

Collective navigation can facilitate passage through human-made barriers by homeward migrating Pacific salmon

Connie Okasaki^{1,2*}, Matthew L. Keefer³, Peter A. H. Westley⁴, Andrew M. Berdahl^{1,2*}

¹Quantitative Ecology & Resource Management Program, University of Washington, Seattle, WA 98195, USA; ²School of Aquatic & Fishery Sciences, University of Washington, Seattle, WA 98195, USA; ³Department of Fish & Wildlife Sciences, College of Natural Resources, University of Idaho, Moscow, ID 83844-1136, USA; ⁴Department of Fisheries, University of Alaska Fairbanks, Fairbanks, AK 99775, USA

Abstract The mass migration of animals is one of the great wonders of the natural world. Although there are multiple benefits for individuals migrating in groups, an increasingly recognized benefit is collective navigation, whereby social interactions improve animals' ability to find their way. Despite substantial evidence from theory and lab-based experiments, empirical evidence of collective navigation in nature remains sparse. Here we used a unique large-scale radiotelemetry dataset to analyze the movements of adult Pacific salmon (*Oncorhynchus* sp.) in the Columbia River Basin, USA. These salmon face substantial migratory challenges approaching, entering, and transiting fishways at multiple large-scale hydroelectric mainstem dams. We assess the potential role of collective navigation in overcoming these challenges and show that Chinook salmon (*O. tshawytscha*), but not sockeye salmon (*O. nerka*) locate fishways faster and pass in fewer attempts at higher densities, consistent with collective navigation. The magnitude of the density effects were comparable with major established drivers such as water temperature, and model simulations predicted that major fluctuations in population density can have substantial impacts on key quantities including mean passage time and fraction of fish with very long passage times. The magnitude of these effects indicate the importance of incorporating conspecific density and social dynamics into models of the migration process. Density effects on both ability to locate fishways and number of passage attempts have the potential to enrich our understanding of migratory energetics and success of migrating anadromous salmonids. More broadly, our work reveals a potential role of collective navigation, in at least one species, to mitigate the effects of anthropogenic barriers to animals on the move.

Introduction

Long distance migration is an iconic and threatened behavior (Wilcove and Wikelski, 2008). Migratory species navigate with incredible precision to and from highly spatially restricted locations (Bingman and Cheng, 2005). To solve these challenging navigational problems, species use mechanisms ranging from an innate sun compass (Reppert et al., 2010) and magnetic maps (Putman et al., 2014) to learned olfactory cues (Dittman and Quinn, 1996; Keefer and Caudill, 2014). However, long-distance migrations are threatened by human influence (Berger, 2004). Fences, highways, and other developments block terrestrial migration pathways (Seidler et al., 2015), light pollution interferes with aerial migrations (Gauthreaux Jr et al., 2006) and dams and de-watering impede passage both upstream and downstream (e.g. Norrgård et al. (2013)). In light of these impacts, it is essential to understand the mechanisms of navigation in order to predict and mitigate human impacts on migratory populations.

Many species migrate in large groups, and it is thought that this may aid navigation (Berdahl et al., 2018). Theory suggests that such *collective navigation* may be the result of a number of mechanisms. For example, groups can increase accuracy by averaging over error-prone individual directional estimates — known as the “many wrongs” principle (Codling et al., 2007). Even without individual-level directional estimates, accurate directional responses can emerge through social interactions between group-mates — known as “emergent sensing” (Berdahl et al., 2013). We direct interested readers to Box 1 of Berdahl et al. (2018) for an overview of these and other mechanisms including leadership (Couzin et al., 2005), and social and collective learning (Fagan et al., 2012; Kao

et al., 2014). A growing body of empirical literature lends compelling support to these hypothesized mechanisms, but evidence from wild populations is rare (*Berdahl et al.*, 2018).

One iconic example of a migratory species is salmon, which home in large numbers back to their natal spawning grounds. Salmon navigation is still not fully understood but is known to include an inherited magnetic map (*Putman et al.*, 2014) and olfactory recognition of natal water (*Dittman and Quinn*, 1996). *Berdahl et al.* (2016b) hypothesized that salmon use collective navigation, based on seven independent studies reporting positive associations between homing accuracy and run size. However, like many migratory species, salmon face an anthropogenic barrier: dams. For example, the impassable Swan Falls Dam on the Snake River in Idaho rendered approximately 25% of mainstem riverine habitat inaccessible to Snake River Chinook salmon. A study of fall-run Chinook spawning habitat on the Columbia River found that between impassable dams and altered flow regimes, less than 20% of historical spawning habitat for fall-run Chinook remained available (*Dauble et al.*, 2003). Many dams have fishways, which allow salmon to pass by these barriers. However, locating a fishway entrance is non-trivial, since salmon use rheotaxis to move upstream, and the main source of flow at most dams is the spillway or turbines. Adult salmon migrations are often delayed in dam tailraces, and this delay may bear important costs, including increased exposure to predation (e.g. *Keefer et al.* (2012)) and increased energy output which can lead to greater mortality (e.g. *Burnett et al.* (2014)). Thus, if collective navigation eases the dam passage process, it may have an important effect on salmon survival and reproductive success, and therefore important implications for population conservation.

Here, we use radiotelemetry data on adult Chinook (*Oncorhynchus tshawytscha*) and sockeye salmon (*Oncorhynchus nerka*) navigating upstream past dams on the Columbia River, combined with daily fish counts at the dams, to evaluate the hypothesis that collective navigation helps salmon overcome the navigational challenges posed by fishways. We find strong evidence that Chinook salmon find and commit to fishways more rapidly on higher-density days. Evidence for density effects in sockeye salmon, and for Chinook salmon navigating within fishways, was weak. Although some prior evidence exists for negative density effects in similar contexts (e.g. *Goerig and Castro-Santos* (2017)), we did not find any prior evidence of negative density effects in either sockeye or Chinook salmon.

System & Methods

Study System

The Columbia River drains >600,000 km-sq of seven western U.S. states and two Canadian provinces and historically supported some of the most abundant Pacific salmon and steelhead runs in the world (*Chapman*, 1986). The basin has been transformed by hydroelectric development, with 14 large dams on the main stem Columbia River and 20 dams on the main stem Snake River, the Columbia's largest tributary by area. The dams, along with overharvest, habitat loss, and artificial propagation, contributed to steep declines in Columbia River salmon populations (*Lichtowich*, 2001) and subsequent threatened or endangered status under the U.S. Endangered Species Act (*NFSC*, 2015).

Upstream-migrating adult salmonids can pass many of the Columbia basin dams via pool-and-weir fishways (*Katopodis and Williams*, 2012) that rise ≈ 17 –56 m per dam. To navigate past the dams, adults first pass through turbulent, high-velocity tailraces that are several kilometers long and >1 km wide. Fish must then locate low-volume fishway openings sited near powerhouses or adjacent to spillways, move through a series of collection channels and junction pools, ascend a fish ladder, and then exit into the upstream reservoir (Figure 1). The spatial scale and hydraulic complexity of dam tailraces and fishways present several navigational and physiological challenges. The combination of searching for passage routes and fishway exit and re-entry behaviors, for example, is energetically demanding, particularly when fish make multiple passage attempts (*Brown et al.*, 2006; *Crozier et al.*, 2017). Typical upstream migration rates for Chinook and sockeye salmon in undammed sections of the Columbia basin range from ≈ 18.5 –52.7 km/day (*Fryer et al.*, 2012). In contrast, adult salmonids take ≈ 1 –3 days to pass each main stem dam along their Columbia River migration route (*Keefer et al.*, 2004). These tailrace and dam reaches range in length from 0.5–3.2 km, such that, on average, the fish are travelling 0.17–3.2 km/day during dam passage (a ≈ 10 –100-fold reduction in up-stream passage speed), potentially delaying timely arrival at spawning sites.

Data Collection

Data used in this study were from salmon collected and radio-tagged at Bonneville Dam in 2013 and 2014 using previously-described methods (*Keefer et al.*, 2004; *Caudill et al.*, 2007). Bonneville Dam is at Columbia River kilometer (rkm) 235.1 and is the first dam returning adult salmon encounter during their upstream migration. Telemetered fish were monitored at multiple dams and in tributaries, but analyses focused on data collected as fish entered tailraces and passed through fishways at The Dalles Dam (TD;

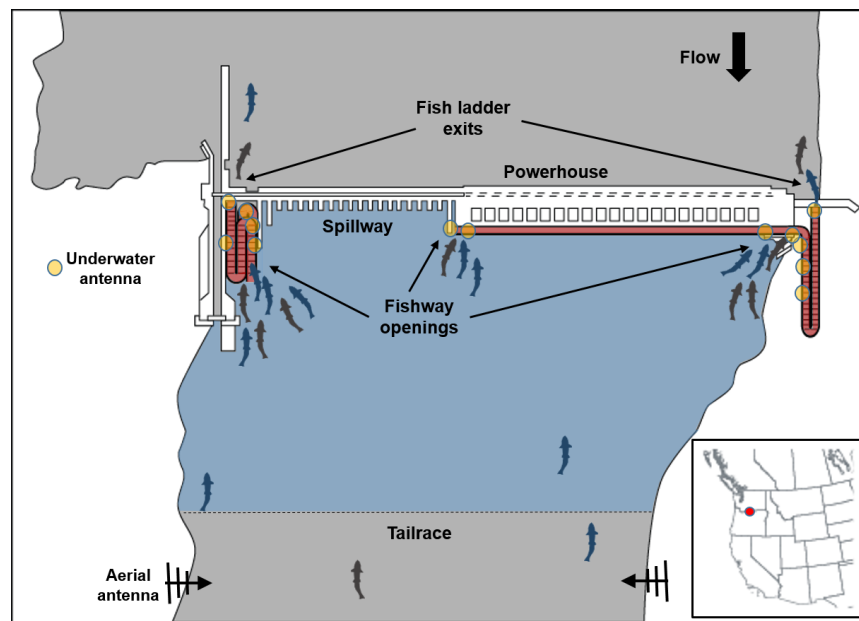


Figure 1. Schematic of John Day Dam. Layout of The Dalles Dam is qualitatively similar. The John Day facility is 2,327-m long and 56-m high and has two adult fishways: one on each shoreline. The tailrace antennas were 1.8 km downstream from the dam (3.2 km at The Dalles Dam). Multiple underwater antennas were used to monitor fish passage into and through the fishways. Components of this schematic are not to scale. We modeled three processes: the “finding” time from when a fish enters a tailrace (blue) to when it first enters a fishway (red); the “fishway” time from when a fish last enters a fishway to when it exits into the upstream reservoir; and the “commit” probability that a fish passes all the way through a fishway on its first attempt.

rkm 308.1) and John Day Dam (JD; rkm 346.9), the second and third dams from the Pacific. Monitoring arrays at the two projects included aerial 9-element Yagi antennas sited on tailrace shorelines 1.8–3.2 rkm downstream from the dams and underwater coaxial cable antennas at fishway openings, inside fishway collection channels and junction pools, and in fish ladders (Keefer *et al.*, 2004, 2013b). Detection ranges for the aerial antennas ranged from 100s of m to >1 km, depending on fish depth (Melnichuk, 2012). Ranges for the underwater antennas were 5–15 m. The raw telemetry data from all antennas were assembled, filtered, and coded using established methods (Keefer *et al.*, 2004; Caudill *et al.*, 2007); files of coded records were then used to identify when salmon entered and exited tailraces and fishways.

We obtained daily counts of salmon from the Columbia Basin Research Data Access in Real Time (DART) database (CBR, 2015) and environmental data including water temperature and spillway discharge from the US Geological Survey’s (USGS) National Water Inventory System (NWIS) database (<https://waterdata.usgs.gov/nwis>). This synthesis of several different sources of data was crucial for our analysis. Daily counts are collected by human observers watching through windows, and are able to capture a large fraction of passing fish. These data are therefore suited to measuring density, but not to modeling individual passage rates. On the other hand, telemetry arrays are more expensive and technical, capturing only a small fraction of fish, but allow much more detailed observations of those fish which are tagged. These data allowed us to model passage rates for individual fish. Although the synthesis of these datasets was of great benefit, it also introduced several challenges, discussed in the following section. Most notably, counts were *not* a direct measurement of fish density.

Modeling Approach

We split the process of passing a dam into a sequence of three distinct stages: i) the “finding” process which starts at a fish’s first detection in a tailrace and continues until its first detection at a fishway opening; ii) the “committing” process which models the probability that a fish actually passes all the way through a fishway to the upstream exit on its first attempt, rather than exiting back into the tailrace; and iii) the “fishway” process which starts when a fish enters a fishway and commits (i.e. the last fishway entrance) and continues until the fish exits from the top of the ladder.

We modeled the “finding” and “fishway” processes using a time-to-event analysis framework (for a general introduction, see Kleinbaum and Klein (2010)). We modeled the “committing” process using a logistic regression. A detailed technical description of our models and diagnostics can be found in the electronic supplementary materials (ESM).

We will now briefly explain the concepts underlying time-to-event analysis before discussing the special challenges we faced. A time-to-event dataset consists of a series of observations through time of an individual along with a set of covariates for that individual. Generally, we were interested in one or more “events” and we wished to understand how long it took for these events to occur. This type of data is very common in medical studies where “events” are often negative patient outcomes such as death; for this reason time-to-event models are often referred to as “survival” models. In our case we were interested in two events: the event of entering a fishway, and the event of exiting a fishway into the upstream reservoir. We must also define the starting time for each analysis: respectively, the entrance to the tailrace and the last entrance to the fishway. In other words, our first model was designed to answer the question: “how quickly does a fish find and subsequently enter a fishway after entering a tailrace, and how does this rate vary with salmon density, temperature, and other covariates?” Our second model was similarly designed to answer the question “how quickly does a fish navigate and subsequently exit a fishway after entering it and committing to passage?” More complex “multi-state” models tie together all these events in a sequence (*Andersen et al., 2002*), but to simplify the rest of our analysis we used more tractable single-process models. The remainder of this section discusses the mathematical underpinnings of the time-to-event modeling framework, as well as the special challenges we faced in our analysis.

We used a common time-to-event model known as the proportional hazards (PH) model. A hazards model assumes that the time-to-event process is essentially an exponential decay, with an event rate $\lambda(t|X)$ (the “hazard function”) which changes depending on both how long it has been since the fish entered the system, t , and with a set of covariates X . The PH model assumes that this rate depends on covariates according to the equation

$$\lambda(t|X) = \lambda_0(t) \exp(X\beta).$$

The function $\lambda_0(t)$ is known as the baseline hazard function. A common variant of these time-to-event models are models with time-varying covariates. In our case, covariates such as temperature, spillway discharge, and fish density were constantly changing and the rate at which fish passed through the dam was assumed to vary proportionately. An advantage we had over many time-to-event analyses was that our time-varying covariates were environmental rather than individual. This gave us the ability to simulate from our model, even if the simulation dictated that individuals should “survive” longer than they were truly observed, since we could continue to assign time-varying covariates correctly.

Our focus was on the effect of density, which we quantified using daily counts of individuals passing observation windows within the fish ladder portion of the fishway, obtained from the separate, much larger DART database (*CBR, 2015*). This use of counts introduced two major problems. First, our count covariate was a product of density and hazard: when fish were passing through the fishway more quickly, a higher proportion of them would be counted over the course of a day. This introduced reverse causality: a high rate (the response) caused our counts (a predictor) to be higher. Moreover, since hazard varied substantially over the course of a day, the relationship between counts and density was inconsistent. Second, the fish observation windows are placed near the middle of the fish ladders. Thus there was an unknown amount of time between when a fish triggered a telemetry reading and when it and its nearest neighbors were counted by the fish count observers. A third concern, not related to our use of counts, was that density is related to hazard through time: when fish are passing through a fishway more quickly, fewer of them remain behind to contribute to density. In other words, high passage rates deplete density over time. This introduced another source of reverse causality.

These three issues posed a substantial challenge. The first and last were particularly worrisome, since reverse causality has the potential to bias model fits and produce spurious results. Even if there was no true causal effect of density, we might observe significant density coefficients in our models. For example, suppose that due only to other unmeasured covariates or random chance, some days have a higher than average rate of fish movement into a fishway. On those days we would observe a higher count, so that empirically that rate of passage would positively correlate with count. However, this association would be purely due to the fact that counts increase with passage rate.

We took two major steps to account for these modeling challenges. First, although hourly count data was available, we used daily count data as our estimate of density. Since a consistently high proportion of radio-tagged fish in our dataset passed within 24 hours (>97%), and relatively few fish passed overnight (<10% entering the fishway and <5% exiting to the reservoir), the daily count provided a roughly accurate assessment of daily density while smoothing out any within-day variation in passage rate. On the other hand, hourly counts are far more dependent on random chance and are systematically biased due to strong diel behavioral and environmental effects. Moreover, hourly counts introduce the potential for greater biases due to the time lag between a tagged fish triggering a telemetry event and being counted by a count observer.

Second, we used a parametric bootstrap to account for reverse causality. Our bootstrap analysis was justified using the following chain of logic. First, our system violated modeling assumptions and our models may therefore produce biased inference. Second,

if density truly has no effect then counts have no effect. In this case we need not include counts as a covariate, and our models should provide valid unbiased fits. Therefore, simulations from models with no count covariates produce valid null distributions. By fitting models *with* count covariates to these null-model simulations, we obtained a null distribution for the count coefficient. Even if the above problems induced reverse causality in our dataset, our null distribution remains valid, since it assumes no effect of density. Therefore we can use such a null distribution to conduct valid inference. Due to reverse causality, the power of our tests remains unknown, but we may correctly calculate the p -values. For a more detailed introduction to bootstraps in general see [Efron and Tibshirani \(1994\)](#). From here on we will use *null model* to mean a model without a count covariate (sometimes, the best fitting such model) and *full model* to mean a null model with the addition of a count covariate.

Statistical Analysis

To satisfy model assumptions, we split our initial 6 models (2 species \times 3 processes) into 13 models: 11 PH models and 2 logistic regression models. By splitting a model, we mean we split the dataset for that model into disjoint subsets and fit separate but structurally identical models to all datasets that came from the same original species/process dataset. We split our PH (finding; fishway) models by dam (TD; JD). We further split our Chinook fishway models by run (spring; summer) and our Sockeye fishway TD model by specific fishway (East; North). These submodels are referenced in Table 1 and are explained in further detail in the ESM. One PH model (Sockeye fishway TD North) was discarded due to low sample size, leaving us with 12 final models. In each of those 12 models we conducted one set of null model simulations (bootstraps) to test for the presence of a density effect as well as a set of secondary bootstraps to calculate confidence intervals for the count coefficients.

Upon conducting model diagnostics, we added a threshold density effect ($\text{count} \leq 150$) to our Chinook finding model. This successfully accounted for a series of large positive residuals, possibly modeling a strong crowding effect (i.e. negative density effect). However, this effect was highly confounded with fishway identity, with 88 out of 89 fish under the threshold passing at The Dalles's east fishway, and because of this we do not feel that any strong conclusions can be made about this effect. We used this effect as part of the null model, prior to testing for a linear density effect.

To ensure that our fitted density effects were biologically important as well as statistically significant, we produced simulations for a variety of density scenarios ranging from zero density (near-extirpation) to twice current density, which can be found in Figure 3. Each density scenario is obtained by multiplying observed counts by a fixed factor, and then producing model simulations. We did this for both the PH models and the logistic regression models.

For additional technical details regarding our statistical analysis, please refer to the ESM.

Results

Of our twelve tests, three detected highly significant ($p < 0.001$) density effects. Two were Chinook PH models for finding the fishway, and the third was a Chinook logistic regression model for committing to a fishway. Two other effects were statistically significant at the $p < 0.05$ or 0.1 levels (Summer-run Chinook navigating the fishway at The Dalles; and Sockeye navigating the fishway at The Dalles' East Fishway). However, since these two effects are statistically weak and did not display any consistent pattern with other models of the same species and process, we feel these associations were spurious. All significant density effects (including the two statistically weak effects) were positive, meaning that an increase in density facilitates faster predicted completion of the modeled process, and therefore faster overall passage past the dam.

Our simulated null distributions for the count coefficients are shown in Figure 2, compared to the actual count coefficient fitted to our true (non-simulated) dataset. These results along with our confidence intervals, are shown in Table 1. Coefficients are reported after standardizing the covariates so that magnitudes can be compared to other covariates such as temperature. Full model summaries are available in the ESM.

These results provide strong evidence for the existence of positive density effects, particularly in Chinook salmon. No evidence was found for negative density effects. Evidence for sockeye salmon was ambiguous and did not support a density effect.

Our density scenario simulations for the "finding" models can be found in Figure 3. These simulations predict a 20-30% increase in finding times for Chinook under the extirpation scenario compared to present conditions, and 50-115% more fish with high finding times of >24 hours. Conversely, if salmon densities were to double compared to 2013/2014 levels we predicted a 15-19% decrease in finding times and 31-46% fewer fish with high (>24 hr) finding times. Our density scenario simulations for the "committing" model predicted a linear increase in commit rates with densities, with doubling densities bringing an increase of almost 5% commit rate from the current level of 43% to 47.7%. However, lower density predictions from this model were unreliable, due to the threshold effect we assumed in our null model. Because this effect was only evident in one model, and was confounded with fishway identity

Species	Process	Dam	Subset	<i>p</i> -value	95% CI	Sample Size
Chinook	Find	JD	.	< 5e-04	(0.36 , 0.75)	804
		TD	.	< 5e-04	(0.16 , 0.49)	751
	Commit	.	.	< 5e-04	(0.29 , 1.2)	930
	Fishway	JD	Spring Run	> 0.1	(-0.088 , 0.49)	439
			Summer Run	> 0.1	(-0.59 , 1.1)	345
		TD	Spring Run	> 0.1	(-0.17 , 0.2)	415
			Summer Run	0.061	(-0.054 , 1.2)	332
Sockeye	Find	JD	.	> 0.1	(-0.032 , 0.04)	609
		TD	.	> 0.1	(-0.023 , 0.042)	616
	Commit	.	.	> 0.1	(-0.053 , 0.075)	678
	Fishway	JD	.	> 0.1	(-0.047 , 0.028)	605
		TD	East Fishway	0.037	(0.00067 , 0.039)	553
			North Fishway	.	.	59

Table 1. Results for the 13 models considered after model splitting. Final model was not fit due to small sample size. All *p* values calculated using parametric bootstraps from the AICc-selected null model. All 95% CIs calculated using parametric bootstrap from the full model (selected null model plus a density effect). Sample size reflects the number of radio-tagged fish. Note that the *p* values are not Bonferroni corrected; see ESM for more details.

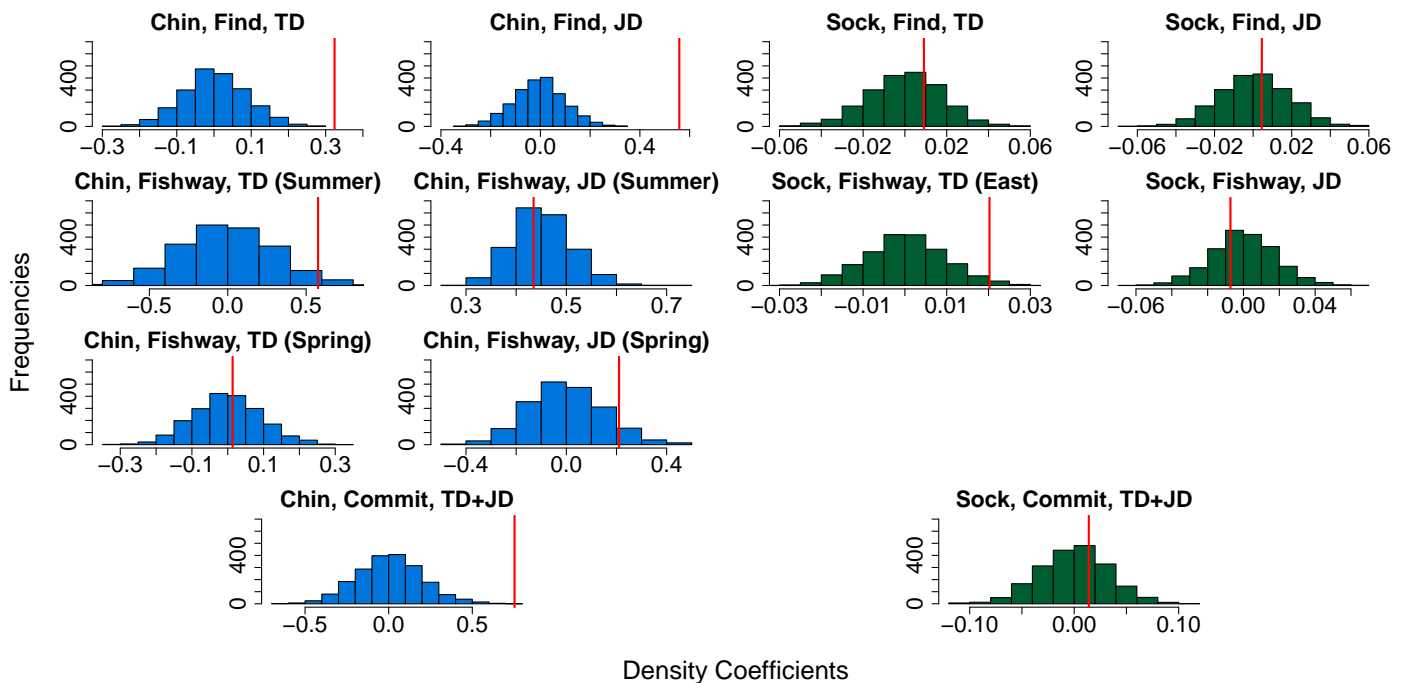


Figure 2. The results of our null distribution simulations. Histograms represent fitted density coefficients from over 2000 simulations of the best fitting null model (with no density effect). Red lines represent the density coefficient fitted to our actual data. *Chin* refers to models of Chinook salmon; *Sock* refers to models of sockeye salmon. *Find*, *Fishway*, and *Commit* refer to our three different process models (see Figure 1). *TD* and *JD* refer to The Dalles and John Day dams. *Summer* and *Spring* refer to models in which summer-run and spring-run Chinook were separated. *East* refers to the east fishway at The Dalles Dam. Separation of models beyond species and process were the result of model diagnostic procedures.

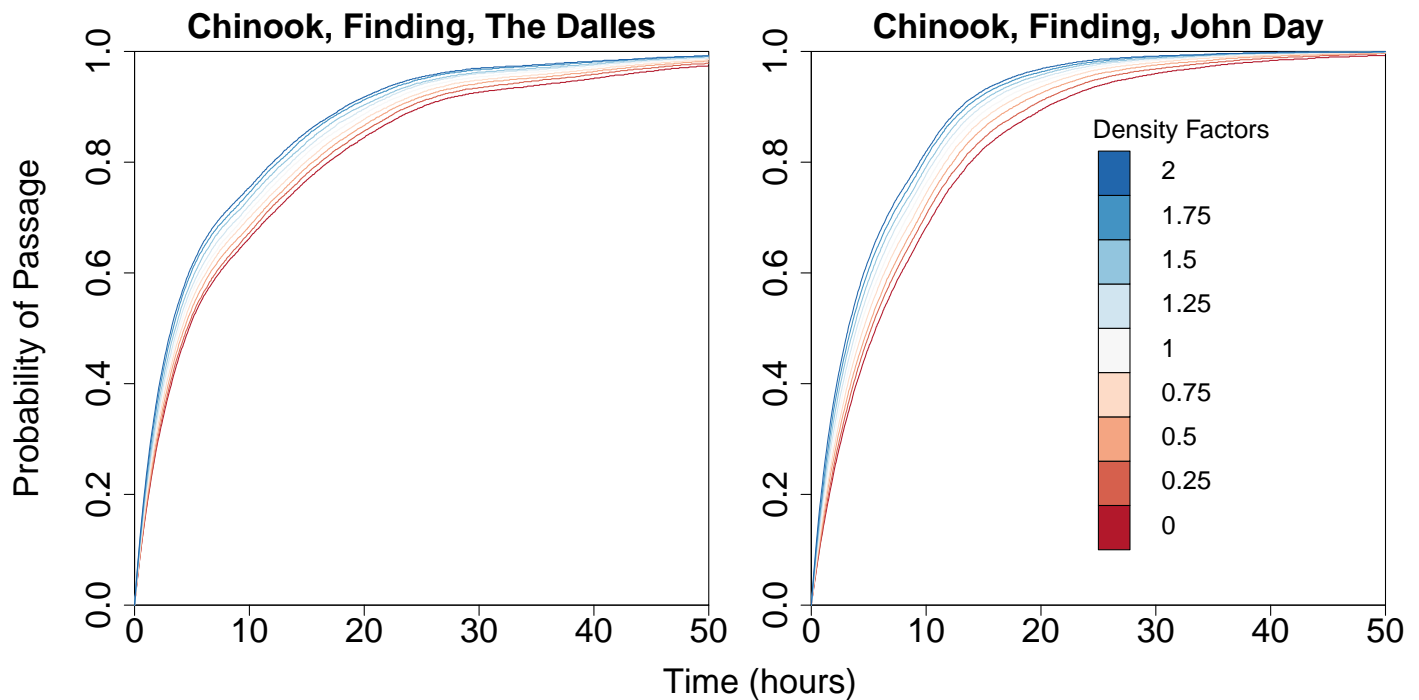


Figure 3. Predictions from our two Chinook “finding” models under various fish density scenarios. Densities were chosen to be a factor (see legend) multiplied against measured counts, to simulate a realistic scenario of higher or lower densities. Factors ranged from 0, to simulate near-extirpation up to twice current levels. Curves at each density factor were generated by simulating from the fitted model 192 times and calculating the median probability of passage at each time point.

we were not able to fully investigate this possible density effect, and it cannot be used for reliable predictions. However, we feel this effect is worth investigating more deeply in future work.

Consistent with previous studies in the same system (*Keefer et al., 2004, 2013a*), we also observed strong temperature ($0.22 < |\beta| < 1.29$; negative in 2/4 Chinook fishway models, otherwise positive) and very strong diel ($1.22 < \beta < 2.96$; higher passage during the day) effects in our PH models. We also observed a strong temperature effect ($\beta = -1.23$) in our Chinook committing model. Our significant density coefficients were of roughly the same order of magnitude as our temperature coefficients, indicating that density may have a substantial impact, comparable to other established drivers. Since these other variables were not our focus, we did not conduct any further analysis of these environmental effects.

Discussion

Human modifications of the global landscape have increased the migratory challenge facing animals on the move (*Hardesty-Moore et al., 2018*). Salmon returning to spawning grounds in the Columbia River basin are confronted with multiple main stem dams. While offering fish passage facilities in the form of fishways, passage remains a daunting challenge as fish need to locate a fishway entrance and then ascend a ladder to continue their migration. Here we reveal evidence that Chinook, but not sockeye, salmon appeared to benefit from social interactions during this challenge consistent with collective navigation (*Berdahl et al., 2018*). We demonstrated, using a bootstrap method to account for several sources of reverse causality, a positive effect of density on two key quantities for Chinook salmon: rates of locating fishway entrances, and probability of committing to passage of a fishway. In contrast, we found no density effect for passage rates through a fishway, or for any aspect of dam passage for sockeye salmon.

Our results can alternatively be explained by an effect of migratory motivation or run-timing, as other studies have noted (*Caudill et al., 2007*). Fish on peak density days may be more motivated, or may have timed their migration better with respect to unmeasured environmental conditions than earlier- or later-migrating fish. Controlling for these effects without directly manipulating density is difficult. Given the consistency of variation between species, we feel that the most plausible explanation is the presence of a true density effect in Chinook salmon, rather than an effect of motivation or timing, which we might expect to see more strongly in both species. Generally, we see our lack of statistically “significant” results for sockeye salmon as adding support to our results for Chinook salmon. We do not expect density effects to exist in all processes or for all species, but do expect these effects to apply

consistently. This expectation was borne out in our results.

It is nevertheless somewhat counter intuitive that the species with a stronger tendency to school would benefit less from collective navigation. Here we provide two, plausible, yet admittedly speculative, explanations. First, having a strong tendency to migrate in groups (*Berdahl et al., 2017*), sockeye salmon might be in sizeable groups regardless of the population density — i.e. their local density is not highly dependent on global (~daily) density. In contrast, the less-social Chinook salmon's local density might be more governed by the global density. Thus for Chinook the number of social interactions may scale with daily fish density whereas for sockeye social interactions may be relatively constant. Second, casual observations by the authors suggest another potential mechanism. In tailraces, Chinook salmon typically move slowly and periodically in small groups. They also tend to hold near fishway entrances before entering. This holding behaviour seems to result in loose shoal-like aggregations near fishway entrances, potentially leaving a sort of social signpost that may draw subsequent Chinook towards an entrance. This situation has the potential to lead to positive feedback and thus higher finding rates at higher fish densities (*Torney et al., 2011*). On the other hand, sockeye salmon's increased tendency to school might inhibit their ability to take advantage of such a social effect (as in *Lemasson et al. (2014)*). By travelling in large, highly cohesive and polarized schools sockeye salmon may have trouble transitioning from a large tailrace to a relatively small fishway. The social “momentum” of the school may prevent individuals who did spot a fishway entrance from stopping to explore it further. This possible mechanism also explains why we observed no strong effects within the fishways, although it does not explain the effect we observed for commit probabilities.

The effect of density on fishway passage rates was first studied over 60 years ago, but has largely focused on the effects of overcrowding (i.e., deleterious effects of density). The possibility of a positive effect of density on fishway passage rates was discussed by *Lander (1959)* in the context of a model for overcrowding, and saw some experimental work in a study of alewives (*Alosa pseudoharengus*), also primarily in the context of overcrowding (*Dominy, 1973*). Unfortunately, although *Dominy (1973)* reported a positive density effect, they analyzed their data in a way that was inconsistent with our analysis¹. More recent work in the context of culvert passage has found negative (*Goerig and Castro-Santos, 2017*), and no (*Johnson et al., 2012*) density effects for brook trout (*Salvelinus fontinalis*) and Coho salmon (*O. kisutch*) respectively. These study systems were most similar to our “fishway” system, involving little difficulty in finding the entrance to the culvert (e.g. in both studies fish were confined at the downstream extremity, as opposed to our open system). Thus our null results for “fishway” are consistent with these studies, while our positive result for “finding” is not contradictory since it involves a fundamentally different, relatively unstudied system. A study by *Caudill et al. (2007)* on Chinook salmon and steelhead (sea-run *O. mykiss*) reported several positive associations with density, but density effects were not the focus of their analysis, and their model encompassed the entire dam passage process from tailrace entry to fishway exit. A study of juvenile palmetto bass (*Morone saxatilis x chrysops*), *Lemasson et al. (2014)* found that fish in schools took much longer than lone individuals to pass an artificial barrier when moving downstream and thus showed a strong negative influence of density on passage rate.

Given the diversity of findings in this literature, and in our own results, there is scope for additional work in this area. Our methods can be applied to other systems and other species, where “finding” and “committing” behavior has rarely been isolated for analysis. For example, controlled navigation experiments investigating these behaviors, where density can be manipulated systematically, are a promising avenue. Further, emerging technologies including sonic tags, acoustic cameras and computer vision will make more detailed analysis of individual and collective movement of fish around dams possible and also yield local (i.e. actual group size, rather than estimated fish density in tailraces) measures of conspecific density (*Hughey et al., 2018*). Such studies could also shed light on the specific mechanisms driving any collective navigation. Revealing individual and collective search algorithms may contribute general principles to the fields of animal movement and bio-inspired engineering, but may also contribute specific insights for dam management of fish passage. For example, mechanisms such as the “social signpost” hypothesis for Chinook might motivate management interventions designed to promote more efficient salmon migration past fishways. One simple and inexpensive hypothetical intervention might simulate a holding pattern of fish about fishway entrances using model fish tethered near a fishway entrance. These decoys could provide a social signpost, attempting to activate our hypothesized social behaviors even at lower densities.

When conducting our model-building and analyses we included an additional threshold density effect in our Chinook “commit” model, possibly modeling a strong crowding effect. However, we did not conduct an in-depth analysis of this variable, since it was highly confounded with use of The Dalles’ east fishway. One possible explanation for this effect is that it truly was a density effect associated with overcrowding in the fishway — however it is unclear why overcrowding would be represented by a threshold

¹ *Dominy (1973)* used a numerical response (number passing per unit time) rather than the rate response (proportion passing per unit time) used here. Although they reported a sigmoidal (positive at low densities, then negative at high densities) density effect in alewives, a visual analysis of their data appears more consistent (in our framework) with either no density effect or a negative effect, although there is a large group of outliers that could indicate a positive effect.

effect rather than a more gradual decline in commit probabilities. Furthermore, even if this density effect were associated with overcrowding in a single fishway, we would expect such an effect to vary significantly among fishways, both in magnitude and in location of the threshold, making it difficult to generalize this effect to make predictions elsewhere. This being the only evidence we found for negative density effects, we recommend this as an avenue for further research, connected with negative density effects reported elsewhere in the literature.

Our analysis faced three substantial challenges, rarely encountered in time-to-event modeling: counts were confounded with hazard, counts were a time-delayed estimate of density, and density was confounded with hazard across time. We addressed these challenges using our bootstrap approach to circumvent concerns about reverse causality, and by using smoother daily counts rather than hourly counts which are more subject to concerns about time-delay and inconsistent relationships with density. These were the more unique roadblocks we encountered, but of course, like any statistical analysis, there are some other caveats to consider. For example, other covariates such as flow velocity may have played an important role but were not included, and some variables such as migratory motivation are all but impossible to measure quantitatively in any case. Like any model, ours was an imperfect representation of reality. We feel it was close enough to reality to provide useful insight. We are also open to some criticism in our use of the PH model, since we dropped fish with missing measurements from our analysis of each model. However, we used only “entry” and “exit” data points, making a proper censoring analysis impossible. Furthermore, since data points were likely missing independently at random due to missed radiotelemetry signals, we incurred little bias in this manner.

To our knowledge, our results provide the first demonstration of a positive density effect for fish passing riverine obstacles. This is in contrast to the prevailing wisdom that overcrowding is the dominant effect. More broadly, it is one of only a handful of examples of collective navigation in freely-migrating populations. Given the ubiquity of social movement during migration, we expect many more examples of collective navigation to be uncovered, especially as new technologies improve our ability to quantify collective movement *in situ* (Hughey *et al.*, 2018). Such studies underscore the need for further investigation of density effects, since these processes could have important ecological implications. For example, if populations decline, densities at dams will decline: will this alleviate overcrowding or reduce collective benefits? In the first case, population decline is buffered, while in the other it is magnified, potentially generating critical transitions that may lead to sudden population collapses (Fagan *et al.*, 2012; Berdahl *et al.*, 2016a). As anthropogenic disturbances simultaneously increase navigational difficulty in a variety of contexts and decrease population densities, understanding the role of density-dependent processes, such as collective navigation, may therefore yield critical insights for sound management and conservation (Westley *et al.*, 2018).

Acknowledgments

Telemetry data were collected with funding from the US Army Corps of Engineers, Portland District and with assistance from the NW Fisheries Science Center (NOAA-Fisheries and the University of Idaho Fish Ecology Research Lab. This material is based upon work supported by the NSF-GRFP under Grant No. DGE-1762114. We thank David Smith and Christa Woodley for assistance obtaining data and to Christy Contreras for preliminary analysis as part of an NSF REU project at the Santa Fe Institute. Finally, we thank Chris Caudill for invaluable support.

Data Accessibility

All data used in this article are from publicly available repositories. All data for this article have been made publicly available at DOI (10.6084/m9.figshare.13010072), along with links to source datasets and R code which reproduces our data preprocessing, analysis, model diagnostics, and results.

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Electronic Supplementary Material for: Collective navigation can facilitate passage through human-made barriers by homeward migrating Pacific salmon

Connie Okasaki, Matthew L. Keefer,
Peter A. H. Westley & Andrew M. Berdahl

September 25, 2020

1 Statistical Analysis

We fit two proportional hazards (PH) models and one logistic model: these models are termed “finding,” “ladder,” and “committing” respectively. Each model was fit for Chinook and sockeye separately, since we expected inter-species differences in most or all coefficients. The PH models were fit in R [7] using the `phreg` function from the `eha` package [1]. All models included daily counts of conspecifics. Since counts are available for each ladder, we used ladder-specific counts for the “ladder” and “commit” processes; however since a fish might approach either ladder upon entering the tailrace we used dam-level counts for the “finding” process.

All models controlled for temperature [3], dam identity, and a binary diel effect [4]. For the finding and committing processes we included a spill effect, but since fish cannot detect spill from within the fishway, no spill effect was included in the ladder models.

For all models we included a binary covariate (`middle`) indicating whether a fish’s tailrace entry was in the middle (2nd and 3rd) quartiles. This variable controlled for the effect of run timing on fish condition and passage speed, since timing is highly correlated with density (very high densities near the modal date) and might otherwise confound our analysis.

For Chinook we included a binary variable (`spring`) indicating whether a fish was labeled spring- or summer-run. For sockeye we included a three-level factor variable indicating whether a fish was sourced to the Wenatchee, the Okanogan, or to any other site. The Wenatchee and Okanogan tributaries each accounted for about a third of the sockeye in our sample.

Two of our predictors — `temperature` and `day` — had strong prior evidence from the literature [3, 4]. To reduce the number of variables being selected and the risks associated with model dredging, we included these variables a priori. The remainder of the predictors we selected using AICc. For consistency, however, we wished to fit structurally identical models to each set of species/process submodels. We examined the AICc for each set of models and

subjectively chose what seemed to be the best-fitting overall model. Due to the extremely long tails of the count predictor, we then considered adding either an un-transformed or a log-transformed count variable to the best-fitting null model. In most cases there was no discernible difference in AICc between the two, but in several cases the un-transformed variable was selected. For consistency, despite the long tails, we used the un-transformed version to conduct the remainder of our analysis.

The classical form of the PH model uses a partial likelihood function and does not specify the baseline hazard function, but in order to simulate from our bootstrapped distributions we assumed a constant baseline hazard $\lambda_0(t) = \lambda_0$. This was visually consistent with the empirical hazard functions. However, since there is a small but non-trivial minimum time to complete each task, the empirical hazard functions are zero for a short period of time. To account for this discrepancy, we truncated each fish’s timeline by a constant amount (per model) such that the minimum passage time was less than 1 minute, effectively assuming a piecewise constant baseline hazard function with the first section fixed at zero hazard. In several models there were outlier individuals detected as passing through the fishway in as little as 2 minutes. Since such passage times are implausible (fast passage times are ≈ 1 hour), we attribute this to data error and remove all records which show passage in <10 minutes. This approach conservatively includes several extraordinarily fast passage times of ≈ 30 minutes.

For each model, we dropped any fish with censored measurements. Censoring is a standard concern for time-to-event models, and occurs when an event is not observed to occur because an individual leaves observation. This could occur when a fish passed but was not detected by a telemetry antenna, or because a fish died in a tailrace. Incorrect assumptions regarding censoring are known to bias inference in PH models [5]. We did not account for censoring because, for each system, we used essentially only two measurements for each fish: “entry” and “exit.” A censoring analysis would require follow-up measurements between entry and exit to verify that an individual is still being detected but has not yet exited. Although the aerial tailrace antenna misses a large number of measurements, the underwater fishway antennas miss far fewer. Only a very small portion ($\approx 1\%$) of fish are observed to enter but not exit the fishway. Since a very similar portion of fish are observed to exit but not enter, we attribute this censoring almost entirely to randomly missed telemetry detections rather than mortality. Since individuals were therefore dropped from the dataset independently of hazard we lose little information and incur very little bias in this manner.

Finally, we conducted a parametric bootstrap test on the count coefficient to detect density effects, using our best-fitting null models. Since these models do not contain reverse causality, they provide valid, unbiased fits under the null hypothesis. To each simulation, we fit a model with an effect of count. Assuming our null model is correctly specified, comparing our fitted count coefficients to these null distributions provide valid p -values to test for density effects. We do not Bonferroni correct these p -values because by the nature of our split models a single false-positive result is not statistically convincing, as we note when discussing our two marginally significant results. Instead we demand consistency between matching models, and indeed we found that several models were consistently highly significant (and would remain so even with a Bonferroni correction).

To ensure that our null models were well-specified, we conducted standard model diagnostics. For our PH models we tested the proportional hazards assumption using the

`cox.zph` function in the `survival` package [8], applied to the partial-likelihood model fits. Since the `cox.zph` function tests the proportional hazards assumption for each covariate as well as globally for each model we made 36 tests. Using a Bonferroni correction, this test identified strong differences (corrected $p < 10^{-5}$) in baseline hazard functions between dams, likely caused by differences in the layout of the monitoring arrays. We thus split our models by dam. Retesting these sub-models, we made an additional 59 tests. These tests caused us to split our Chinook ladder models by run ($p < 10^{-5}$) and to split our `sockeye.ladder.TD` models by site ($p < 0.005$; East (TDE) vs. North (TDN)). Since all of these were individual-level variables, we could not assign interactions with time, since this could (and did) result in predictions of effectively infinite survival time. We also added interaction effects between temperature and time ($p < 0.001$) in all of the Chinook ladder models. Finally we made an additional 41 tests after conducting this second level of model-splitting, with no significant results. After splitting, the Chinook ladder models each contained between 330 and 440 fish. All other models contained over 500 fish, with the exception of `sockeye.ladder.TDN` which had only 59. Our bootstrap simulations frequently produced ill-conditioned fits for this model, and we subsequently removed it from our analysis. A diagram of our analysis can be found in Figure 1.

For the `commit` models we fit one logistic regression model per species, without splitting by dam. We plotted binned residuals from the null model, which motivated the addition of a threshold variable (count ≤ 150) to the Chinook model, due to substantially higher-than-expected commit rates for these low-density fish. Of these 89 individuals, 88 of them were detected at The Dalles’s east ladder. Elevated commit probability was not observed at TDE at higher densities.

Although we hypothesized positive density effects, we conducted two-sided tests in all cases to allow for the possibility of negative effects (e.g. overcrowding in the fishway).

Because of the reverse causality in our system, the null modeling approach we took was the most reliable way we knew to detect a density effect. However, this approach provides only p -values, and not confidence intervals for the true magnitude. In order to quantify magnitude, we conducted another parametric bootstrap to produce 95% confidence intervals for the count coefficient. To produce these intervals we sampled from the full model (i.e. the model with a count coefficient) and fit to these simulations new count coefficients. We calculate the confidence intervals using the hybrid method, recommended in [2] for use when estimating regression coefficients in Cox models. In all cases, the bootstrapped distribution was symmetric and centered on the fitted coefficient. This secondary bootstrap also roughly reproduced the p -values of our primary bootstrap. These two metrics lend credibility to this bootstrap, despite possible biases that might enter due to reverse causality. Thus, we also report approximate 95% confidence intervals for the magnitude of the density coefficient, calculated from these bootstrapped distributions. All bootstraps included >2000 simulations.

To speed up calculation we did bootstrap simulations in parallel using 24 cores of a 48 core Windows compute server. We parallelized using the R package `parallel` [7] and set our random seeds using [6]’s method.

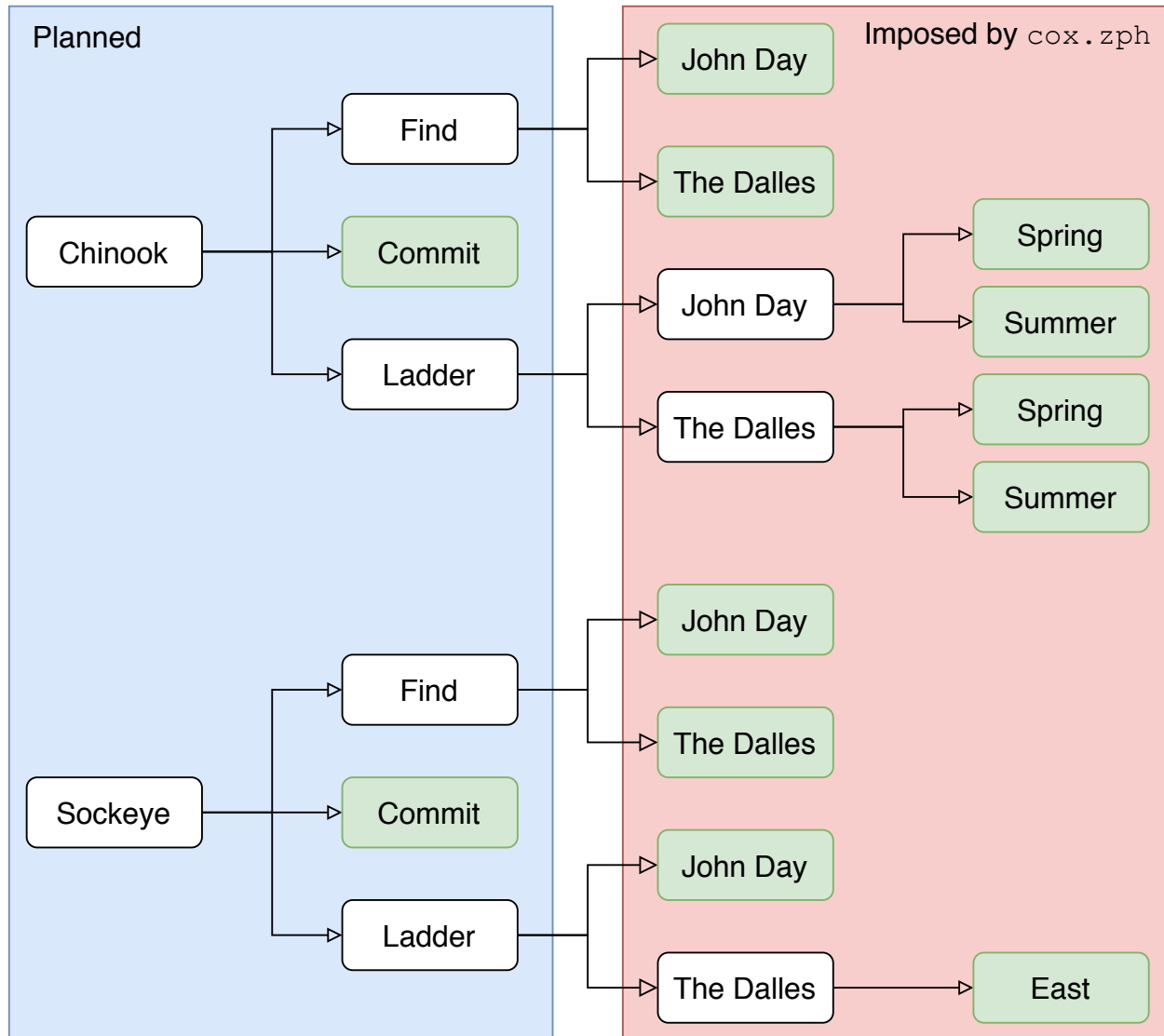


Figure 1: A diagram of the models we fit. Originally we planned to fit the 6 models shown in blue on the left. However, due to model diagnostic violations (specifically violations detected by `cox.zph`) we were forced to split further to allow baseline hazard functions to differ between factors. These more specific final models are shown in red. Our final set of models which passed all model diagnostics are shown in green.

2 Model Summaries

Below, we have included the model output for our final selected models. For the three models where a highly significant density effect was detected we include that density effect. Otherwise we include the best-fitting null model.

Find Chin JD

Call:

```
phreg(formula = Surv(tstart, tstop, success) ~ day + middle +
      spring + temp.c + spill + chin, data = find.chin.JD.trunc,
      dist = "pch")
```

Covariate		W.mean	Coef	Exp(Coef)	se(Coef)	Wald p
day		0.577	2.245	9.445	0.134	0.000
middle						
	FALSE	0.375	0	1	(reference)	
	TRUE	0.625	-0.523	0.593	0.075	0.000
spring						
	FALSE	0.364	0	1	(reference)	
	TRUE	0.636	0.044	1.045	0.113	0.697
temp.c		-0.297	0.616	1.852	0.120	0.000
spill		0.682	0.204	1.227	0.108	0.058
chin		-0.048	0.559	1.748	0.090	0.000

Events	804
Total time at risk	5255.9
Max. log. likelihood	-1997.2
LR test statistic	632.58
Degrees of freedom	6
Overall p-value	0

Find Chin TD

Call:

```
phreg(formula = Surv(tstart, tstop, success) ~ day + middle +  
      spring + temp.c + spill + chin, data = find.chin.TD.trunc,  
      dist = "pch")
```

Covariate		W.mean	Coef	Exp(Coef)	se(Coef)	Wald p
day		0.575	2.889	17.978	0.187	0.000
middle						
	FALSE	0.484	0	1	(reference)	
	TRUE	0.516	0.155	1.168	0.079	0.051
spring						
	FALSE	0.345	0	1	(reference)	
	TRUE	0.655	0.654	1.923	0.164	0.000
temp.c		-0.322	1.299	3.667	0.191	0.000
spill		0.777	-0.075	0.928	0.191	0.695
chin		0.093	0.324	1.383	0.082	0.000

Events	751
Total time at risk	6445.7
Max. log. likelihood	-2030.9
LR test statistic	669.09
Degrees of freedom	6
Overall p-value	0

Fishway Chin JD Spring

Call:

```
phreg(formula = Surv(tstart, tstop, success) ~ day + site.JDN +  
      temp.c + temp.ct, data = ladder.chin.JD.spring.trunc, dist = "pch")
```

Covariate		W.mean	Coef	Exp(Coef)	se(Coef)	Wald p
day		0.755	2.945	19.002	0.382	0.000
site.JDN						
	FALSE	0.738	0	1	(reference)	
	TRUE	0.262	0.203	1.225	0.102	0.047
temp.c		-0.578	0.296	1.344	0.154	0.055
temp.ct		-2.409	-0.003	0.997	0.012	0.798

Events	439
Total time at risk	1707
Max. log. likelihood	-935.96
LR test statistic	198.41
Degrees of freedom	4
Overall p-value	0

Fishway Chin JD Summer

Call:

```
phreg(formula = Surv(tstart, tstop, success) ~ day + site.JDN +  
      temp.c + temp.ct, data = ladder.chin.JD.summer.trunc, dist = "pch")
```

Covariate		W.mean	Coef	Exp(Coef)	se(Coef)	Wald p
day		0.797	2.360	10.594	0.282	0.000
site.JDN						
	FALSE	0.436	0	1	(reference)	
	TRUE	0.564	-0.024	0.977	0.110	0.829
temp.c		0.292	-0.651	0.521	0.249	0.009
temp.ct		0.619	0.437	1.548	0.048	0.000

Events	345
Total time at risk	1101.5
Max. log. likelihood	-681.38
LR test statistic	128.25
Degrees of freedom	4
Overall p-value	0

Fishway Chin TD Spring

Call:

```
phreg(formula = Surv(tstart, tstop, success) ~ day + site.TDN +  
      temp.c + temp.ct, data = ladder.chin.TD.spring.trunc, dist = "pch")
```

Covariate		W.mean	Coef	Exp(Coef)	se(Coef)	Wald p
day		0.589	2.783	16.161	0.257	0.000
site.TDN						
	FALSE	0.820	0	1	(reference)	
	TRUE	0.180	0.108	1.114	0.130	0.405
temp.c		-0.520	-0.342	0.711	0.191	0.074
temp.ct		-2.105	0.063	1.065	0.021	0.003

Events	415
Total time at risk	1115.4
Max. log. likelihood	-659.5
LR test statistic	331.65
Degrees of freedom	4
Overall p-value	0

Fishway Chin TD Summer

Call:

```
phreg(formula = Surv(tstart, tstop, success) ~ day + site.TDN +  
      temp.c + temp.ct, data = ladder.chin.TD.summer.trunc, dist = "pch")
```

Covariate		W.mean	Coef	Exp(Coef)	se(Coef)	Wald p
day		0.784	2.101	8.172	0.310	0.000
site.TDN						
	FALSE	0.671	0	1	(reference)	
	TRUE	0.329	-0.224	0.799	0.127	0.076
temp.c		0.234	0.337	1.401	0.260	0.196
temp.ct		0.658	0.048	1.049	0.047	0.309

Events	332
Total time at risk	1017.7
Max. log. likelihood	-654
LR test statistic	99.77
Degrees of freedom	4
Overall p-value	0

Find Sock JD

Call:

```
phreg(formula = Surv(tstart, tstop, success) ~ day + middle +  
      wenatchee + okanogan + temp.c + spill, data = find.sock.JD.trunc,  
      dist = "pch")
```

Covariate		W.mean	Coef	Exp(Coef)	se(Coef)	Wald p
day		0.459	1.951	7.034	0.111	0.000
middle						
	FALSE	0.461	0	1		(reference)
	TRUE	0.539	-0.211	0.810	0.084	0.012
wenatchee		0.187	0.381	1.463	0.114	0.001
okanogan		0.456	0.195	1.215	0.094	0.039
temp.c		0.220	0.668	1.950	0.113	0.000
spill		0.546	-0.456	0.634	0.143	0.001

Events	609
Total time at risk	1836.4
Max. log. likelihood	-1067.7
LR test statistic	426.88
Degrees of freedom	6
Overall p-value	0

Find Sock TD

Call:

```
phreg(formula = Surv(tstart, tstop, success) ~ day + middle +  
      wenatchee + okanogan + temp.c + spill, data = find.sock.TD.trunc,  
      dist = "pch")
```

Covariate		W.mean	Coef	Exp(Coef)	se(Coef)	Wald p
day		0.589	2.703	14.926	0.190	0.000
middle						
	FALSE	0.525	0	1		(reference)
	TRUE	0.475	0.122	1.129	0.082	0.137
wenatchee		0.195	0.400	1.491	0.112	0.000
okanogan		0.432	0.131	1.140	0.094	0.164
temp.c		0.301	0.759	2.135	0.221	0.001
spill		0.677	-0.269	0.765	0.219	0.221

Events	616
Total time at risk	3905.7
Max. log. likelihood	-1524.1
LR test statistic	459.16
Degrees of freedom	6
Overall p-value	0

Fishway Sock JD

Call:

```
phreg(formula = Surv(tstart, tstop, success) ~ day + site.JDN +  
      temp.c, data = ladder.sock.JD.trunc, dist = "pch")
```

Covariate		W.mean	Coef	Exp(Coef)	se(Coef)	Wald p
day		0.786	1.533	4.634	0.182	0.000
site.JDN						
	FALSE	0.676	0	1	(reference)	
	TRUE	0.324	0.743	2.102	0.082	0.000
temp.c		0.300	0.214	1.239	0.179	0.231

Events	605
Total time at risk	2347.6
Max. log. likelihood	-1320.5
LR test statistic	209.60
Degrees of freedom	3
Overall p-value	0

Fishway Sock TD East

Call:

```
phreg(formula = Surv(tstart, tstop, success) ~ day + temp.c,  
      data = ladder.sock.TDE.trunc, dist = "pch")
```

Covariate	W.mean	Coef	Exp(Coef)	se(Coef)	Wald p
day	0.784	1.199	3.315	0.156	0.000
temp.c	0.219	0.872	2.391	0.156	0.000

Events	553
Total time at risk	1871.9
Max. log. likelihood	-1169
LR test statistic	116.59
Degrees of freedom	2
Overall p-value	0

Commit Chin

Call:

```
glm(formula = success ~ day + site + spring + temp.c + thresh +  
    chin.specific, family = binomial, data = prob.chin)
```

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.7907	-1.0415	-0.6673	1.1420	2.1301

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.03122	0.28168	-0.111	0.91176
day	-0.04247	0.23845	-0.178	0.85863
siteJDS	-1.02322	0.17067	-5.995	2.03e-09 ***
siteTDE	0.04591	0.16864	0.272	0.78544
siteTDN	0.11066	0.28167	0.393	0.69442
springTRUE	-0.31638	0.22854	-1.384	0.16625
temp.c	-1.22897	0.26553	-4.628	3.68e-06 ***
threshTRUE	1.50867	0.28215	5.347	8.94e-08 ***
chin.specific	0.75259	0.21903	3.436	0.00059 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 2129.1 on 1554 degrees of freedom
Residual deviance: 1898.2 on 1546 degrees of freedom
AIC: 1916.2

Number of Fisher Scoring iterations: 4

Commit Sock

Call:

```
glm(formula = success ~ day + site + temp.c, family = binomial,  
     data = prob.sock)
```

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.7249	-1.1053	0.7476	0.7485	1.3937

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.911939	0.243638	3.743	0.000182 ***
day	0.319363	0.202688	1.576	0.115110
siteJDS	-1.401290	0.183263	-7.646	2.07e-14 ***
siteTDE	-0.098865	0.180317	-0.548	0.583497
siteTDN	-0.313573	0.375813	-0.834	0.404064
temp.c	-0.006558	0.314959	-0.021	0.983387

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 1564.5 on 1224 degrees of freedom
Residual deviance: 1457.1 on 1219 degrees of freedom
AIC: 1469.1

Number of Fisher Scoring iterations: 4

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