall, Sherman Swanson, Wilson Yee, Don Kozlowski, Michael J. Philbin, Daniel T. Heggem, et al. 2019. “Assessing Dungeness River Functionality and Effectiveness of Best Management Practices (BMPs) Using an Ecological Functional Approach.” *American Journal of Environmental Engineering* 9 (2): 36–54.

Heim, Kurt C., Mark S. Wipfli, Matthew S. Whitman, and Andrew C. Seitz. 2016. “Body Size and Condition Influence Migration Timing of Juvenile Arctic Grayling.” *Ecology of Freshwater Fish* 25 (1): 156–66. https://doi.org/10.1111/eff.12199.

Hillman, T. W., and J. W. Mullan. 1989. “Effect of Hatchery Releases on the Abundance and Behavior of Wild Juvenile Salmonids.” Final Report to Chelan County Public Utility District. Summer and Winter Ecology of Juvenile Chinook Salmon and Steelhead Trout in the Wenatchee River, Washington. McCall, Idaho: Don Chapman Consultants.

Hoar, William S. 1958. “The Evolution of Migratory Behaviour among Juvenile Salmon of the Genus *Oncorhynchus*.” *Journal of the Fisheries Research Board of Canada* 15 (3): 391–428. https://doi.org/10.1139/f58-020.

———. 1976. “Smolt Transformation: Evolution, Behavior, and Physiology.” *Journal of the Fisheries Research Board of Canada* 33 (5): 1233–52. https://doi.org/10.1139/f76-158.

Holtby, L. Blair, Thomas E. McMahon, and J. Charles Scrivener. 1989. “Stream Temperatures and Inter-Annual Variability in the Emigration Timing of Coho Salmon (*Oncorhynchus Kisutch*) Smolts and Fry and Chum Salmon (*o* . *Keta*) Fry from Carnation Creek, British Columbia.” *Canadian Journal of Fisheries and Aquatic Sciences* 46 (8): 1396–1405. https://doi.org/10.1139/f89-179.

Hvidsten, Nils Arne, Arne J. Jensen, Helga Vivas, Bakke Oyvind, and Tor G. Heggberget. 1995. “Downstream Migration of Atlantic Salmon Smolts in Relation to Water Flow, Water Temperature, Moon Phase and Social Interaction.” *Nordic Journal of Freshwater Research*, no. 70, 38–48.

Kastl, Brian, Mariska Obedzinski, Stephanie M. Carlson, William T. Boucher, and Theodore E. Grantham. 2022. “Migration in Drought: Receding Streams Contract the Seaward Migration Window of Endangered Salmon.” *Ecosphere* 13 (12): e4295. https://doi.org/10.1002/ecs2.4295.

Kerwin, John. 1999. “Salmon Habitat Limiting Factors.” Puyallup River Basin. Olympia, Washington: Citeseer.

Kuruvilla, Maria, Thomas P. Quinn, Joseph H. Anderson, Mark D. Scheuerell, Erika M. Miller, Andrew G. Berger, Connie Okasaki, et al. 2024. “Social Influences Complement Environmental Cues to Stimulate Migrating Juvenile Salmon.” Unpublished manuscript.

Macan, T. T. 1958. “The Temperature of a Small Stony Stream.” *Hydrobiologia* 12 (2): 89–106. https://doi.org/10.1007/BF00034143.

Maher, Susannah, and Curt Veldhuisen. 2023. “Stream Temperature Monitoring in Forested Tributaries of the Skagit River Basin: 15-Year Update and Analysis.”

Moss, Jamal H., David A. Beauchamp, Alison D. Cross, Katherine W. Myers, Edward V. Farley Jr., James M. Murphy, and John H. Helle. 2005. “Evidence for Size-Selective Mortality after the First Summer of Ocean Growth by Pink Salmon." *Transactions of the American Fisheries Society* 134 (5): 1313–22. https://doi.org/10.1577/T05-054.1.

Oestreich, William K., Kanoe M. Aiu, Larry B. Crowder, Megan F. McKenna, Andrew Berdahl, and Briana Abrahms. 2022. "The Influence of Social Cues on Timing of Animal Migrations." *Nature Ecology & Evolution* 6 (11): 1617–25. https://doi.org/10.1038/s41559-022-01866-0.

Okasaki, Connie, Matthew L. Keefer, Peter A. H. Westley, and Andrew Berdahl. 2020. "Collective Navigation Can Facilitate Passage through Human-Made Barriers by Homeward Migrating Pacific Salmon." *Proceedings of the Royal Society B: Biological Sciences* 287 (1937): 20202137. https://doi.org/10.1098/rspb.2020.2137.

Parker, Robert R. 1962. "Estimations of Ocean Mortality Rates for Pacific Salmon (*Oncorhynchus*)." *Journal of the Fisheries Research Board of Canada* 19 (4): 561–89. https://doi.org/10.1139/f62-037.

Polyakov, Anne Y., Thomas P. Quinn, Katherine W. Myers, and Andrew Berdahl. 2022. "Group Size Affects Predation Risk and Foraging Success in Pacific Salmon at Sea." *Science Advances* 8 (26): eabm7548. https://doi.org/10.1126/sciadv.abm7548.

Quinn, Thomas P. 2018. *The Behavior and Ecology of Pacific Salmon and Trout*. 2nd ed. Seattle: University of Washington Press.

Rickbeil, Gregory J. M., Jerod A. Merkle, Greg Anderson, M. Paul Atwood, Jon P. Beckmann, Eric K. Cole, Alyson B. Courtemanch, et al. 2019. "Plasticity in Elk Migration Timing Is a Response to Changing Environmental Conditions." *Global Change Biology* 25 (7): 2368–81. https://doi.org/10.1111/gcb.14629.

Roper, Brett B, and Dennis L Scarnecchia. 1999. "Emigration of Age-0 Chinook Salmon (*Oncorhynchus Tshawytscha*) Smolts from the Upper South Umpqua River Basin, Oregon, U.S.A." *Canadian Journal of Fisheries and Aquatic Sciences* 56 (6): 939–46. https://doi.org/10.1139/f99-023.

Rotics, Shay, Michael Kaatz, Sondra Turjeman, Damaris Zurell, Martin Wikelski, Nir Sapir, Ute Eggers, Wolfgang Fiedler, Florian Jeltsch, and Ran Nathan. 2018. "Early Arrival at Breeding Grounds: Causes, Costs and a Trade-off with Overwintering Latitude." *Journal of Animal Ecology* 87 (6): 1627–38.

Scheuerell, Mark D., Richard W. Zabel, and Benjamin P. Sandford. 2009. "Relating Juvenile Migration Timing and Survival to Adulthood in Two Species of Threatened Pacific Salmon (*Oncorhynchus* Spp.)." *Journal of Applied Ecology* 46 (5): 983–90. https://doi.org/10.1111/j.1365-2664.2009.01693.x.

Sirot, Etienne, and Frédéric Touzalin. 2014. "Temporal Patterns of Arrival from Migration as a Response to Competition for Breeding Space." *Journal of Avian Biology* 45 (1): 109–12. https://doi.org/10.1111/j.1600-048X.2013.00184.x.

Sykes, Gregory E., Chris J. Johnson, and J. Mark Shrimpton. 2009. "Temperature and Flow Effects on Migration Timing of Chinook Salmon Smolts." *Transactions of the American Fisheries Society* 138 (6): 1252–65. https://doi.org/10.1577/T08-180.1.

Weinheimer, Joshua, Joseph H. Anderson, Mark Downen, Mara Zimmerman, and Thom Johnson. 2017. "Monitoring Climate Impacts: Survival and Migration Timing of Summer Chum Salmon in Salmon Creek, Washington." *Transactions of the American Fisheries Society* 146 (5): 983–95. https://doi.org/10.1080/00028487.2017.1321580.

Wilson, Samantha M., Joseph H. Anderson, and Eric J. Ward. 2023. "Estimating Phenology and Phenological Shifts with Hierarchical Modeling." *Ecology* 104 (7): e4061.

https://doi.org/10.1002/ecy.4061.

Wilson, Samantha M., Jonathan W. Moore, Eric J. Ward, Clayton W. Kinsel, Joseph H. Anderson, Thomas W. Buehrens, Charmaine N. Carr-Harris, et al. 2023. "Phenological Shifts and Mismatch with Marine Productivity Vary among Pacific Salmon Species and Populations." *Nature Ecology & Evolution* 7 (6): 852–61. https://doi.org/10.1038/s41559-023-02057-1.

3.7 SUPPLEMENTARY INFORMATION

3.7.1 *Chinook salmon*

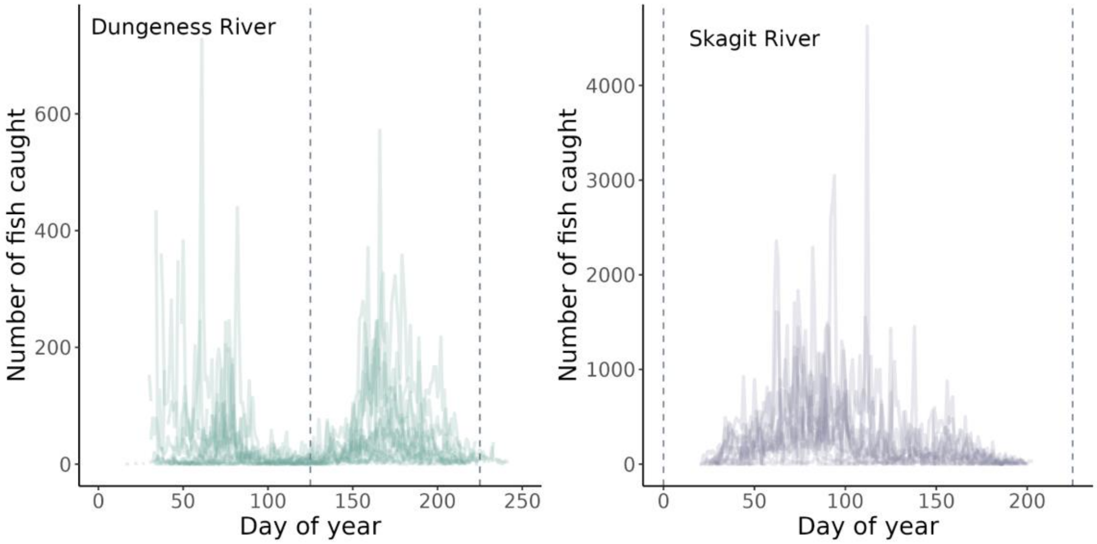


Figure 3.9. Daily catches for wild sub-yearling Chinook salmon in the Dungeness (years 2005-2020) and Skagit rivers (years 2010-2022). Data from every year available is overlaid. The vertical dashed lines bracket the period when wild salmon were caught in the trap, which was the portion of data we used for the analysis.

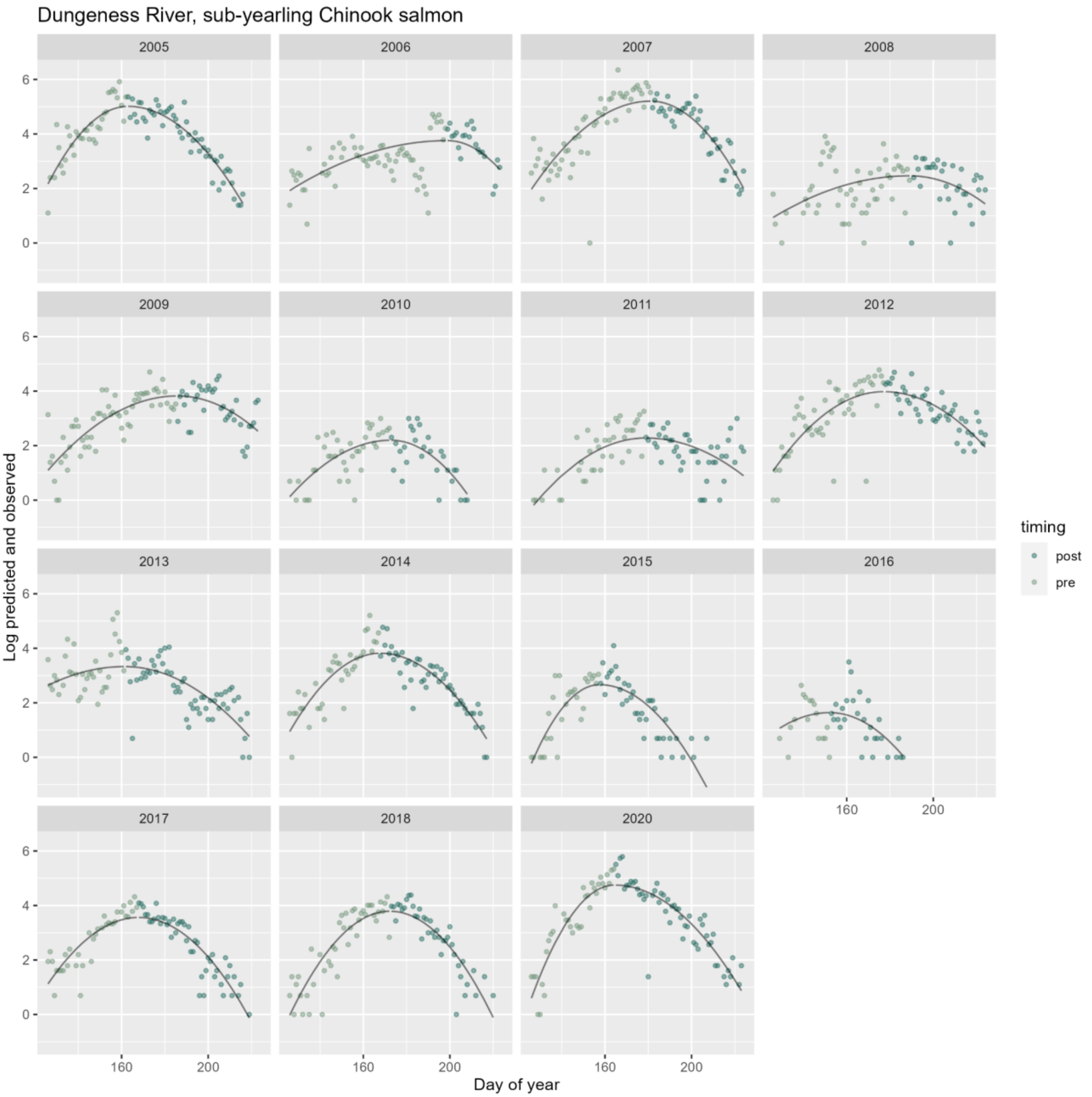


Figure 3.10. Observations and fitted values of sub-yearling Chinook salmon in the Dungeness River. The model with the lognormal family and gaussian tails had the lowest AIC.

Figure 3.11. Observations and fitted values of sub-yearling Chinook salmon in the Skagit River. The model with the lognormal family and student-t tails had the lowest AIC.

3.7.2 *Coho salmon*

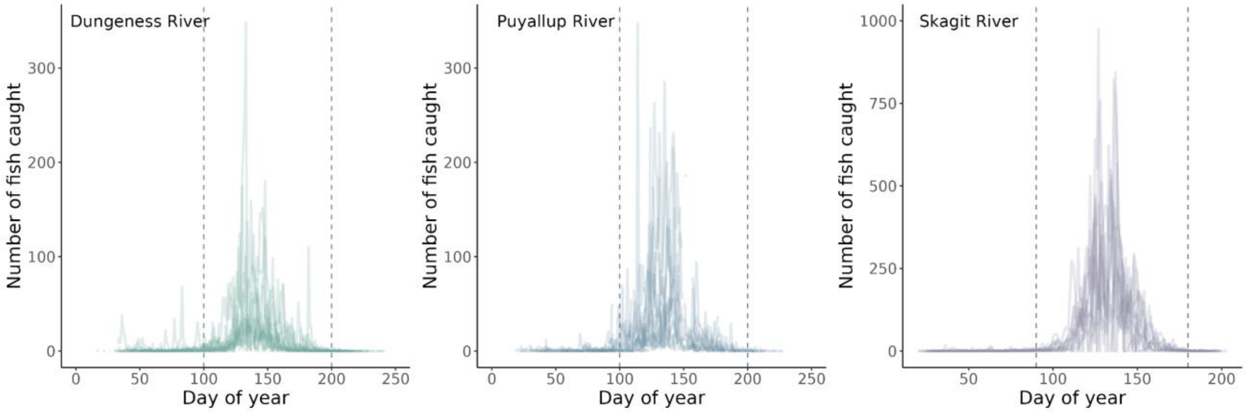


Figure 3.12. Daily catches for wild yearling coho salmon in the Dungeness (years 2005-2020), Puyallup (years 2004-2021), and Skagit rivers (years 2010-2022). Data from every year available is overlaid. The vertical dashed lines bracket the period when wild salmon were caught in the trap, which was the portion of data we used for the analysis.

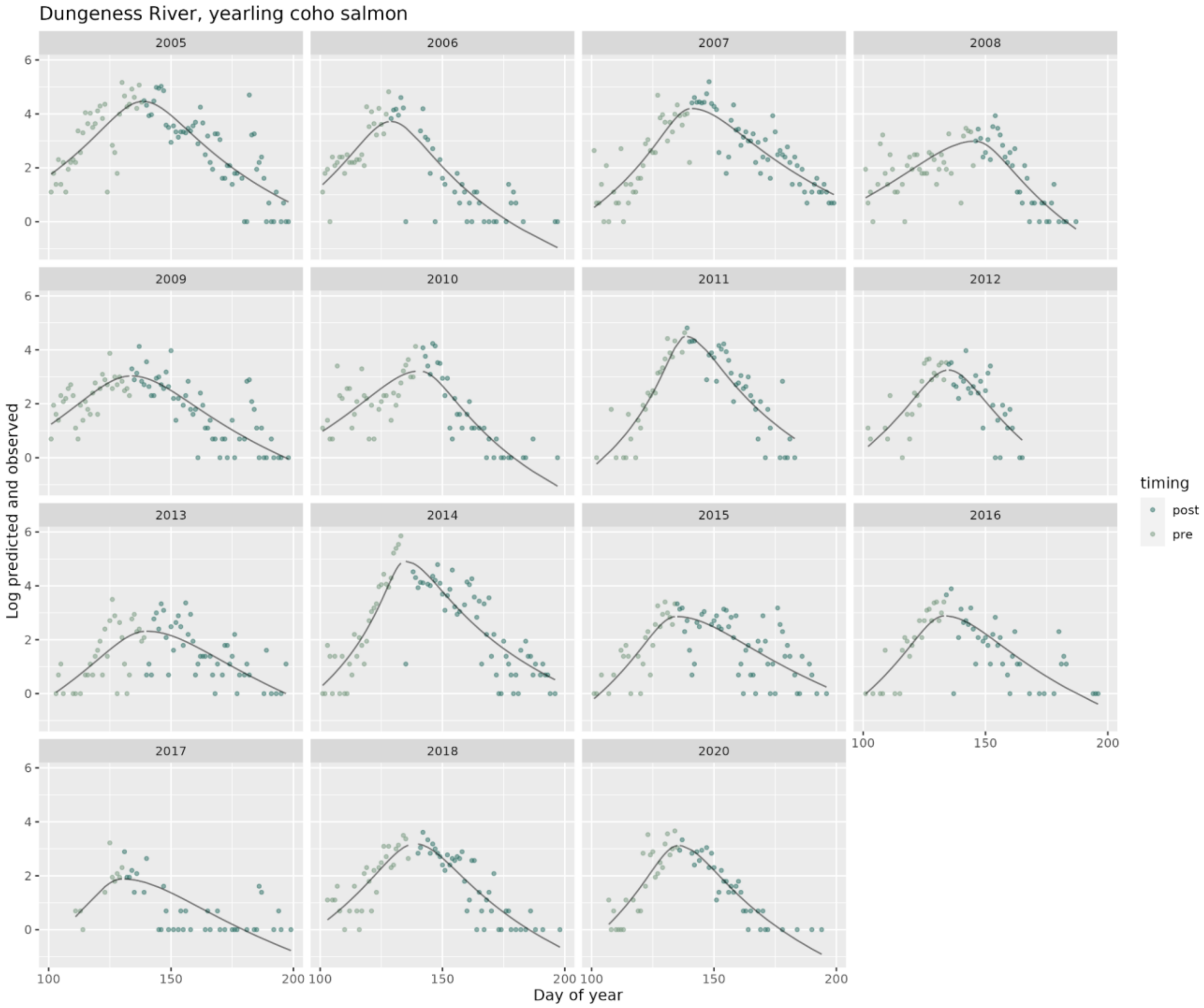


Figure 3.13. Observations and fitted values of yearling coho salmon in the Dungeness River. The model with the lognormal family and student-t tails had the lowest AIC.

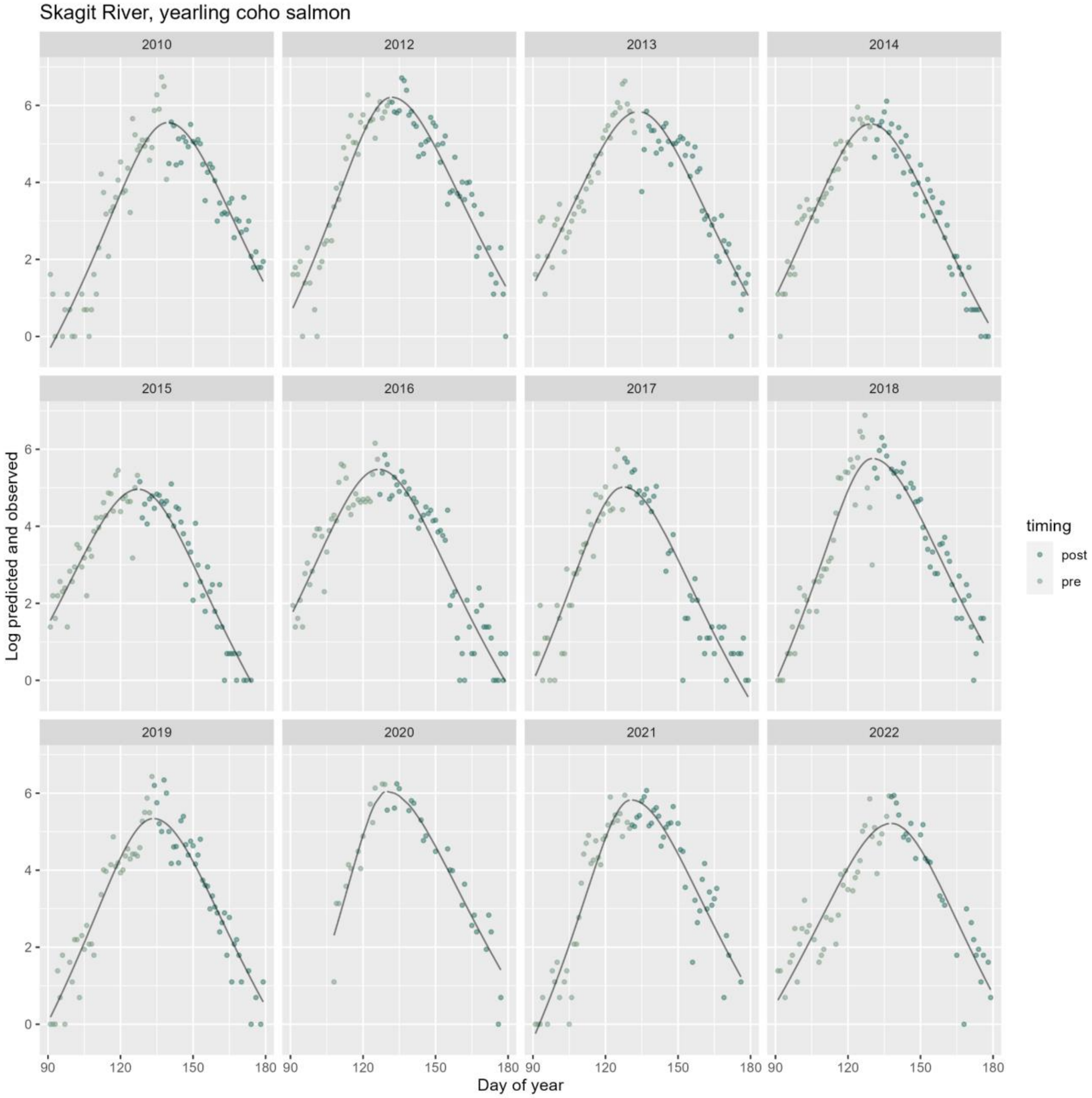


Figure 3.14. Observations and fitted values of yearling coho salmon in the Skagit River. The model with the lognormal family and student-t tails had the lowest AIC.

3.7.3 *Chum salmon*

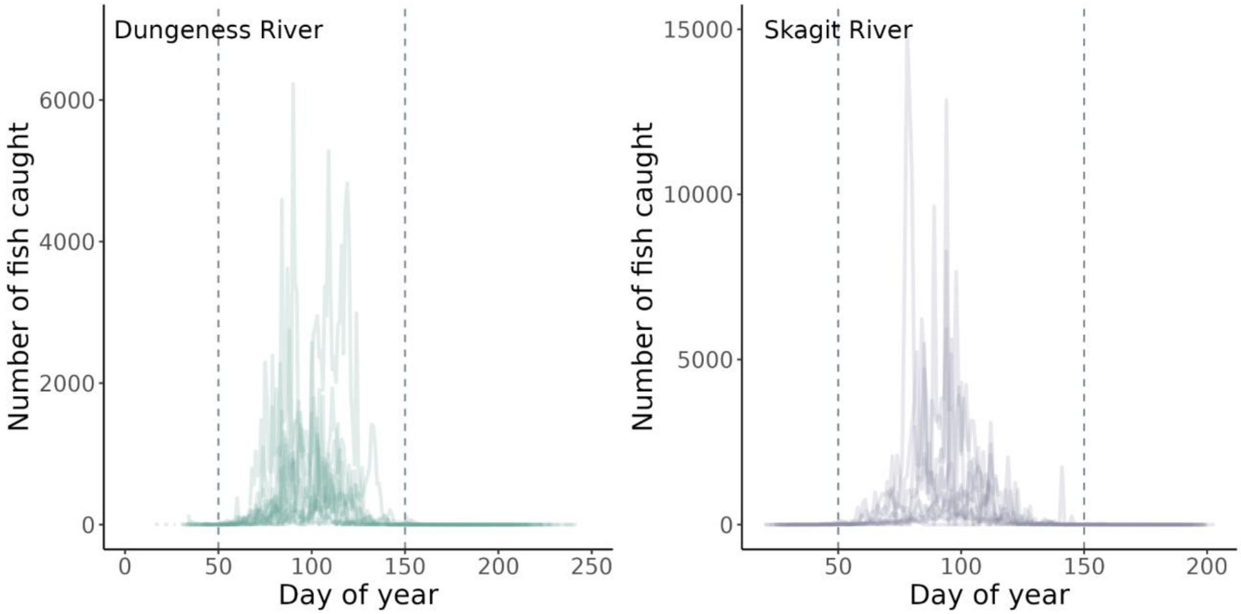


Figure 3.15. Daily catches for wild sub-yearling chum salmon in the Dungeness (years 2005-2020) and Skagit rivers (years 2010-2022). Data from every year available is overlaid. The vertical dashed lines bracket the period when wild salmon were caught in the trap, which was the portion of data we used for the analysis.

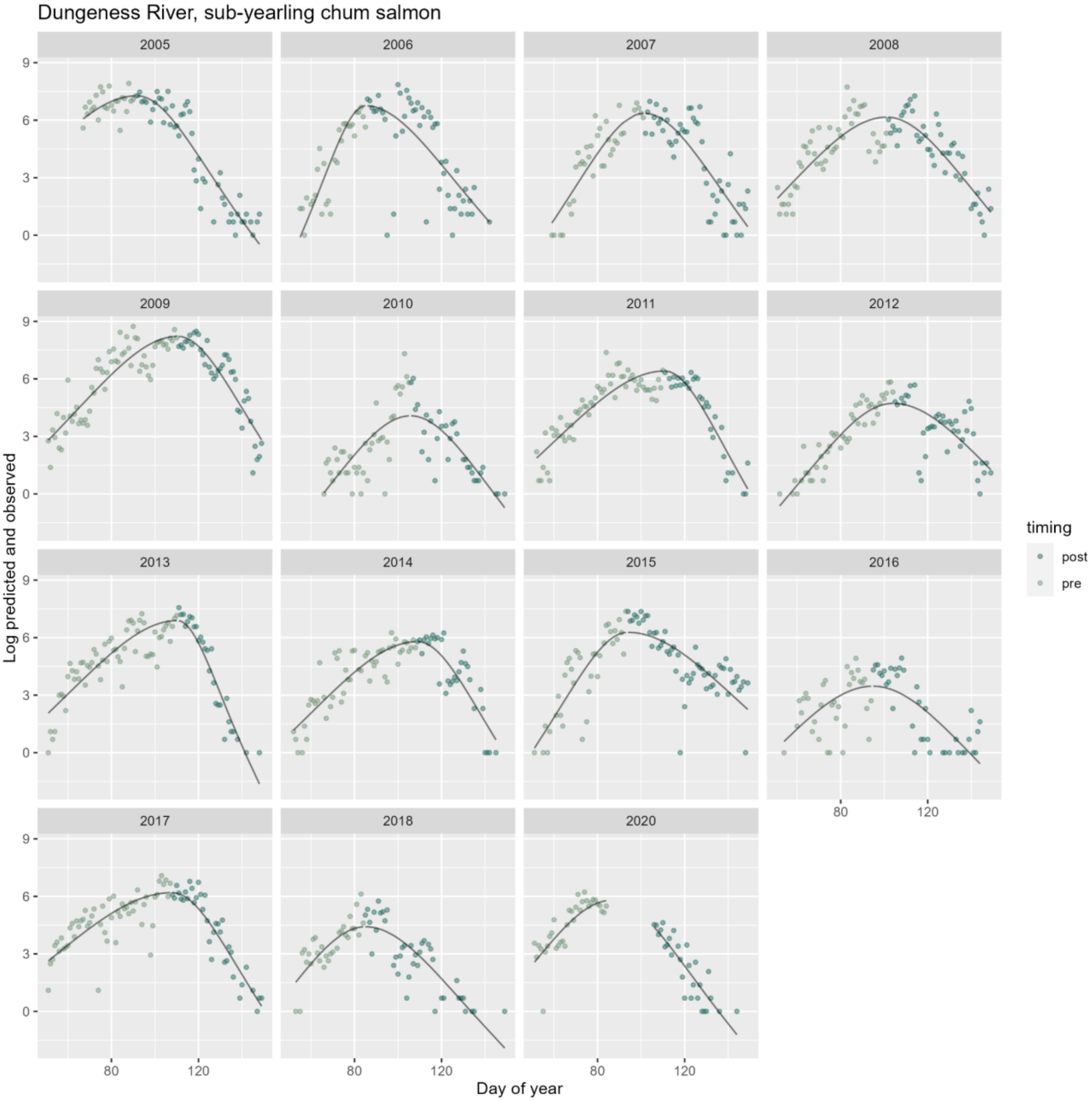


Figure 3.16. Observations and fitted values of sub-yearling chum salmon in the Dungeness River. The model with the lognormal family and student-t tails had the lowest AIC.

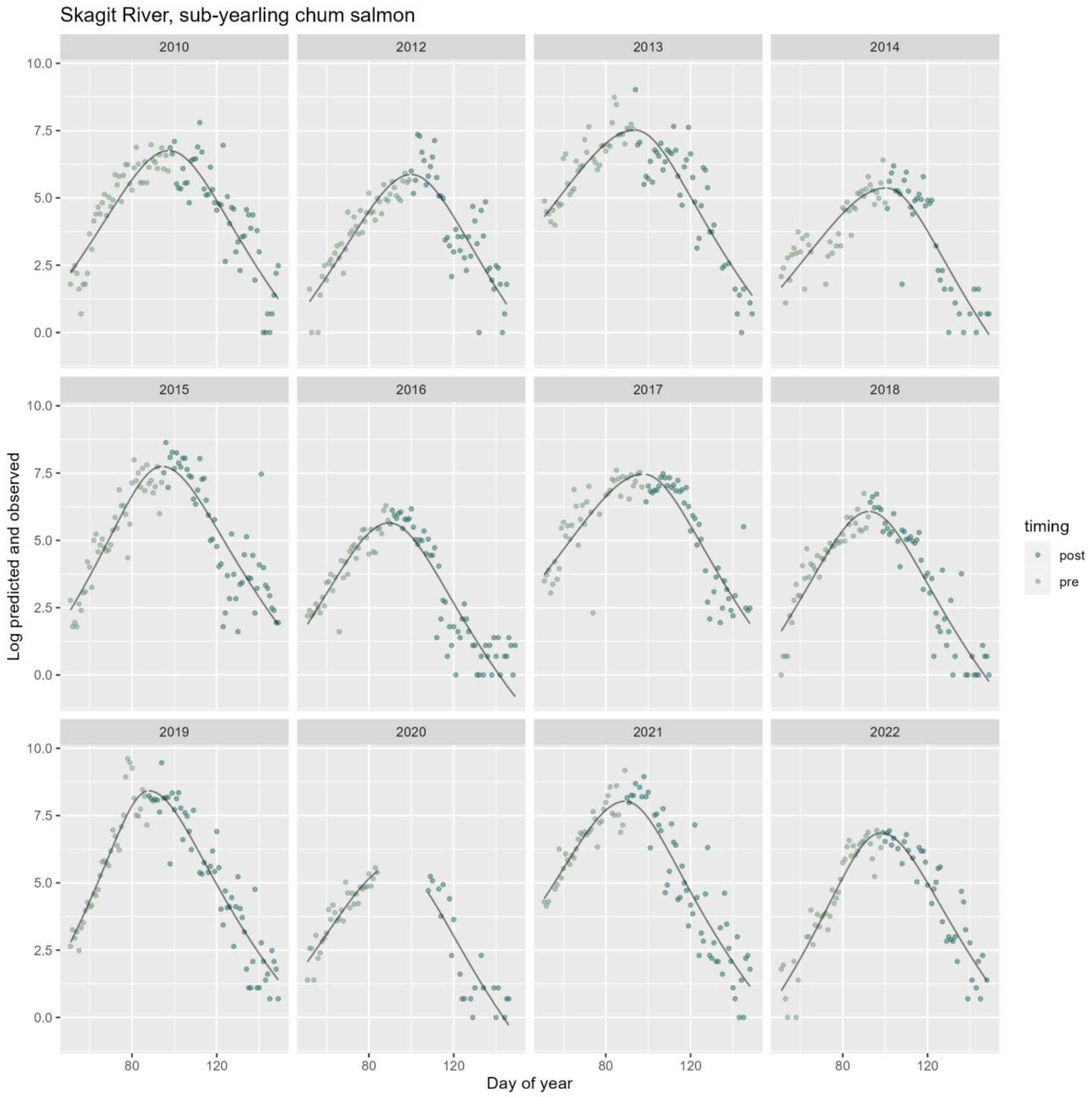
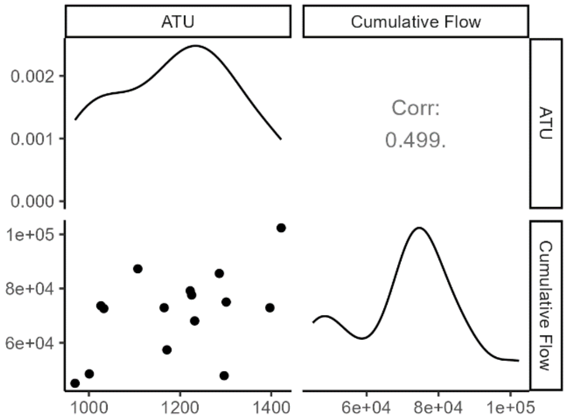


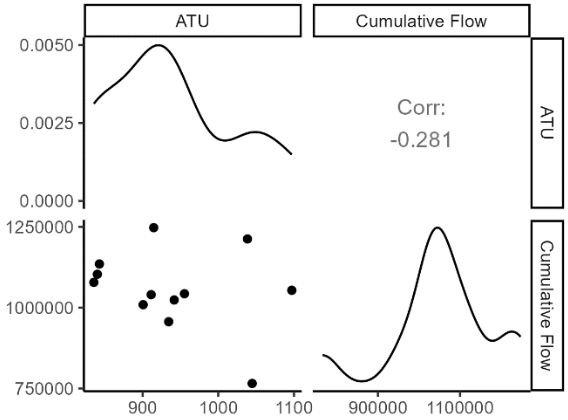
Figure 3.17. Observations and fitted values of sub-yearling chum salmon in the Skagit River. The model with the lognormal family and student-t tails had the lowest AIC.

3.7.4 *Correlation between ATU and Flow*

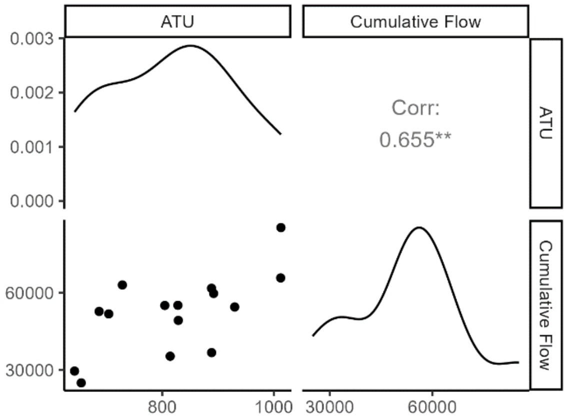
3.7.4.1 Chinook salmon, Dungeness River



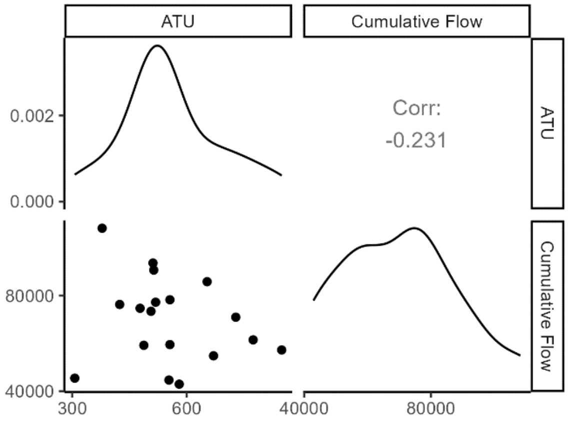
3.7.4.2 Chinook salmon, Skagit River



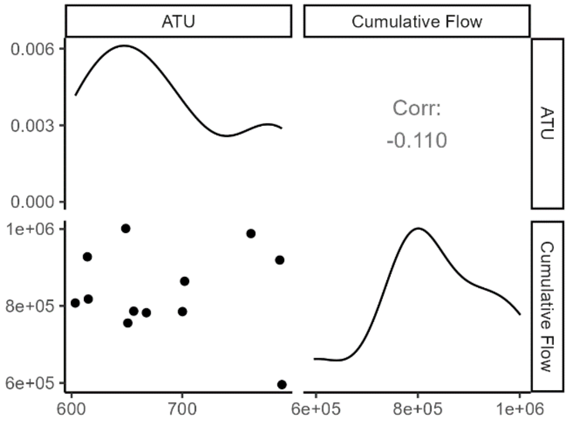
3.7.4.3 Coho salmon, Dungeness River



3.7.4.4 Coho salmon, Puyallup River



3.7.4.5 Coho salmon, Skagit River



3.7.5 *Estimates from phenomix models*

Species	River	Covariate	Estimate	Standard error	p value
Chinook	Dungeness	atu	-7.35	2.9	0.01
		hatchery_sigma1	-3.59	2.46	0.14
		hatchery_sigma2	-1.55	1.28	0.23
	Skagit	atu	-7.5	2.29	0
		flow	-2.85	2.22	0.2
Coho	Dungeness	flow	-2.78	1.23	0.02
		hatchery_sigma1	-0.65	1.46	0.66

		hatchery_sigma2	2.25	1.51	0.13
	Puyallup	atu	-0.8	0.96	0.41
		flow	-1.63	0.84	0.05
		hatchery_sigma1	-0.14	1.5	0.93
		hatchery_sigma2	-6.01	2.47	0.02
	Skagit	atu	-0.28	1.08	0.8
		flow	-2.2	1.08	0.04
		hatchery_sigma1	-2.3	0.69	0
		hatchery_sigma2	0.44	0.43	0.31
Chum	Dungeness	atu	-5.66	2.1	0.01
	Skagit	atu	-1.06	1.3	0.41
		flow	-1.66	1.29	0.2

VITA

Maria Kuruvilla was trained as a physicist at the University of Delhi, and then later at IUPUI at Indianapolis. Maria spent a year in between at the National Center for Biological Sciences, where she was introduced to studying living phenomena. While at the University of Washington, Maria specialized in using statistical methods towards understanding ecological problems, more specifically collective behavior. Maria feels privileged to have spent six years in the Pacific Northwest and is looking forward to a few more years just north of the border at the University of Victoria and the Salmon Coast Field Station.