PREDICTING STREAM ATTRACTIVENESS TO STRAY HATCHERY-ORIGIN CHUM SALMON TO AID IN UNDERSTANDING SALMON DISPERSAL AND INFORMING HATCHERY MANAGEMENT

By

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Abstract

Understanding the processes underlying dispersal propensity in animal populations is a fundamental goal of ecologists. In metapopulations of wild Pacific (*Oncorhynchus spp*) and Atlantic salmon (*Salmo salar*, hereafter collectively referred to as "salmon"), it is recognized that dispersal, or straying, exists in tandem with philopatry and provides benefits such as gene flow and colonization of new habitat. However, straying by hatchery-produced salmon into streams can negatively affect the genetic integrity and reproductive success of wild salmon populations. Straying by hatchery-origin salmon may also confound fishery management procedures around assessing wild spawner escapement, given the difficulty in identifying hatchery salmon in the field. A first step in mitigating and managing the consequences of straying by hatchery salmon is to understand where and why hatchery salmon stray. In this study, I described the relationship between the number of hatchery-origin strays received by streams and the characteristics of those streams based on the hypothesis that certain characteristics are attractive to hatchery strays.

An extensive dataset documenting the number of stray hatchery-origin chum salmon (*Oncorhynchus keta*) that spawned in 57 streams in Southeast Alaska was produced from hundreds of field surveys conducted over a 10-year period 2008–2019. I used these data in a generalized linear mixed effects modeling framework to predict how "attractive" a given stream was to hatchery strays based on hypothesized influential stream characteristics, such as streamflow, distance and numbers of hatchery releases, and conspecific density. I found that some streams were more attractive than others to hatchery strays: 10 of 57 streams surveyed had mean observed attractiveness indices of 39 recipient strays over time (range: 12–115) in a given survey, while the remaining 47 sites only attracted two recipient strays on average (range: 0–8). Furthermore, stream attractiveness to hatchery strays was predicted to increase by 44% with a 1-

SD (27.6 million) increase in the number of hatchery-origin chum salmon released near the stream and increase non-linearly with elevated levels of intra-annual variability (CV > 0.55) of stream discharge. These results corroborate results from other studies that distance to a source population (e.g., a hatchery release site) influences the number of dispersing immigrants, or strays, received by the stream. However, additional ecological factors such as streamflow also affect the distribution of hatchery strays, indicating that inclusion of distance is necessary but not sufficient for accurate prediction.

In the second part of this study, I expanded predictions to 558 additional streams throughout Southeast Alaska in 2008–2019 and in a hypothetical future year given increased hatchery releases. Only a small subset of streams (~10%) was predicted to be attractive, with mean predicted attractiveness indices of 57 recipient hatchery strays (range: 9–600). Bootstrapped coefficients of variation described uncertainty around predictions. Uncertainty was modest for predictions for streams in 2008–2019 (CV range: 0.21–0.62) but high for predictions of hypothetical future stream attractiveness (CV range: 0.70–1.15). These results suggest that the predictive modeling framework may be useful in describing patterns of stream attractiveness beyond the spatial range of the observed data, but not beyond its temporal range. Taken together, the results of this study elucidate the role of stream ecology and spatial location in attracting dispersing hatchery-origin salmon and provide insight into how predictions of stream attractiveness may be incorporated into hatchery management.

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Introduction

Understanding causes and patterns of movement in animal populations helps ecologists and resource managers comprehend how animals interact with their environment and persist under changing conditions (Hanski 1998, Morales et al. 2010, Liedvogel et al. 2013). This information is essential for effective conservation and management of species that move among habitats within a landscape. For instance, Arctic caribou (*Rangifer tarandus*) return annually to the same fine-scale calving locations depending on the distribution and availability of resources in the landscape. The availability of resources may be attenuated by habitat loss, climate change, or other factors. Thus, recognizing how resource availability potentially affects calving success and protecting that resource access is critical to the persistence of the species (Cameron et al. 2020, Joly et al. 2021).

Philopatry and dispersal are two specific types of movement within the context of animal migrations. Philopatry is defined as the behavior of animals remaining permanently within their home range, or as individuals who migrate but later return to the same site for feeding or reproduction (Hendry et al. 2004). Within the context of this thesis, I discuss natal philopatry of migratory individuals for reproductive purposes. Natal philopatry benefits individuals by returning them to sites with which they are familiar and/or adapted, thereby enabling higher breeding success (Thompson and Hale 1989, Hendry et al. 2004, Helfer et al. 2012). Conversely, dispersal is the movement of an individual to a place of reproduction other than the natal site and is an important mechanism for allowing gene flow between breeding populations (Matthysen 2012). Because each strategy plays a different and necessary role in metapopulation persistence, natal philopatry and dispersal often exist in a balance with one another in animal metapopulations (Berdahl et al. 2015). One prime example is the interplay between homing and straying in metapopulations of Pacific (*Oncorhynchus spp*) and Atlantic salmon (*Salmo salar*, hereafter collectively referred to as "salmon"). For salmon that *home*, or exhibit philopatric behavior, the spawning migration culminates in the natal stream. Homing returns locally adapted salmon to the streams where they will have the highest probability of successful reproduction (Taylor 1991, Fraser et al. 2011, Peterson et al. 2014, May 2022). Freshwater streams and tributaries are inherently isolated from one another, so in the event that all salmon home, spawning populations are isolated from one another as well. Dispersal, or straying enables gene flow (Hendry et al. 2004), as well as colonization of new habitat (Milner and Bailey 1989, Pess et al. 2012) and avoidance of degraded habitat in the home stream (Whitman et al. 1982). As in other taxa (Thompson and Hale 1989, Helfer et al. 2012), homing (philopatry) and straying (dispersal) exist simultaneously in salmon metapopulations and are both essential to the persistence of a metapopulation.

But the balance that has evolved to exist between homing and straying in salmon metapopulations can become problematic within the framework of hatcheries and aquaculture. Across hatchery programs, straying is defined as adult hatchery-produced fish returning and attempting to spawn at sites, whether those be hatcheries, release sites, or streams, other than those to which they were intended to return. Although the extent of straying varies among species and hatchery programs (Westley et al. 2013), no existing hatchery program will be able to completely preclude straying by hatchery-produced salmon, given that straying is a fundamental biological attribute of salmon. In programs where hatchery fish are not intended to stray into streams where natural-origin fish spawn, interactions between hatchery- and natural-origin fish may result in additional competition experienced by natural-origin fish (Grant 2012, Anderson et al. 2020), fitness declines of natural-origin fish from interbreeding and hybridization

(Christie et al. 2014), and inflated spawner escapement assessments by hatchery and fishery managers (Johnson et al. 2012). In the interest of mitigating these effects, hatchery and fishery managers would benefit from understanding the factors that influence straying by hatchery-origin salmon.

Hatchery practices and salmon demographics are currently recognized to influence the magnitude of straying by hatchery-origin salmon. For instance, human transportation of juvenile hatchery salmon, typically by barge over long river distances, tends to produce a higher proportion of strays when that cohort of juveniles returns as adults (Keefer et al. 2008, Bond et al. 2017). In species with variation in age of returning adults, older salmon sometimes stray more than younger salmon, possibly due to memory loss or changes in freshwater odors over time (Quinn and Fresh 1984, Hard and Heard 1999). However, our understanding of site characteristics that influence straying parameters is incipient at best, with a critical question remaining: Are sites that receive many hatchery-origin strays *attractive* to those strays? Evidence from the Columbia River system showed that among five hatchery sites, each located on their own tributary, two of the sites were clearly more attractive than the others because they received hundreds of strays (range: 396–526) from the other sites. The three less populous, or attractive sites only received 85, four, and one stray, respectively, from other locations. There was no apparent correlation between tributary distance from the ocean or the number of returning wild fish that could explain the marked attractiveness of the two populous sites, but it was noted that the least attractive tributary consistently had lower flow than the others (Quinn et al. 1991, Pascual and Quinn 1994). Thus, it would appear that ecological characteristics of the most populous hatchery tributaries may have played a role in attracting strays from other locations.

I therefore undertook an analysis to identify which factors make sites attractive to stray hatchery-origin salmon. This work sought to elucidate a poorly understood driver of dispersal in salmon metapopulations with the ultimate goal of informing hatchery and salmon fishery management practices. Identifying attractive streams by their characteristics would enable 1) planning hatchery activities, such as situating remote release sites far from attractive streams and 2) detecting streams where wild escapement estimates are likely to be confounded due to hatchery straying. As such, the objective of my first chapter is to identify factors that are attractive to stray hatchery-origin salmon through literature review and developing a predictive modeling framework. The objective of my second chapter is to formally apply the predictive model developed in first chapter to other locations within my study region to generate additional estimates of stream attractiveness to stray hatchery-origin salmon. By developing a predictive model to estimate stream attractiveness, my results are a first step towards a tool that will help guide hatchery and fishery managers in understanding the extent and distribution of straying by hatchery-origin salmon.

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Chapter 1: Going beyond the distance: streamflow alters site attractiveness to stray hatchery-origin chum salmon in Southeast Alaska[1]

Abstract

Dispersal ("straying") of hatchery-produced Pacific (*Oncorhynchus spp*) and Atlantic salmon (*Salmo salar*) complicates fishery management and can erode wild salmon productivity and resilience, yet relatively little is known about what makes certain sites apparently attractive to strays. In this study, we sought to identify stream characteristics associated with higher numbers of stray hatchery-origin chum salmon (*Oncorhynchus keta*) in Southeast Alaska. We compiled a dataset of approximately 45,000 chum salmon sampled from 57 streams in the region during the spawning seasons of 2008–2019. Of these, 8,300 fish, or 18% of the total, were confirmed to be of hatchery-origin by otolith thermal markings. A generalized linear mixed-effects model was fit to the data and confirmed an important role of distance to a source population and numbers of fish released in proximity to sites on the numbers of strays observed in streams. Specifically, by increasing nearby releases of hatchery-origin juveniles by 1-SD (27.6 million fish), we estimated a 44% increase in the predicted number of hatchery-origin strays in nearby streams. Beyond distance, non-linear stream discharge effects were detected, with the numbers of strays being particularly low in streams with intermediate coefficients of variation of flow (0.48–0.55). We interpret the flow effect to possibly reflect other stream characteristics, such as stream water source, that we did not account for in this study. For instance, attractive CVs of flow were primarily associated with snowmelt-fed streams, indicating a possible role of

[1] Payne, M. K., C. C. Cunningham, M. V. McPhee, and P. A. H. Westley. (In prep). Going beyond the distance: streamflow alters site attractiveness to stray hatchery-origin chum salmon in Southeast Alaska. Ecosphere.

temperature regulation during warm summer spawning seasons as an attractive stream characteristic. In addition to providing new insights into habitat-mediated dispersal and colonization dynamics by straying salmon, our results are the first step towards incorporating stream attractiveness in spatial planning of release locations for hatchery fish.

Introduction

The management and conservation of Pacific (*Oncorhynchus spp*) and Atlantic (*Salmo salar*) salmon necessitates consideration of metapopulation frameworks informed by theory (Cooper and Mangel 1999, Schtickzelle and Quinn 2007, Bradford and Braun 2021). A metapopulation is broadly defined as a population of local populations living in discrete habitat patches that exhibit dynamics of colonization and extinction and are connected by dispersal (Hanski 1998). Within salmon metapopulations, most individuals are philopatric and exhibit homing to natal patches (Quinn and Fresh 1984, Jonsson et al. 2003). Homing coupled with site-specific patterns of natural and sexual selection facilitates local adaptation (Taylor 1991) where philopatric individuals have higher fitness on average than foreign individuals spawning in the same site (Peterson et al. 2014). Even though the fitness of dispersing individuals is expected to be low on average compared to homing individuals, straying may benefit the metapopulation by introducing novel genetic diversity and even genetically rescuing otherwise isolated breeding populations (Hendry et al. 2004). At an individual level, straying may allow a fish to have higher breeding success in specific instances than it would at home (Whitman et al. 1982). Straying also facilitates the colonization of new habitat (Milner and Bailey 1989, Pess et al. 2012). In salmon metapopulations, homing and straying exist in a dynamic equilibrium that is thought to be one mechanism by which salmon populations have been able to persist in the face of environmental and demographic stochasticity (Cooper and Mangel 1999, Fullerton et al. 2011, Berdahl et al. 2015, Yeakel et al. 2018).

While straying is clearly a fundamental aspect of salmon ecology and evolution, it has conservation implications in aquaculture and hatchery programs when those programs are designed to minimize hatchery and wild (i.e., natural-origin) salmon interactions. In an average year from 2000 to 2020, 4.8 billion hatchery-produced salmon were released into the North Pacific Ocean (North Pacific Anadromous Fish Commission 2021) to meet enhancement or conservation objectives. Putting this into context, even a small fraction of 4.8 billion hatchery-produced fish that survive to adulthood and stray translates to a perennial source of hatchery-origin individuals that can interact with wild populations. Hatchery-wild interactions may have any number of negative consequences for the natural-origin population, including added competition for stream resources (Grant 2012, Anderson et al. 2020) and/or fitness declines resulting from interbreeding and hybridization (Christie et al. 2014). Furthermore, the presence of hatchery-origin spawners in a stream can complicate the assessment of natural-origin population size for management purposes, as common visual survey methods cannot easily differentiate spawner origin in the absence of external tagging of fish (Johnson et al. 2012). Due to these challenges, understanding the drivers of dispersal in hatchery salmon metapopulations is critical to mitigating straying by hatchery-origin salmon.

Documented rates of straying by hatchery-origin salmon vary greatly across species, populations, and hatchery programs (Quinn et al. 1991, Westley et al. 2013, Keefer and Caudill 2014). Based on studies of donor straying (i.e., straying out of a population), we have a solid understanding of fish characteristics that influence the likelihood of an individual straying. These characteristics include interrupted olfactory imprinting (Keefer et al. 2008, Bond et al. 2017), spawner age (Quinn and Fresh 1984, Unwin and Quinn 1993), and hatchery-origin strays returning to an ancestral home stream (Mclsaac and Quinn 1988, Candy and Beacham 2000). Far less is known about what influences recipient straying (i.e., into a population) of salmon, which is more important from a conservation standpoint since high levels of recipient straying can erode local population productivity through competition and outbreeding depression (Brenner et al. 2012, Keefer and Caudill 2014, Bett et al. 2017). Metapopulation theory (Hanski 1998, Moilanen and Hanski 1998) and empirical examples (Weddell 1991, Jonsson et al. 2003) indicate that the distance between a habitat patch and a source population (i.e., hatchery release site; Heggberget et al. 1993, Josephson et al. 2021) relates directly to the number of dispersers received by the patch. However, factors beyond distance to a release site affect the number of stray hatchery-origin salmon at a site. For instance, work in the heavily altered Columbia River system revealed that among five tributaries where hatchery-origin Chinook salmon (*Oncorhynchus tshawytscha*) were released, the Lewis and Kalama rivers consistently attracted strays from other sites over multiple years, while other sites seemed to repel them for reasons that were unclear and not related to distance from release or the ocean (Quinn et al. 1991, Pascual and Quinn 1994). We hypothesize that habitat characteristics other than distance influence a hatchery salmon's choice of spawning habitat because from an ultimate standpoint, characteristics of the recipient habitat are related to a salmon's probability of reproductive success. Indeed, in a study of dispersal between two spawning populations of wild sockeye salmon (*Oncorhynchus nerka*), Peterson et al. (2016) found that individuals tended to stray away from the creek that had less vegetative cover and more bear predation wherein the likelihood of surviving to successfully spawn was lower. Furthermore, sockeye salmon that ultimately strayed were often previously observed at the mouths of their natal creeks, which suggests that these individuals had the ability to find the natal site but chose an alternative preferred location for eventual spawning.

In this study, we sought to test the hypothesis that spawning habitat characteristics influence dispersal dynamics of hatchery salmon metapopulations. We undertook this study in Southeast Alaska, where an average of 447 million hatchery-origin chum salmon (*Oncorhynchus keta*) were released as juveniles annually 2003–2017 (Wilson 2021). Identifying the factors that influence straying of hatchery-origin chum salmon is particularly pertinent in this system because regional hatcheries form a fishery enhancement program, where hatchery- and natural-origin salmon can mingle at sea in shared ocean foraging habitats but are intended to avoid interaction on spawning grounds to prevent impacts to wild salmon populations while making hatchery salmon available for harvest (Josephson et al. 2021). Pervasive straying of hatchery-origin chum salmon in Southeast Alaska (Piston and Heinl 2012, Josephson et al. 2021) indicates that not all goals of the program are being met. Fortuitously, the framework of hatchery production in Southeast Alaska facilitates the study of factors that influence straying because most hatchery-produced chum salmon in Southeast Alaska are released at remote sites located in open estuaries (Wilson 2021), and since returning hatchery-origin adults have no home stream they appear to be uniquely primed for seeking out and straying into suitable spawning habitat. Moreover, nearly 100% of all released hatchery fish are marked (Wilson 2021). During the fish's embryonic stage, otoliths are thermally marked with episodic temperature fluctuations, resulting in a unique banding pattern that identifies individuals as hatchery-origin (Volk et al. 1999). This enables identification of hatchery-origin individuals virtually without error, and, due to the internal nature of the mark, successfully eliminates observer bias during field sampling.

In this paper, we use the estimated number of dead hatchery-origin strays that spawned in 57 streams over a 10-year period to 1) determine which sites consistently attract more hatchery-origin chum salmon in Southeast Alaska, and 2) assess the role of spawning site characteristics that may be associated with attractiveness. By doing so we aim to provide insight into the role of local spawning site features in mediating metapopulation dispersal dynamics and to use this information as a first step towards informing the management of hatchery release sites to minimize hatchery-wild interactions.

Materials and Methods

Study system

Southeast Alaska comprises 135,000 km^2 of temperate terrestrial and aquatic habitat that has been sustainably stewarded for millennia by the Eyak, Łingít, Haida, and Tsimshian Peoples. Small, mountainous watersheds with short streams characterize the region and provide excellent habitat for several anadromous fish species, particularly pink salmon (*O. gorbuscha,* cháas' in the Łingít language), chum salmon (téel'), and coho salmon (*O. kisutch*, l'ook, Giefer and Blossom 2020). There are currently 7,118 documented streams that support spawning populations of natural-origin (often referred to as "wild," although some individuals could have hatchery ancestry) chum salmon (Giefer and Blossom 2020). Beyond production in nature, twelve chum salmon enhancement hatcheries with 27 release sites currently operate in Southeast Alaska (Fig. 1.1) with the goal of augmenting harvest in common-property commercial fisheries.

Hatchery-produced chum salmon are of high commercial value to the region; in 2021 they contributed 92% of the total commercial harvest of all chum salmon in Southeast Alaska, which translated to $11 million in commercial ex-vessel value (Wilson 2021). Hatchery salmon that stray can also make up a substantial portion (up to 87% within a single year) of the total escapement to certain stream spawning populations (Piston and Heinl 2012, Josephson et al. 2021). To document the extent and possible impacts of hatchery production on wild stocks, a consortium of partners comprised by the aquaculture industry, the Alaska Department of Fish and Game, and the University of Alaska established the Alaska Hatchery Research Project in 2011 (AHRP; Alaska Department of Fish and Game n.d.). The AHRP has three primary objectives: 1) to describe the genetic stock structure of chum salmon in Southeast Alaska; 2) to measure the extent and annual variability of straying by hatchery-produced chum salmon; and 3) to quantify the impact of straying of hatchery chum salmon on the reproductive success (per capita productivity) of wild chum salmon stocks in Southeast Alaska. Josephson et al. (2021) addressed these questions using a portion of the AHRP data (2013–2015 surveys). They found that stray hatchery salmon were widespread in Southeast Alaska streams but varied widely in occurrence, with 22 out of 32 streams having less than 5% of the recipient escapement comprised by strays on average during 2013–2015, while 10 of 32 streams had a mean of 20% (range: 6–71%). Our analyses expand upon the work of Josephson et al. (2021), which fully describes field sampling methods, thus we only briefly describe them here.

Foot crews surveyed 33 chum salmon-spawning streams throughout Southeast Alaska 2013–2019 during chum salmon spawning seasons (Fig. 1.1). Survey streams were randomly selected from a set of 81 continually monitored index streams defined by Piston and Heinl (2014). Twenty-nine of the streams were only sampled 2013–2015 and were sampled twice on average (range: 1–6 surveys) in any given year. The two surveys occurred early and then late in the spawning season, such that surveyors would be able to account for most of the spawners from the peak of the run by accessing carcasses immediately afterwards. If only one survey occurred on a stream in a given year, it occurred at or near the peak run timing, which ranges from mid-July to mid-August for chum salmon in Southeast Alaska (Eggers and Heinl 2008). Surveyors had a target carcass sample size of 384 fish, after which efforts would be focused on other streams. Four of the 33 streams were additionally sampled in 2017–2019 and were sampled either every day or every other day with no maximum number of fish to sample (i.e., sample as many fish as possible). These four streams were also sampled 2013–2015, but in 2014 they were sampled daily or every other day as logistics allowed. A separate study conducted in 1 of the 4 streams (Sawmill Creek) in 2015 also sampled all carcasses possible on a daily or semi-daily basis as weather and stream conditions allowed (McConnell et al. 2018).

During surveys, crews collected otoliths from every chum salmon carcass encountered along the entire length of the stream used by chum salmon for spawning. If a stream sampled 2013–2015 with a threshold of 384 fish contained more than 384 carcasses, the crews would spread sampling effort throughout the extent of the stream. The carcasses were later identified as hatchery- or natural-origin via the presence/absence of a hatchery thermal mark. Thus, a "stray" in this study was conservatively defined as a marked salmon found naturally dead in the stream of recovery, as opposed to live fish assumed to remain in the stream. Furthermore, this study quantified the extent of recipient rather than donor straying, meaning that the number of strays was considered relative to the size of the recipient stream population, rather than the total hatchery population (Keefer and Caudill 2014, Bett et al. 2017).

Hatchery- and natural-origin spawner data from an additional 31 streams in Southeast Alaska were available from an earlier study that collected data 2008–2011 (no temporal overlap with AHRP surveys; Piston and Heinl 2012). The carcass sampling methods were identical, except that 2008–2011 surveys had a target carcass sample size of 192 chum salmon. Combined data from the Alaska Hatchery Research Project and Piston and Heinl (2012) yielded a total of 64 streams and 48,665 individual salmon sampled across 10 years (2008–2011, 2013–2015, and 2017–2019). Of these, 8,538 fish (17.5% of the total) were confirmed to be of hatchery-origin by otolith thermal markings. Our final dataset included 45,401 chum salmon from 624 surveys across 57 streams after removing streams surveyed outside of the chum salmon spawning season in Southeast Alaska (Eggers and Heinl 2008).

Quantifying straying

We described the number of stray hatchery-origin chum salmon detected in each stream as a function of a suite of ecological and spatial variables and defined site attractiveness as the number of strays present in a stream relative to other sites. We note that the number of strays detected in a stream was biased low in streams where proportionally less of the total number of carcasses was sampled, particularly in 2008–2011 and 2013–2015 streams with predetermined sampling thresholds of 192 and 384 fish, respectively (Fig. S1.1). To account for the bias, we divided the number of hatchery strays detected in a survey by the proportion of total carcasses sampled during each survey, thereby expanding the number of hatchery strays in streams proportional to the actual number of dead chum salmon. Counts of total dead were unavailable for 2008–2011 surveys, so we estimated the number of carcasses for these surveys using a simple linear regression fit ($F = 340.7$, $df = 1$, $r^2 = 0.63$) with 2013–2015 data that predicted the dead count dependent on the number of fish sampled. The number of hatchery strays detected in a survey divided by the proportion of carcasses sampled may be considered a reasonable estimate of the effective number of dead hatchery strays expected to be within a stream on a given sampling occasion.

Further, because the number of sampling events varied considerably across streams and years (Fig. 1.1), we ultimately defined the model response variable, or attractiveness index, as the average effective number of stray hatchery-origin chum salmon in a stream each year. The attractiveness index (A_{iy}) was calculated for each stream and year as the total effective number of hatchery strays summed over the season divided by the number of carcass surveys conducted in stream i in year y.

Thus, our model response variable should be interpreted as the total count of hatchery-origin spawners one would expect to find in a single survey if a stream was randomly sampled at peak chum salmon run timing. Data used to calculate the attractiveness index were derived directly from Josephson et al. (2021) and Piston and Heinl (2012). We considered using pHOS (the proportion of hatchery-origin spawners) in each stream as the response variable but given the challenge of readily interpreting the number of strays in a stream using pHOS, we instead chose to use the absolute (effective) number of strays as an index of attractiveness.

Factors associated with attractiveness

To explain variation in the attractiveness index among streams within years, we considered the following covariates, each with an associated biological hypothesis (Table 1.1):

1) Stream distance to the nearest chum salmon hatchery: the hydrographic distance in km from the mouth of the stream to the closest chum salmon hatchery.
2) Stream distance to the nearest chum salmon hatchery release site: the shortest hydrographic distance in km from the mouth of the stream to the closest chum salmon hatchery release site.

3) Number of hatchery chum salmon released within 40 km of the stream: the weighted moving average of the number, in millions, of hatchery-origin juvenile chum salmon released 2–5 years prior to the year of sampling within 40 km of the stream mouth. The 40 km threshold was derived from an approximate average of the threshold distances for elevated levels of straying by Pacific and Atlantic salmon in other studies (Pascual and Quinn 1994, Jonsson et al. 2003, Piston and Heinl 2012, Josephson et al. 2021). Hatchery chum salmon are released the year following their brood year in Southeast Alaska, so releases 2–5 years prior correspond to chum salmon ages 3–6 spawning in streams. The weighted moving average of the number of hatchery-origin juveniles released 2–5 years prior was based on the age distribution of hatchery-origin strays in the stream in question.
4) Conspecific (natural-origin chum salmon) abundance: the estimated escapement of natural-origin chum salmon in the stream in the year of sampling, less the estimated hatchery contribution. Hatchery contribution to the escapement of each stream was estimated as the number of hatchery-origin strays out of the total number of fish sampled in each stream in the AHRP dataset (Josephson et al. 2021).
5) Pink salmon abundance: the estimated escapement of natural-origin pink salmon in the stream in the year of sampling. Pink salmon abundance was not adjusted for hatchery contribution. We assumed that most pink salmon in Southeast Alaska are wild since hatchery production of pink salmon is small in scale for this region (Stopha 2018).
6) Mean watershed discharge: long-term (1979–2012; Table 1.1) whole-watershed average discharge estimates. The assigned watersheds occasionally include other

freshwater channels, so a caveat of our research is that any significant discharge effect in the model relates to the hydrologic regime of the surrounding watershed. However, we expected that watershed-level hydrologic conditions provide a reasonable proxy for those at the stream level. Further, discharge data were derived from a separate model (Sergeant et al. 2020) and were only estimated at the stream level (did not vary annually), so we assessed the effect of overall long-term flow characteristics on straying patterns.

7) The coefficient of variation (CV) of watershed discharge: the mean-adjusted standard deviation in long-term whole-watershed estimates of freshwater discharge. The CV was calculated from the entire distribution of modeled daily stream discharge estimates from 1979 to 2012.
8) Fishery harvest of chum salmon in Southeast Alaska: The total annual commercial harvest of chum salmon in each management subregion in Southeast Alaska. Hatchery-produced chum salmon comprise most of the commercial chum salmon harvest and are targeted for 100% removal at remote release sites designated as terminal harvest areas (Wilson 2021). To control for the potential effect of fishery harvest on the number of hatchery chum salmon strays in the study streams, we included this covariate under the hypothesis that years of higher harvest may result in reduced numbers of hatchery-origin salmon straying into index streams.

Exploratory data analysis revealed that stream distance to the nearest hatchery, stream distance to the nearest release site, and the number of fish released within 40 km of the stream were collinear with one another (Spearman's rank correlation coefficient $\rho > 0.5$; Table S1.1). We retained the number of fish released within 40 km because it provided information on both the distance to a potential source of hatchery-origin chum salmon and on the size of that source, as opposed to just a measure of distance. No other pairs of variables were correlated ($\rho > 0.5$). The final set of covariates considered in the model were 1) the number of fish released within 40 km of the stream, 2) conspecific abundance, 3) pink salmon abundance, 4) mean watershed discharge, 4) the coefficient of variation of watershed discharge, and 5) fishery harvest by subregion.

Stream attractiveness analysis

We fit a generalized linear mixed-effects model with a negative binomial error distribution and log-link following the general formula:

(1)

$$\begin{aligned}\eta_{iy} = \log(\hat{A}_{i,y}) \\ &= \alpha + a_y + \beta_1(40\ km\ release_{i,y}) + \beta_2(conspecific\ abundance_{i,y}) \\ &+ \beta_3(pink\ abundance_{i,y}) + \beta_4(mean\ flow_i) + \beta_5(mean\ flow_i)^2 \\ &+ \beta_6(CV\ flow_i) + \beta_7(CV\ flow_i)^2 + \beta_8(harvest_{i,y}) + \varepsilon_{i,y}\end{aligned}$$

$$a_y \sim N(0, \sigma_y)$$

$$A_{i,y} \sim NB(e^{\eta_{iy}})$$

where $\hat{A}_{i,y}$ is the predicted attractiveness index; average (effective) number of strays of stream *i* in year *y*, a_y is the randomly varying intercept for the effect of year, and β_n are the coefficient estimates for model effects. Year was included in the model as a random effect so that it was possible to make predictions outside of the time series while quantifying and propagating the common among-year variation in expected stream attractiveness. We explored possible nonlinear relationships for the two flow effects by testing quadratic terms, given that we recognize that stream discharge influences spawning site selection on small scales (Bjornn and Reiser 1991, Beechie et al. 2008), but it was unclear how that relationship would manifest in hatchery chum salmon seeking out spawning streams.

Prior to modeling, we standardized all covariates to the same scale by subtracting the mean and dividing by the standard deviation (i.e., z-score). All covariates were continuous variables. The response variable represented an average of hatchery-origin abundances in streams. However, as the attractiveness index is intended to reflect the expected count in a given survey, continuous attractiveness was rounded to the nearest even integer. Data were modeled with a negative binomial error distribution because the conditional variances were greater than the conditional means in the data, resulting in a worse fit with a Poisson error distribution (Table S1.2). Further, incorporating zero-inflation structure into the model was considered, but ultimately deemed unnecessary based on the distribution of model residuals (Fig. S1.3). We used AIC_c-based model selection with the package *MuMIn* in the R programming language (Bartoń 2020) to select the best model to predict stream attractiveness to stray hatchery-origin chum salmon. Our selection process included evaluation of biologically plausible interaction terms as well as the hypothesized quadratic terms for stream discharge. All possible combinations of fixed effects were evaluated as candidate models, and we included the null model (no fixed effects) in our calculation of AIC_c values. All models were compared with maximum likelihood (ML) estimation and the final model was also derived using ML (as opposed to REML) because the variance bias was expected to be small given the number of covariates versus observations.

We interpreted and defined the “final” model as the most parsimonious model within 2 AIC_c units of the lowest AIC_c. We considered covariate effect sizes to be strong if their approximate 95% confidence interval did not overlap with zero. Approximate 95% confidence intervals were calculated using the standard error around each coefficient estimate. We cross-validated the model by randomly removing 30% of the original stream-year observations and using the remaining 70% to predict the withheld values. We repeated this removal and refitting process over 500 iterations and calculated the mean absolute error (MAE) for each retained observation.

Results

Observations of stream attractiveness in Southeast Alaska

Despite variation in straying rates across space and time, we found that a subset of sites consistently attracted or repelled stray hatchery-origin chum salmon in Southeast Alaska (Fig. 1.1, Table 1.2). There was an apparent break in the data in which the most attractive streams (n = 10) had mean observed attractiveness indices (averaged over years) of 12 or more hatchery-origin strays (range: 12–115), while all other streams (n = 47) were less attractive with mean observed indices < 8 strays (range: 0–7.6; Table 1.2, Table S1.4). Among the attractive sites, Fish Creek was the most attractive: it had the highest attractiveness index relative to all other streams in 6 out of the 8 years it was surveyed, with a mean attractiveness index of 115 strays (range: 31–332). Similarly, Ketchikan Creek and Sawmill Creek were the second and third most attractive over time with mean attractiveness indices of 76 (only one observation) and 50 (range: 2–147) hatchery-origin strays, respectively. Within years, Ketchikan Creek was the second most attractive stream behind Fish Creek in 2010. Sawmill Creek had the highest attractiveness index in three out of nine years surveyed and was consistently within the top ten in all years surveyed.

At the other end of the continuum, many streams were apparently unattractive to strays. Out of 57 sites analyzed, the 10 least attractive streams across time had mean attractiveness indices of 0.4 strays (range: 0–1; Table 1.2). Some of the apparently unattractive streams were only surveyed once in 10 years, thus it is difficult to truly assess their level of attractiveness, but several sites with few strays that were sampled consistently confirmed that certain streams are indeed unattractive (Table 1.2). For instance, no hatchery-origin strays were found in Little Goose Creek in seven surveys over three years. No more than two strays in total were observed in Kadashan River in any one year across six years of consistent survey effort.

Factors influencing stream attractiveness

Two models contributed equally to the total AIC_c weight ($\Delta AIC_c = 0.00$). We retained the more parsimonious of the two as our final model. This model explained stream attractiveness as a function of the number of hatchery chum salmon released within 40 km and a quadratic effect of the coefficient of variation of stream discharge. This model was estimated to explain 37% of the total variation from its fixed effects and had a standard deviation around its year random effect of 0.75 (Table 1.3). Further candidate models which included additional effects were unlikely to predict the attractiveness index of a given stream.

Consistent with the importance of site distance to source populations, the number of fish released within 40 km of a stream was strongly positively related to the number of stray hatchery-origin chum salmon found within a stream. A 1-SD (27.6 million fish) increase in the number of fish released within 40 km resulted in a 44% increase in the average number of hatchery-origin chum salmon in the stream, conditional on the values of the other covariates being held constant at their mean values. We further noted that the streams with the highest attractiveness indices were close to remote hatchery release sites rather than close to hatcheries where rearing and release occurred at the same location (Fig. 1.2), although the effect of release site type on attractiveness was not statically significant ($t = -0.991$, $df = 13.9$, $p = 0.339$; Fig. 1.2). The coefficient of variation of stream discharge was strongly related to the attractiveness index as well, though the relationship was nonlinear (Fig. 1.3). At the lowest CVs of river discharge (< 0.48), the number of hatchery-origin strays in a stream increased slightly and at the highest levels (> 0.55), the number of strays increased sharply.

The mean absolute error (MAE) of the model for all stream-year observations was 10.98 hatchery-origin strays and 6.31 strays for observations < 40 strays, indicating lower predictive accuracy for higher observed values of stream attractiveness (Table 1.3). Predictions from the final model were more accurate than those made by the null model, which had an MAE of 14.89 for all observations and 8.27 for observations below 40 strays (Table 1.3). The final model was qualitatively accurate at predicting the relative attractiveness of streams. For example, while the model did not accurately predict the exact observed attractiveness index in Fish and Sawmill Creek, it did predict that Fish Creek was more attractive than Sawmill Creek (Table 1.2).

Discussion

Explaining stream attractiveness to hatchery strays

Using a decade of data on the number of hatchery-origin strays spawning in streams in Southeast Alaska, we identified attributes of spawning streams that were associated with increased attractiveness to hatchery-origin chum salmon. We revealed that proximity to large releases of hatchery salmon and below- or above-average intra-annual variability in streamflow were associated with increased attractiveness of spawning sites to hatchery strays. These results both corroborate the importance of distance between sources and sinks and emphasize the additional roles of site characteristics in influencing the dispersal of individuals within salmon metapopulations.

Across our study system of 57 streams in Southeast Alaska, we identified sites that were consistently attractive or consistently unattractive to stray hatchery-origin chum salmon across multiple years. Most sites were relatively unattractive, i.e., 47 out of 57 streams had observed attractiveness indices of less than eight strays, while only 10 out of 57 had indices of 12 strays or greater. Thus, based on our dataset, most streams are not at great risk of receiving large numbers of hatchery-origin spawners. However, the potential conservation implications of straying by hatchery-origin salmon should not be discounted, especially for the attractive sites, as the effect of straying into a stream depends on the size of the wild population. Even a modest increase in the number of hatchery-origin spawners in a stream from one year to the next could have significant impacts on a small natural-origin population spawning in the same stream (Bett et al. 2017).

Our observations of stream attractiveness align with the results of other studies in which some spawning sites are clearly important or appealing to dispersing hatchery-origin salmon across time, while others are not. In a study of hatchery salmon dispersal among five tributaries in the Columbia River system, the Lewis and Kalama tributaries attracted hundreds of strays from three of the other tributaries over a 6-year period, while Washougal and Abernathy tributaries only attracted zero and 1 stray, respectively (Quinn et al. 1991). These observations suggest that there is some set of characteristics, rather than just random chance, that makes spawning streams inherently attractive or unattractive to dispersing salmon.

The importance of stream proximity to hatchery release sites may be explainable in part by metapopulation theory, which predicts that patch proximity to a source population increases the probability that dispersers are received by that patch (Hanski 1998, Moilanen and Hanski 1998). We observe this in salmon populations, in which streams that are close to a source of hatchery salmon (e.g., a release site) have higher numbers of recipient strays (Jonsson et al. 2003, Piston and Heinl 2012, Josephson et al. 2021). This is consistent with the result in our study that streams with more hatchery-origin strays are within 40 km of hatchery release sites, and, as would be expected, larger releases of fish result in proportionally more strays in nearby streams.

We also noted that proximity to remote hatchery release sites further increased the number of hatchery-origin strays compared to hatchery on-site releases. Remote release sites are sites where hatchery juveniles are released after being transported by barge away from the rearing hatchery, as opposed to being released directly from the hatchery. The difference was not statistically significant, possibly due to limited statistical power and an influential observation of the on-site release type, but we found that streams within 40 km of a remote hatchery release site had a maximum attractiveness index twice that of streams within 40 km of a release site located at the hatchery (Fig. 1.2). This result is consistent with the results of other studies in which transporting hatchery-origin juveniles increased stray rates of those fish as adults due to navigational impairment (Keefer et al. 2008, Bond et al. 2017). In Southeast Alaska, transportation through the estuarine environment may confuse the fish's perception of where 'home' is, leading to increased straying. However, the lack of release site-specific thermal marks for all hatcheries producing chum salmon in Southeast Alaska precludes definitive assessment of the relationship of straying with release site type. This is a fruitful area for future research.

Counter to our predictions, we found that intermediate coefficients of variation of stream discharge were least attractive to hatchery-origin chum salmon, while high and low values greatly increased the number of strays in a stream. The effect of CV of flow was strong (Fig. 1.3). It is possible that low CVs of streamflow over time are indicative of habitat stability, though it is unclear if this would be detectable to a migrating hatchery salmon present in the short-term. We think it more likely that the effect of CV of flow on stream attractiveness represents an artifact of another factor for which we did not test. One such possible artifact may be the water source of the stream, i.e., if the stream is fed by rain, snow, or glacier meltwater. We noted that the highest and lowest CVs were associated with snowmelt-fed streams (Fig. 1.4). However, snow-5 streams were not associated with high or low CVs of flow (Fig. 1.4), so the effect of CV of flow may not be entirely attributable to snowmelt as a water source alone. Note that the number assigned to watershed classifications (e.g., "snow-5", "rain-6") are arbitrary. We posit that the possible effect of snowmelt as a water source on attractiveness may be due to temperature control. Snowmelt streams are generally more temperature-stable because they vary less with summer air temperature compared to rain-fed streams (Lisi et al. 2015), so perhaps the snowmelt streams provided a more amenable and attractive temperature regime for prospective hatchery strays. As the climate warms, watersheds in Southeast Alaska are expected to increasingly shift to being rain-dominated as opposed to snowmelt (Sergeant et al. 2020), so if snowmelt-fed streams are indeed attractive to hatchery strays, then the increasingly small subset of snowmelt-fed streams could become even more attractive to hatchery-origin spawners. Larger numbers of strays in attractive streams could have consequences ranging from increased opportunity for interbreeding and admixture (Grant 2012) to reduced dissolved oxygen availability due to spawner over-abundance in small streams (Sergeant et al. 2017).

We did not find significant relationships between the number of hatchery strays in a stream and the other variables we considered, including fishery harvest, mean stream discharge, and the abundance of natural-origin chum salmon in the stream. We were particularly surprised to not see an effect of conspecific abundance on the number of recipient hatchery strays, given evidence in other populations that salmon are often attracted to conspecifics (Hard and Heard 1999, Jonsson et al. 2003, Brenner et al. 2012) and that salmon may navigate in groups back to freshwater streams (Berdahl et al. 2016). The lack of significance of this effect may be suggestive of the importance of abiotic, in this case streamflow characteristics over biotic characteristics in influencing habitat choice.

Several caveats warrant mention in this study. First, we assumed that sites with few or no strays were unattractive for the purpose of modeling, but effort varied considerably across streams and years. As demonstrated in Candy and Beacham (2000), increased survey effort can lead to increased detection of hatchery-origin spawners. We accounted for this to the extent possible by averaging the number of strays detected by the number of surveys to calculate our attractiveness index. However, we recognize that while we can assess stream (un)attractiveness with relative confidence for sites with surveys across multiple years (e.g., Ushk Bay W End and Prospect Creek, Table 1.2) and for sites that had large attractiveness indices in a single year (e.g., Ketchikan Creek), we cannot know if ostensibly unattractive sites that were sampled once or twice in a decade were truly unattractive. Therefore, to adequately assess stream attractiveness for all sites, it would be necessary to survey across multiple years. Second, it is unclear if the patterns of straying we report in this study would be generalizable beyond the hatchery chum salmon populations in Southeast Alaska. Future researchers should evaluate patterns of stream attractiveness in other regions to see if the effects of stream characteristics on attractiveness are observed (and therefore applicable) elsewhere. Notwithstanding these caveats, we provide a salient explanation for hatchery chum salmon distribution among spawning habitat patches in a landscape.

Conclusions

Studies of metapopulation dynamics draw on patch area and isolation as the most important (and sometimes only) characteristics that influence dispersal between habitat patches (Hanski 1998, Moilanen and Hanski 1998). We have confirmed that isolation, i.e., proximity to a source population of hatchery-origin salmon, does affect the number of immigrants into a recipient habitat patch. But, consistent with studies of breeding habitat selection in other species (Fleishman et al. 2002, Cameron et al. 2020), additional characteristics of the habitat patch also matter.

Our results have several important implications for the management of chum salmon enhancement in Southeast Alaska. First, it is clear in this study and in similar work in the region (Piston and Heinl 2012, Josephson et al. 2021) that straying of hatchery-produced chum salmon can be substantial in Southeast Alaska, particularly at attractive sites like Fish Creek and Sawmill Creek (Table 1.2). Straying of hatchery-origin chum salmon could have consequences for the genetic integrity of the wild chum salmon population (Grant 2012). Second, we know that there are several extremely attractive streams in Southeast Alaska, and we can further identify other attractive streams with the collection of additional data. We suggest that hatchery release site planning be expanded to avoid not only important wild populations but also attractive streams in the area.

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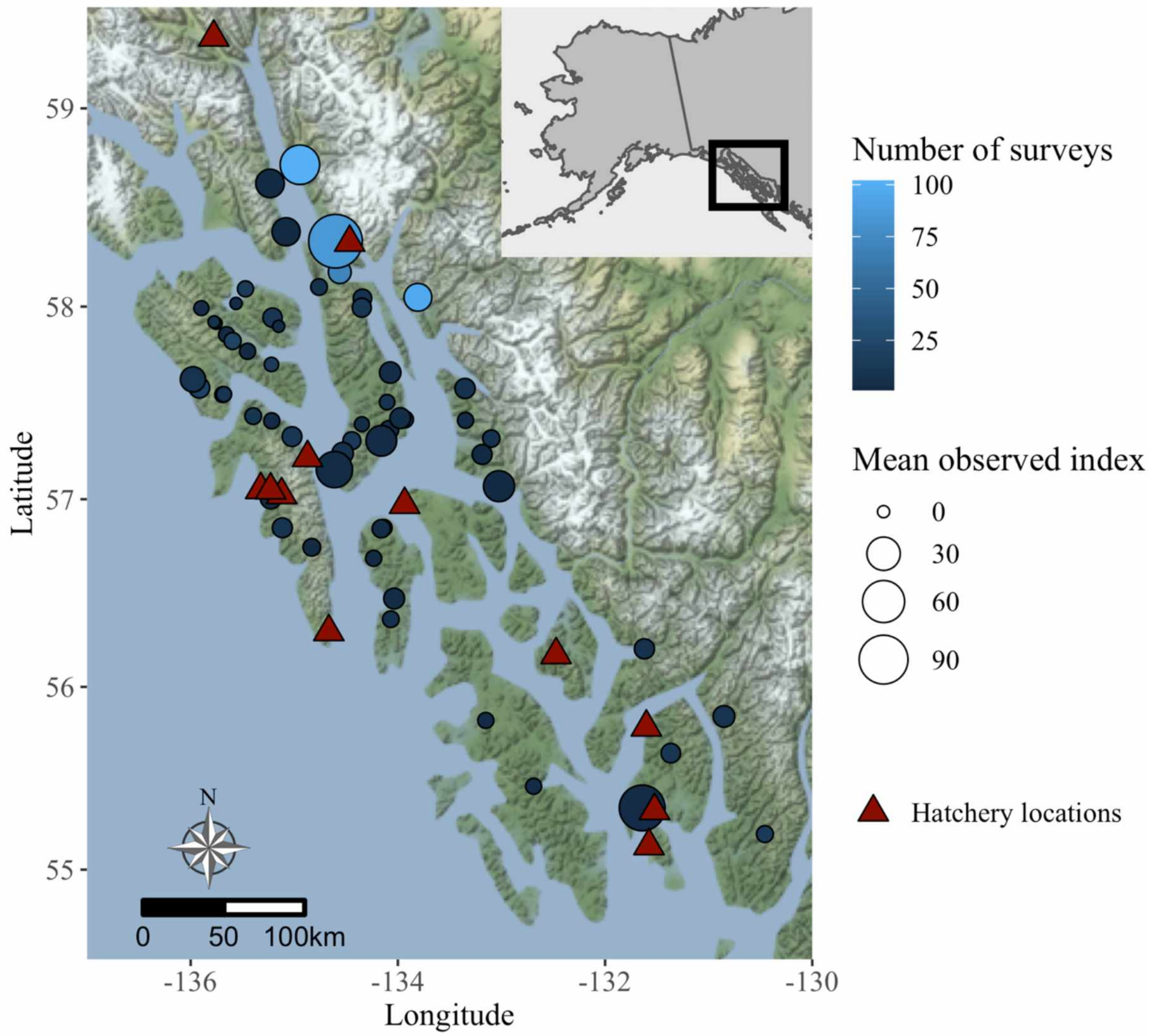

Figure 1.1 Streams in Southeast Alaska that were included in the stream attractiveness model. The mean observed attractiveness index is the mean of the attractiveness indices for each year a stream was surveyed, defined as the effective number of strays detected divided by the number of surveys in a given year. A higher number of surveys indicates greater confidence in the average number of hatchery chum salmon straying to a site over time. This map was created using the R package 'ggmap' (Kahle and Wickham 2013).

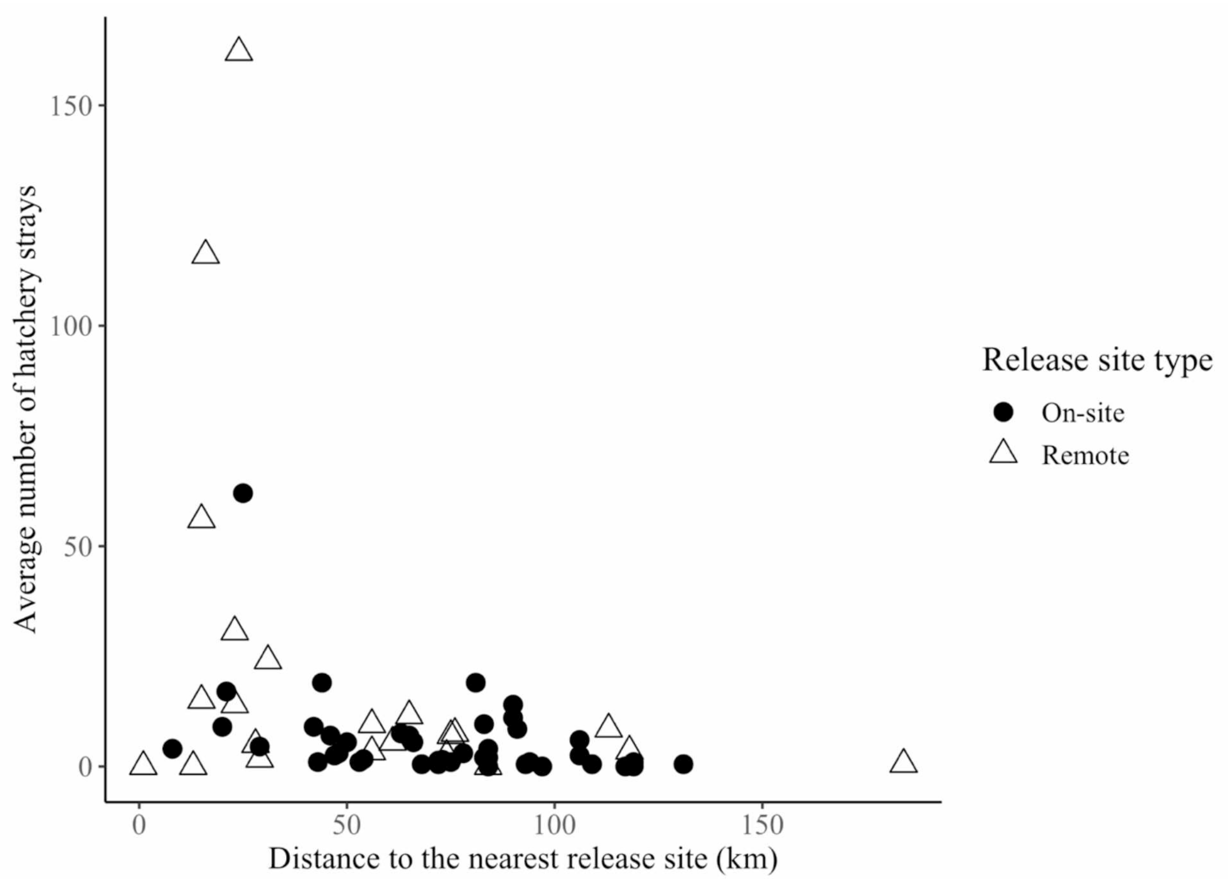

Figure 1.2 The maximum observed value of the model response variable (attractiveness index) for each stream in Southeast Alaska plotted as a function of the distance to the nearest chum salmon hatchery release site. Release sites are either located at or directly in front of the hatchery of origin (on-site), or they are remote.

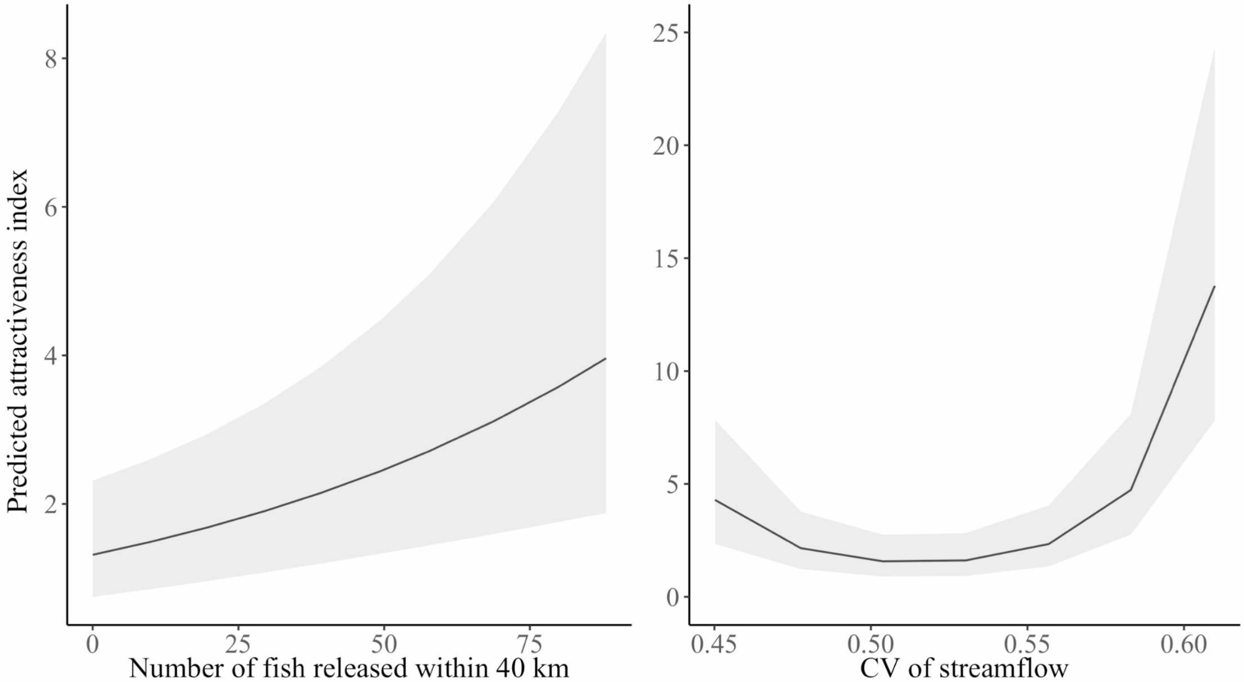

Figure 1.3 The log-transformed model predicted attractiveness index is plotted as a function of the two covariates included in the final model. The shaded region indicates the approximate 95% confidence interval around the model predictions on the scale of each linear predictor.

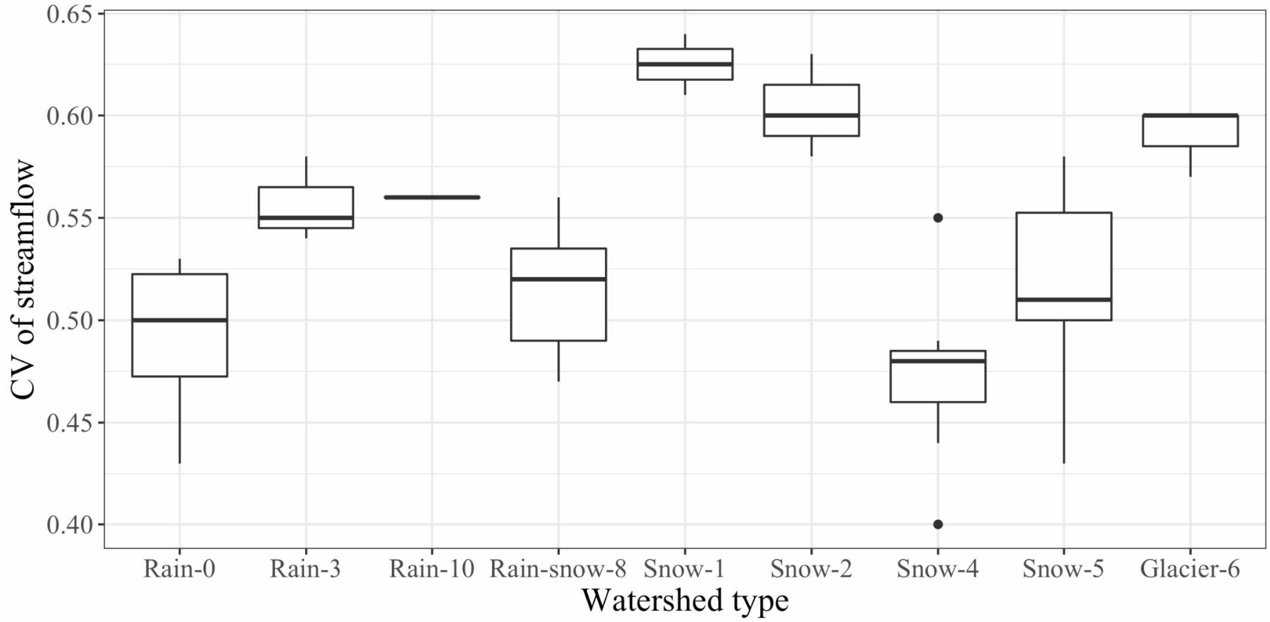

Figure 1.4 The coefficient of variation of streamflow plotted by streamflow class as identified in Sergeant et al. (2020). Sergeant et al. (2020) provides more detailed descriptions of the characteristics of each runoff type for each watershed; note that the class number (e.g., 0 in Rain-0) is an arbitrary value assigned during the classification process.

Table 1.1 Definitions and hypothesized effects of ecological and spatial covariates on the average predicted number of stray hatchery-origin chum salmon in recipient streams in Southeast Alaska. Northern Southeast Inside (NSEI), Northern Southeast Outside (NSEO), and Southern Southeast (SSE) refer to the management subregions in Southeast Alaska (Fishery harvest).

Covariate	Description	Hypothesis	Varied by year	Mean (range)	Data source(s)
Distance to the nearest hatchery	Stream mouth distance (km) to the nearest hatchery	Proximity to hatcheries results in greater numbers of strays	Yes	74 (7–145) km	Hatchery and release locations: Hatchery websites, such as **Northern Southeast Regional Aquaculture Association**
Distance to the nearest hatchery release site	Stream mouth distance (km) to the nearest hatchery release site	Proximity to hatchery release sites results in greater numbers of strays	Yes	62 (8–131) km	Hatchery and release locations: Hatchery websites, such as **Northern Southeast Regional Aquaculture Association**
Number of fish released within 40 km of the stream	Weighted moving average of number of hatchery chum salmon released within 40 km of stream 2–5 years prior to stream sampling	Greater numbers of hatchery salmon released within 40 km of a stream results in greater numbers of strays	Yes	16 (0–88.2) million juvenile chum salmon	Chum salmon age distribution: Alaska Hatchery Research Project (AHRP) data, i.e., Josephson et al. 2021 **Hatchery release site data**
Conspecific abundance	Natural-origin (conspecific) abundance of stream	Greater conspecific abundance results in greater numbers of strays	Yes	3021 (45–22106) chum salmon	Chum salmon escapement: Piston and Heinl 2020a Stream proportion of hatchery-origin spawners (pHOS): Josephson et al. 2021
Pink salmon abundance	Pink salmon abundance of stream	Greater pink salmon abundance results in greater numbers of strays	Yes	47275 (0–$5x10^5$) pink salmon	Pink salmon escapement: Piston and Heinl 2020b)

Table 1.1, continued.

Mean flow	Long-term average discharge from all freshwater channels in the surrounding watershed of stream	Higher average stream discharge will result in more hatchery strays, as high flows can serve as an attractive surrogate for a home stream	No	11.5 (0.32–184.2) m^3/s	Sergeant et al. 2020
Coefficient of variation (CV) of flow	Long-term average coefficient of variation of discharge from all freshwater channels in the surrounding watershed of stream	Low to intermediate coefficients of variation of watershed discharge result in greater numbers of strays	No	0.53 (0.40–0.64)	Sergeant et al. 2020
Fishery harvest	Total number of chum salmon harvested in mixed stock fishery of the corresponding management subregion of stream	NA	Yes	NSEI: 4.8 (3.1–7.2) million NSEO: 1.7 (0.76–2.7) million SSE: 3.5 (2.2–5.3) million	Piston and Heinl 2020a

Table 1.2 The top 10 (above the line) and bottom 10 (below the line) most and least attractive model-predicted streams to chum salmon in Southeast Alaska, respectively. The rows are in descending in order based on the observed attractiveness indices. Model predictions were made individually for each stream in each year, but here we show the average model predicted and observed effective number of strays (attractiveness indices) across all 10 years. The average abundance refers to the mean number of carcasses (hatchery and natural origin together) in each stream in any given survey.

Stream Name	Mean predicted index	Mean observed index	Minimum observed number of strays	Maximum observed number of strays	Average abundance	Total number of surveys	Number of years surveyed
Fish Creek	115.2	115.3	31	323	149	86	8
Ketchikan Creek	13.4	76.0	76	76	115	2	1
Sawmill Creek	81.3	50.0	1	148	89	102	9
Wilson River	12.6	39.0	8	70	91	3	2
Dry Bay Creek	35.4	24.0	24	24	186	1	1
Cannery Cove-Pybus Bay	4.8	23.0	23	23	133	2	1
St. James Bay NW Side	10.5	18.0	18	18	114	1	1
Robinson Creek	10.5	17.0	17	17	98	1	1
Prospect Creek	10.5	16.4	1	36	51	97	7
Sister Lake SE Head	6.2	11.5	1	20	574	8	4
Ushk	2.2	1.0	1	1	107	2	1
Johnston Creek	1.2	0.7	0	1	71	9	3
Ushk Bay W End	1.6	0.7	0	1	47	9	3
Tenakee Inlet Head	1.1	0.5	0	1	86	4	2
Weir Creek N Arm Hood Bay	4.0	0.5	0	1	17	4	2
Kadashan River	1.9	0.3	0	2	4	15	6

Table 1.2, continued.

Big Goose Creek	0.6	0.0	0	0	64	3	1
Kennel Creek	1.3	0.0	0	0	0	2	2
Little Goose Creek	1.3	0.0	0	0	29	7	3
Seagull Creek	0.5	0.0	0	0	0	2	1

Table 1.3 Coefficient estimates for the top two candidate models (in ranked order) to predict the number of stray hatchery-origin chum salmon in a stream in Southeast Alaska. The approximate 95% confidence interval for each estimate is included in the parentheses. AIC_c criteria used for model selection, model weights, cross validation results (MAE; mean absolute error), and pseudo-R^2 values are shown in the bottom half of the table for both models as well as the null model.

	Model 1	Model 2	Null model (Year random effect only)
40km_release	0.345 (0.163, 0.527)	0.364 (0.182, 0.546)	NA
Cons_Abundance	-0.178 (-0.413, 0.057)	NA	NA
CV_flow	0.416 (0.234, 0.598)	0.463 (0.291, 0.635)	NA
CV_flow^2	0.769 (0.612, 0.926)	0.800 (0.641, 0.959)	NA
df	7	6	3
$\log(L_i)$	-468.42	-469.50	-548.54
ΔAIC_c	0.00	0.00	151.71
$w_i(AIC_c)$	0.36	0.36	< 0.01
MAE (all values)	10.51	10.98	14.89
MAE ($x < 40$)	6.18	6.31	8.27
Marginal R^2	0.38	0.37	0.00
Conditional R^2	0.52	0.52	0.04
Intercept (SD)	0.48 (0.73)	0.48 (0.75)	0.41 (0.64)

Supplemental Material

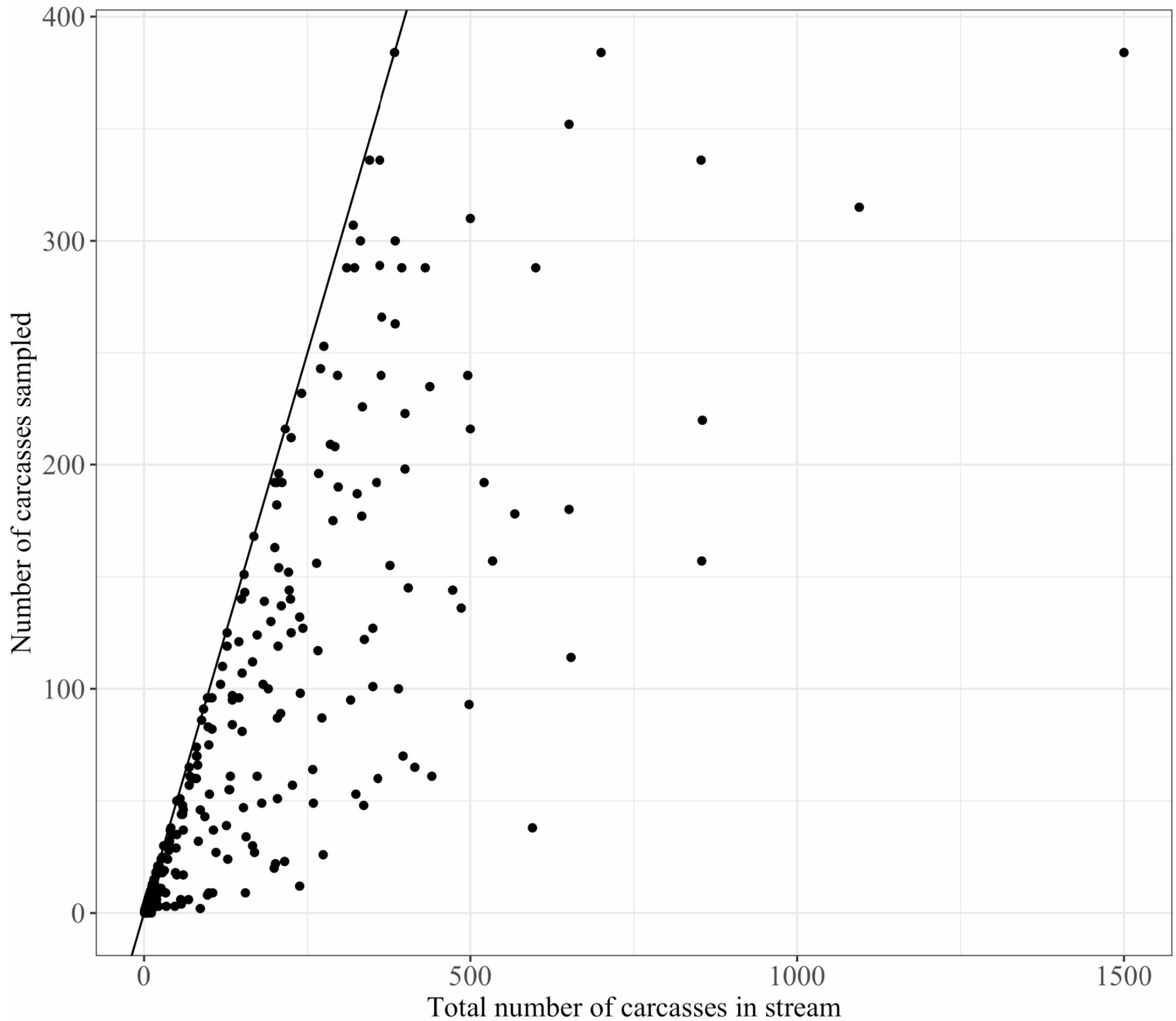

Figure S1.1 The number of chum salmon carcasses that were sampled for otoliths in a stream plotted against the total dead count, or total number of carcasses present in the stream. The solid black line is a 1:1 line indicating streams where 100% of carcasses were sampled for otoliths.

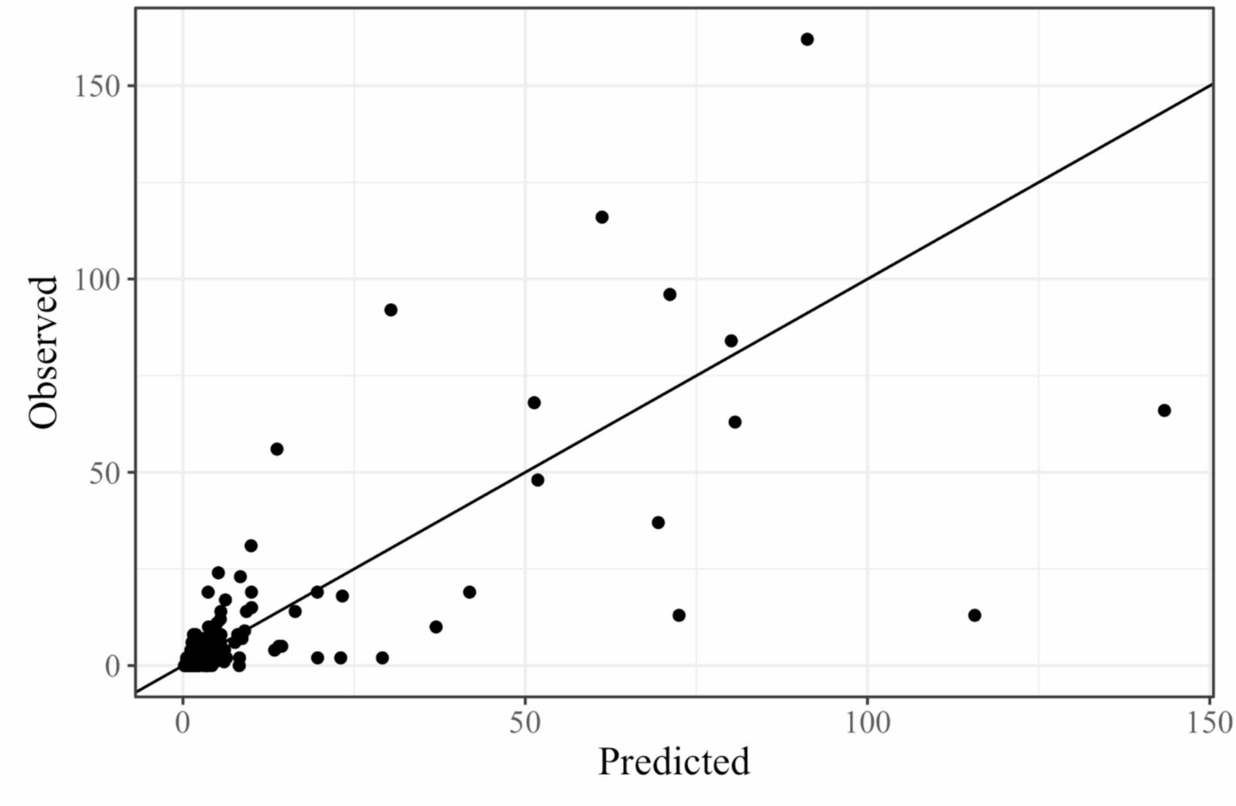

Figure S1.2 Observed attractiveness indices plotted as a function of model predicted attractiveness indices. The solid black line is a 1:1 line.

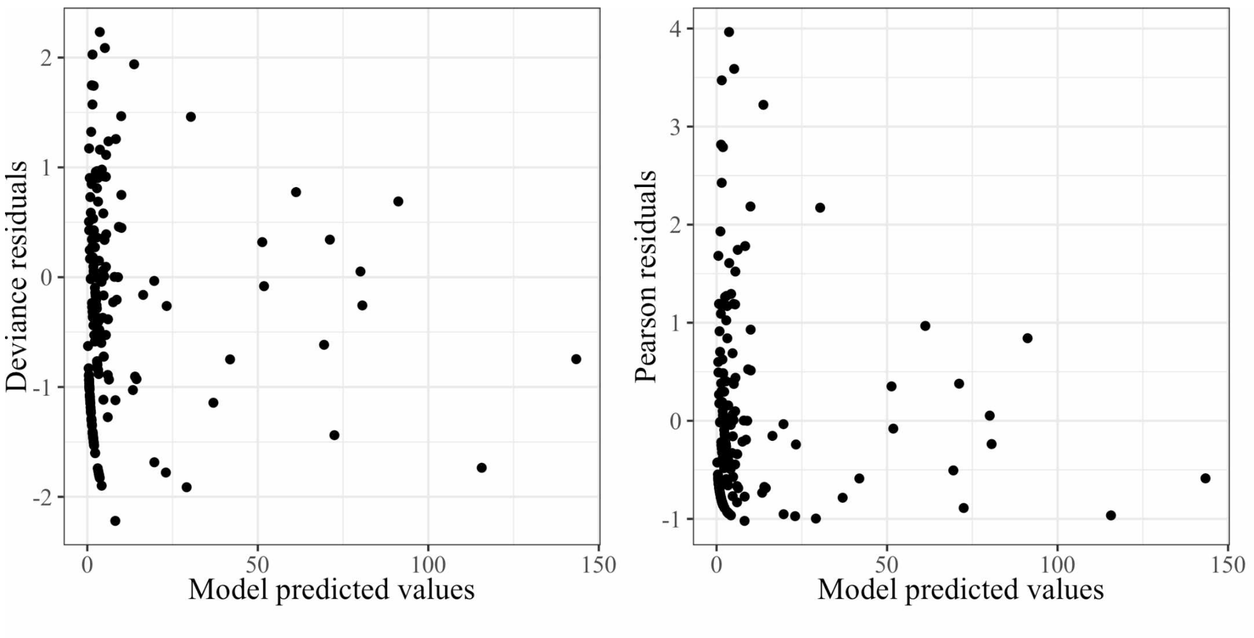

Figure S1.3 Deviance and Pearson residuals from the final model plotted against their predicted values.

Table S1.1 Correlation matrix showing the amount of correlation, or collinearity between proposed model covariates. The bold font indicates correlations that were > 0.5, for which we removed a model covariate.

	Fishery_harvest	**Cons_Abundance**	**Cons_Density**	**Pink_Abundance**	**Pink_Density**	**40km_releas**	**Dist_nearest_H**	**Dist_nearest_R**	**mean_flow**	**CV_flow**
Fishery_harvest	1.000	-0.053	-0.043	-0.070	-0.083	0.154	0.046	-0.075	-0.099	0.248
Cons_Abundance		1.000	**0.889**	0.461	0.326	-0.261	0.175	0.347	0.325	-0.405
Cons_Density			1.000	0.328	0.380	-0.093	0.072	0.192	0.135	-0.360
Pink_Abundance				1.000	**0.885**	-0.291	0.000	0.280	0.346	-0.458
Pink_Density					1.000	-0.106	-0.115	0.132	0.156	-0.412
40km_releas						1.000	**-0.554**	**-0.807**	-0.456	0.180
Dist_nearest_H							1.000	**0.685**	0.322	0.236
Dist_nearest_R								1.000	**0.515**	-0.215
mean_flow									1.000	-0.272
CV_flow										1.000

Table S1.2 Model comparison between the final model fit with a negative binomial error distribution versus a Poisson distribution.

Assumed error distribution	df	AIC_c
Negative binomial	6	951.50
Poisson	5	2280.92

Table S1.3 The form and AIC_c of all candidate models considered. The year random intercept is included in all models and therefore is not shown in the formulae.

Model form	$\log(L_i)$	ΔAIC_c	$w_i(AIC_c)$
40km_releas + Cons_Abundance + CV_flow + CV_flow^2	-468.42	0.00	0.36
40km_releas + CV_flow + CV_flow^2	-469.51	0.00	0.36
40km_releas + Cons_Abundance + CV_flow + $CV\_flow^{2\,+}$ Fishery_harvest	-468.21	1.77	0.15
40km_releas + CV_flow + $CV\_flow^{2\,+}$ Fishery_harvest	-469.43	2.02	0.13
40km_releas + Cons_Abundance + mean_flow + CV_flow + $CV\_flow^{2\,+}$ Fishery_harvest	-468.05	3.67	0.00
Cons_Abundance + CV_flow + $CV\_flow^{2\,+}$ Fishery_harvest	-474.70	12.56	0.00

Table S1.4 Model predicted and observed attractiveness indices in all 56 modeled streams over time. Model predictions were made individually for each stream in each year, but here we show the average model predicted and observed effective number of strays (attractiveness indices) over time for simplicity. Minimum and maximum number of strays are not averaged.

Stream Name	Latitude	Longitude	Mean predicted index	Mean observed index	Minimum observed number of strays	Maximum observed number of strays	Total number of surveys
Fish Creek	58.332728	-134.60176	115.2	115.3	31	323	86
Ketchikan Creek	55.340823	-131.6417	13.4	76	76	76	2
Sawmill Creek	58.71843	-134.94561	81.3	50	1	148	102
Wilson River	57.155757	-134.61229	12.6	39	8	70	3
Dry Bay Creek	57.06871	-133.02373	35.4	24	24	24	1
Cannery Cove-Pybus Bay	57.306248	-134.15955	4.8	23	23	23	2
St. James Bay NW Side	58.624498	-135.23361	10.5	18	18	18	1
Robinson Creek	58.380675	-135.07881	10.5	17	17	17	1
Prospect Creek	58.04737	-133.80631	10.5	16.4	1	36	97
Sister Lake SE Head	57.62557	-135.97804	6.2	11.5	1	20	8
Admiralty Creek	58.1757	-134.56091	4.2	7.6	0	28	71
King Creek	55.84035	-130.85211	6.4	6	2	14	8
Mole River	57.660517	-134.07379	2.6	5.7	3	7	4
Whitewater Creek	57.24227	-134.53249	4.0	5.7	2	11	8
Camp Coogan	57.003894	-135.22678	4.8	5	5	5	1
Sample Creek	56.474244	-134.03588	3.3	5	1	9	4
Snug Cove-Gambier Bay	57.424274	-133.97671	4.6	5	2	8	4
Ford Arm Creek	57.58192	-135.91527	2.9	4.7	0	11	21
Chuck River	57.57833	-133.35174	1.4	4.3	1	8	7
Harding River	56.20498	-131.62061	10.6	4.3	1	6	7
Sanborn Creek	57.234998	-133.18633	2.1	4	4	4	1
W Crawfish NE Arm Hd	56.84966	-135.11491	5.0	4	0	10	9
Ralphs Creek	57.328229	-135.02154	9.0	3.8	0	11	13
Carroll Creek	55.64054	-131.36523	7.5	3.6	0	7	11
Freshwater Creek	57.94333	-135.2097	2.6	3.4	0	13	11
Swan Cove Creek	57.9944	-134.34848	5.2	3.2	0	10	11
Amber Creek	57.362871	-134.08361	2.1	3	3	3	2
King Salmon River	58.042	-134.34145	1.6	2.67	0	7	8

Table S1.4, continued.

Saginaw Creek	56.844679	-134.15974	4.2	2.5	0	5	3
Chaik Bay Creek	57.306752	-134.44392	8.2	2.2	0	6	14
Whale Bay Great Arm Head	56.74647	-134.83079	113.4	2	2	2	1
Glen Creek	57.31787	-133.09792	3.9	1.8	0	4	7
East of Snug Cove	57.41776	-133.93299	3.1	1.7	0	5	8
Seal Bay Head	57.82324	-135.59499	1.7	1.6	0	3	21
Marten River	55.197016	-130.45723	1.9	1.5	0	6	14
Greens Creek	58.099966	-134.76091	3.1	1.3	0	4	7
Petrof Bay W Head	56.36373	-134.06805	1.9	1.3	0	3	6
Rodman Creek	57.43485	-135.39613	1.3	1.3	0	3	10
Saginaw Bay S Head	56.84968	-134.13589	2.3	1.3	0	2	7
Game Creek	58.09042	-135.47092	1.9	1	0	3	15
Harris River	55.459622	-132.68952	5.8	1	1	1	2
Lauras Creek	57.412721	-133.34676	4.2	1	1	1	2
Long Bay Head	57.855908	-135.65309	0.5	1	1	1	2
Rowan Creek	56.688163	-134.23378	4.2	1	1	1	1
Saltery Bay	57.770285	-135.45083	0.6	1	1	1	1
Saook Bay West Head	57.410254	-135.21727	1.7	1	1	1	2
Staney Creek	55.818389	-133.15125	4.5	1	1	1	2
Ushk	57.546422	-135.69007	2.2	1	1	1	2
Johnston Creek	57.50764	-134.1041	1.2	0.7	0	1	9
Ushk Bay W End	57.54824	-135.67862	1.6	0.7	0	1	9
Tenakee Inlet Head	57.99189	-135.89631	1.1	0.5	0	1	4
Weir Creek N Arm Hood Bay	57.392702	-134.34694	4.0	0.5	0	1	4
Kadashan River	57.70235	-135.22044	1.9	0.3	0	2	15
Big Goose Creek	57.914283	-135.75456	0.6	0	0	0	3
Kennel Creek	57.89887	-135.15048	1.3	0	0	0	2
Little Goose Creek	57.92147	-135.77398	1.3	0	0	0	7
Seagull Creek	58.016006	-135.56219	0.5	0	0	0	2

Table S1.5 Yearly individual stream observations of the total number of fish sampled (hatchery- and natural-origin), the number of hatchery fish, the total in-stream dead count, the effective number of hatchery strays, the number of surveys, and the observed attractiveness index, or average number of strays. The total effective number of strays (6th column) is calculated as the number of hatchery fish divided by the proportion of total dead sampled (Total fish sampled/Dead count), and the attractiveness index is calculated as the effective number of hatchery strays divided by the number of surveys.

Year	Stream name	Total fish sampled	Number of hatchery fish	Dead count	Effective number of hatchery strays	Number of surveys	Attractiveness index (average effective number of strays)
2008	Big Goose Creek	172	0	192	0.0	3	0.0
2008	Carroll Creek	190	0	247	0.0	1	0.0
2008	Disappearance Creek	156	0	127	0.0	6	0.0
2008	Ford Arm Creek	184	2	177	2.1	5	0.4
2008	Freshwater Creek	5	0	0	0.0	1	0.0
2008	Kennel Creek	2	0	0	0.0	1	0.0
2008	Long Bay Head	140	1	162	1.2	2	0.6
2008	Ralphs Creek	189	6	230	7.3	2	3.6
2008	Saltery Bay	26	1	21	1.0	1	1.0
2008	Seagull Creek	3	0	0	0.0	2	0.0
2008	Seal Bay Head	188	0	229	0.0	2	0.0
2008	Sister Lake SE Head	192	1	234	1.2	2	0.6
2008	Tenakee Inlet Head	146	1	183	1.3	2	0.6
2008	W Crawfish NE Arm Hd	192	8	234	9.8	2	4.9
2009	Admiralty Creek	117	48	131	56.5	2	28.3
2009	Camp Coogan	94	4	114	4.9	1	4.9
2009	Carroll Creek	202	6	248	7.4	2	3.7
2009	Chaik Bay Creek	11	3	0	3.0	2	1.5
2009	Chilkat River	115	0	128	0.0	2	0.0
2009	Disappearance Creek	235	3	232	3.1	6	0.5
2009	Fish Creek	192	168	234	204.8	2	102.4
2009	Fish Creek-Portland Canal	120	1	147	1.2	2	0.6
2009	Ford Arm Creek	269	8	294	8.0	5	1.6
2009	Game Creek	117	5	135	6.0	2	3.0
2009	Herman Creek	36	0	34	0.0	1	0.0
2009	Hidden Inlet	74	5	87	5.9	1	5.9
2009	Kadashan River	13	0	1	0.0	2	0.0

Table S1.5, continued.

2009	Kennel Creek	11	0	0	0.0	1	0.0
2009	Marten River	87	1	63	1.0	4	0.3
2009	Mole River	12	3	1	3.0	1	3.0
2009	Ralphs Creek	93	9	113	10.9	1	10.9
2009	Robinson Creek	82	14	98	16.7	1	16.7
2009	Sawmill Creek	149	116	190	147.9	1	147.9
2009	Seal Bay Head	182	5	221	6.1	2	3.0
2009	St. James Bay NW Side	94	15	114	18.2	1	18.2
2009	Swan Cove Creek	10	2	0	2.0	1	2.0
2009	W Crawfish NE Arm Hd	96	0	117	0.0	1	0.0
2010	Admiralty Creek	113	14	126	15.9	2	8.0
2010	Black River	92	0	112	0.0	1	0.0
2010	Cannery Cove-Pybus Bay	214	38	265	46.7	2	23.3
2010	Chaik Bay Creek	165	9	197	11.5	2	5.8
2010	Disappearance Creek	239	0	238	0.0	6	0.0
2010	Dry Bay Creek	146	19	186	24.2	1	24.2
2010	Fish Creek	94	66	114	80.0	1	80.0
2010	Ford Arm Creek	291	48	333	52.8	5	10.6
2010	Freshwater Creek	95	11	116	13.4	1	13.4
2010	Glen Creek	50	4	54	4.3	1	4.3
2010	Harding River	188	10	229	12.2	2	6.1
2010	Harris River	84	1	86	1.1	2	0.5
2010	Kadashan River	12	2	1	2.0	1	2.0
2010	Ketchikan Creek	188	124	229	151.1	2	75.5
2010	Marten River	64	1	57	1.0	2	0.5
2010	Mole River	44	7	45	7.2	1	7.2
2010	Prospect Creek	152	28	179	33.1	2	16.6
2010	Ralphs Creek	95	5	116	6.1	1	6.1
2010	Rowan Creek	26	1	21	1.0	1	1.0
2010	Saginaw Creek	57	10	48	10.0	2	5.0
2010	Sample Creek	224	14	278	17.5	2	8.8
2010	Saook Bay West Head	93	9	113	10.9	1	10.9
2010	Sawmill Creek	83	39	68	39.0	3	13.0
2010	Seal Bay Head	188	5	229	6.1	2	3.0
2010	Snug Cove-Gambier Bay	138	14	160	16.2	2	8.1

Table S1.5, continued.

2010	Staney Creek	60	2	52	2.0	2	1.0
2010	Swan Cove Creek	189	17	230	20.7	2	10.4
2010	Weir Creek N Arm Hood Bay	21	1	12	1.0	2	0.5
2010	Whale Bay Great Arm Head	95	2	116	2.4	1	2.4
2010	Wilson River	122	56	153	70.2	1	70.2
2011	Admiralty Creek	190	21	231	25.5	2	12.8
2011	Amber Creek	88	5	91	5.6	2	2.8
2011	Game Creek	63	0	56	0.0	2	0.0
2011	Kadashan River	1	0	0	0.0	1	0.0
2011	Lauras Creek	208	2	256	2.5	2	1.3
2011	Marten River	8	1	0	1.0	1	1.0
2011	Mole River	121	13	136	14.4	2	7.2
2011	North Arm Creek	149	13	175	15.1	2	7.6
2011	Saginaw Creek	17	0	8	0.0	1	0.0
2011	Sample Creek	188	1	229	1.2	2	0.6
2011	Sanborn Creek	191	3	248	3.9	1	3.9
2011	Saook Bay West Head	146	1	171	1.1	2	0.5
2011	Sawmill Creek	209	137	257	176.0	2	88.0
2011	Seal Bay Head	176	3	197	3.2	3	1.1
2011	Snug Cove-Gambier Bay	49	3	50	3.2	2	1.6
2011	Tenakee Inlet Head	139	0	161	0.0	2	0.0
2011	Weir Creek N Arm Hood Bay	62	2	55	2.0	2	1.0
2011	Wilson River	60	15	59	16.3	2	8.1
2013	Admiralty Creek	421	17	424	19.7	9	2.2
2013	Carroll Creek	228	10	90	10.0	2	5.0
2013	Chaik Bay Creek	600	2	740	2.8	3	0.9
2013	Chuck River	453	6	594	7.8	2	3.9
2013	East of Snug Cove	183	0	198	0.0	3	0.0
2013	Fish Creek	767	481	987	830.9	5	166.2
2013	Ford Arm Creek	409	6	245	6.8	2	3.4
2013	Freshwater Creek	172	3	172	3.0	2	1.5
2013	Game Creek	29	1	28	1.0	2	0.5
2013	Glen Creek	148	4	160	4.9	2	2.4
2013	Greens Creek	70	0	79	0.0	2	0.0
2013	Harding River	7	1	7	1.0	1	1.0
2013	Johnston Creek	131	4	170	4.8	4	1.2

Table S1.5, continued.

2013	Kadashan River	64	0	64	0.0	4	0.0
2013	King Creek	342	28	342	28.0	2	14.0
2013	King Salmon River	293	7	542	14.4	2	7.2
2013	Little Goose Creek	140	0	150	0.0	2	0.0
2013	Marten River	111	5	111	5.0	2	2.5
2013	Petrof Bay W Head	475	0	605	0.0	2	0.0
2013	Prospect Creek	485	113	565	137.5	6	22.9
2013	Ralphs Creek	456	3	532	3.6	2	1.8
2013	Rodman Creek	478	5	662	7.6	3	2.5
2013	Saginaw Bay S Head	104	1	137	1.0	2	0.5
2013	Sawmill Creek	441	192	831	371.0	4	92.8
2013	Seal Bay Head	480	2	800	3.1	2	1.6
2013	Sister Lake SE Head	600	8	2000	29.7	2	14.8
2013	Swan Cove Creek	205	5	215	5.6	2	2.8
2013	Ushk Bay W End	492	4	475	4.2	4	1.0
2013	W Crawfish NE Arm Hd	768	11	1084	20.1	2	10.0
2013	Whitewater Creek	238	9	270	10.8	3	3.6
2014	Admiralty Creek	260	12	52	12.0	17	0.7
2014	Carroll Creek	376	7	179	7.0	4	1.8
2014	Chaik Bay Creek	53	0	42	0.0	3	0.0
2014	Chuck River	89	3	11	3.0	3	1.0
2014	East of Snug Cove	13	0	15	0.0	2	0.0
2014	Fish Creek	2633	1742	2634	2452.3	21	116.8
2014	Ford Arm Creek	414	5	455	5.6	2	2.8
2014	Freshwater Creek	119	2	134	2.7	3	0.9
2014	Game Creek	120	0	308	0.0	5	0.0
2014	Glen Creek	3	0	0	0.0	2	0.0
2014	Greens Creek	1	0	0	0.0	2	0.0
2014	Harding River	194	9	93	9.0	2	4.5
2014	Johnston Creek	24	0	11	0.0	2	0.0
2014	Kadashan River	17	1	26	1.0	4	0.3
2014	King Creek	205	5	175	5.0	2	2.5
2014	King Salmon River	290	1	412	1.0	3	0.3
2014	Little Goose Creek	15	0	13	0.0	2	0.0
2014	Marten River	19	1	11	1.0	2	0.5
2014	Petrof Bay W Head	389	2	283	2.0	2	1.0
2014	Prospect Creek	473	34	65	34.0	16	2.1
2014	Ralphs Creek	300	1	343	1.0	4	0.3

Table S1.5, continued.

2014	Rodman Creek	116	1	75	1.0	3	0.3
2014	Saginaw Bay S Head	19	3	8	3.0	2	1.5
2014	Sawmill Creek	124	19	19	19.0	13	1.5
2014	Seal Bay Head	360	10	366	10.7	6	1.8
2014	Sister Lake SE Head	528	17	866	19.1	2	9.6
2014	Swan Cove Creek	96	0	74	0.0	2	0.0
2014	Ushk Bay W End	35	1	21	1.7	3	0.6
2014	W Crawfish NE Arm Hd	442	4	349	4.0	2	2.0
2014	Whitewater Creek	46	4	16	4.0	2	2.0
2015	Admiralty Creek	201	22	175	22.2	3	7.4
2015	Carroll Creek	480	11	678	13.8	2	6.9
2015	Chaik Bay Creek	403	9	401	9.4	4	2.4
2015	Chuck River	153	15	139	15.2	2	7.6
2015	East of Snug Cove	349	15	304	15.4	3	5.1
2015	Fish Creek	629	486	1071	968.1	3	322.7
2015	Ford Arm Creek	487	13	711	17.6	2	8.8
2015	Freshwater Creek	134	4	113	4.0	4	1.0
2015	Game Creek	500	5	735	8.0	4	2.0
2015	Glen Creek	5	2	4	2.0	2	1.0
2015	Greens Creek	262	10	248	12.0	3	4.0
2015	Harding River	92	11	94	11.6	2	5.8
2015	Johnston Creek	503	3	499	3.1	3	1.0
2015	Kadashan River	5	1	5	1.0	3	0.3
2015	King Creek	423	8	415	8.5	4	2.1
2015	King Salmon River	311	3	277	3.1	3	1.0
2015	Little Goose Creek	14	0	19	0.0	3	0.0
2015	Marten River	593	18	559	18.2	3	6.1
2015	Petrof Bay W Head	402	6	448	6.9	2	3.4
2015	Prospect Creek	111	56	88	56.3	3	18.8
2015	Ralphs Creek	442	1	599	1.4	3	0.5
2015	Rodman Creek	385	3	443	3.7	4	0.9
2015	Saginaw Bay S Head	35	5	29	5.1	3	1.7
2015	Sawmill Creek	564	290	597	311.6	29	10.7
2015	Seal Bay Head	328	1	341	1.0	4	0.3
2015	Sister Lake SE Head	513	12	1495	40.3	2	20.1
2015	Straight Creek	0	0	0	0.0	1	0.0
2015	Swan Cove Creek	334	3	323	3.3	4	0.8
2015	Ushk	220	1	214	1.0	2	0.5

Table S1.5, continued.

2015	Ushk Bay W End	32	0	29	0.0	2	0.0
2015	W Crawfish NE Arm Hd	576	5	548	5.4	2	2.7
2015	Whitewater Creek	393	34	387	34.0	3	11.3
2017	Admiralty Creek	872	31	690	34.7	18	1.9
2017	Fish Creek	1931	1067	1035	1182.0	17	69.5
2017	Prospect Creek	1433	550	1417	677.0	19	35.6
2017	Sawmill Creek	1979	562	3054	1165.5	16	72.8
2018	Admiralty Creek	60	6	48	7.0	18	0.4
2018	Fish Creek	1017	344	1322	584.5	19	30.8
2018	Prospect Creek	118	16	94	16.2	19	0.9
2018	Sawmill Creek	112	34	91	43.8	16	2.7
2019	Fish Creek	1634	308	2727	589.4	18	32.7
2019	Prospect Creek	1119	332	1974	539.0	32	16.8
2019	Sawmill Creek	266	137	611	362.8	18	20.2

Chapter 2: Understanding stream attractiveness at a landscape scale: implications for an applied management tool to minimize interactions of hatchery and wild salmon[2]

Abstract

Minimizing the interactions between hatchery and wild salmon is an on-going management challenge in many regions and is impeded by a lack of predictive tools for informing decision-making. In this paper we explore how incorporating information about stream attractiveness to hatchery strays may aid in estimating the distribution and magnitude of straying by hatchery-origin chum salmon (*Oncorhynchus keta*) across a large region of Alaska, USA. Specifically, we quantified the number of streams predicted to be attractive to hatchery-origin strays using a model that incorporates stream proximity to hatchery release sites and abiotic (stream discharge) characteristics. We predicted that most streams across the landscape would be unattractive. Approximately 64 out of 640 streams (~10%) were predicted to be attractive, i.e., predicted to receive an average of 57 (range: 9–600) strays. The remaining sites were moderately attractive or unattractive, i.e., predicted to receive five hatchery strays or less. Most of the attractive streams were located near hatchery release sites releasing 24 (range: 0–107) million hatchery salmon annually, reflecting a strong influence of proximity to a source population on the number of strays received by a stream. However, several sites were predicted to be attractive outside of proximity to hatchery releases due to high or low intra-annual variability of streamflow, indicating the importance of ecological factors beyond distance to a hatchery release site in driving the distribution of strays across the landscape. We further revealed that the predictive model is best suited to predicting stream attractiveness beyond the

[2] Payne, M. K., C. C. Cunningham, M. V. McPhee, and P. A. H. Westley. (In prep). Understanding stream attractiveness at a landscape scale: implications for an applied management tool to minimize interactions of hatchery and wild salmon. Ecosphere.

spatial extent of the observed data but may have more limited use beyond the temporal range due to uncertainty in estimating model random effects. Altogether, our results provide an example of how understanding stream attractiveness to stray hatchery salmon may be used to fill inevitable data disparities in hatchery stray distribution across a landscape and provide some guidance towards hatchery and fishery management goals.

Introduction

In natural Pacific (*Oncorhynchus spp)* and Atlantic salmon (*Salmo salar*) metapopulations, dispersal, or straying, is defined as the return of individuals to non-natal sites for reproduction (Quinn 1993). Straying exists in dynamic equilibrium with its counterpart reproductive strategy, homing, both of which are essential features of salmon evolutionary biology (Quinn 1993, Hendry et al. 2004, Berdahl et al. 2015). Straying functions to allow gene flow among spawning populations (Quinn 1993, Hendry et al. 2004, Matthysen 2012), colonization of new habitat (Milner and Bailey 1989, Anderson and Quinn 2007, Pess et al. 2012), and avoidance of degraded habitat in the natal site (Whitman et al. 1982). In the context of aquaculture, however, straying can have negative fishery and conservation implications, particularly in systems where hatchery- and natural-origin individuals are intended to avoid interaction on the spawning grounds. Such interactions are often unavoidable and can negatively affect natural-origin populations via intensified competition for stream resources (Grant 2012, Anderson et al. 2020) and fitness declines resulting from interbreeding and hybridization (Christie et al. 2014). Furthermore, stray hatchery salmon that successfully reach spawning grounds represent lost fishery yield and can complicate the accurate assessment of wild spawner escapement in the absence of external tagging procedures, making it impossible to identify spawner origin using visual survey methods (Johnson et al. 2012).

Consequently, there is urgent need for tools and information that will predict and potentially help minimize interactions between hatchery- and natural-origin salmon, especially given that many non-supplementation hatcheries along the west coast of North America intend and assume segregation of hatchery- and natural-origin stocks on the spawning grounds for the purposes of wild salmon conservation (Wilson 2021). Existing tools like the “All-H Analyzer” developed by the Hatchery Scientific Review Group incorporate information about large-scale natural-origin salmon productivity, fish passage, hatchery release numbers, and fishery harvest to estimate regional-scale returns and stray rates of hatchery produced salmon (StreamNet n.d.). But to our knowledge, there is not yet a tool that incorporates site-specific information to estimate the level or distribution of straying by hatchery-origin salmon. Given evidence that characteristics of spawning sites such as freshwater discharge influence the magnitude and distribution of straying by hatchery salmon and farmed salmon escapees (Unwin and Quinn 1993, Hard and Heard 1999, Mahlum et al. 2020), the inclusion of site-specific information for predicting straying patterns represents a fruitful avenue for exploration and use in hatchery management. For instance, Atlantic salmon (*Salmo salar*) that escaped from a farming operation in Norway strayed disproportionately to rivers that were close to the farm, had large populations of natural Atlantic salmon, and had greater freshwater discharge, suggesting possible influences of spatial location and river characteristics on habitat selection by the spawning adult Atlantic salmon (Mahlum et al. 2020). The river characteristics in question - proximity to the salmon farm, salmon population abundance, and discharge - might be useful in predicting which rivers have the highest risk of receiving farmed Atlantic salmon spawners and could subsequently inform the potential for farm-wild interactions.

Our goal is to explore the feasibility and utility of using site characteristics as a tool to predict site-specific patterns of straying by hatchery-origin salmon, given that some characteristics are associated with higher numbers of recipient hatchery-origin strays. We undertake this study in Southeast Alaska as a case study, a region where over 400 million hatchery-origin chum salmon are released annually (Wilson 2021). Hatchery salmon are released as part of a fishery enhancement program in which hatchery- and natural-origin individuals rear in a common ocean but are intended to avoid interaction on spawning grounds as much as possible to prevent impacts to wild salmon populations (Josephson et al. 2021, Wilson 2021). Straying by hatchery-origin chum salmon *Oncorhynchus keta* is pervasive in Southeast Alaska (Piston and Heinl 2012, Josephson et al. 2021). We found that in this region there is a relationship between higher numbers of recipient chum salmon hatchery strays in streams and increased releases of hatchery salmon near the stream, as well as (in)variable stream discharge (Chapter 1). This information is not currently incorporated into hatchery management in Southeast Alaska, and juvenile hatchery salmon continue to be released in remote locations to create "terminal fisheries" in which managers generally assume that hatchery fish will be captured in the fishery (Wilson 2021). Here, we predicted the number of hatchery-origin chum salmon straying into streams throughout Southeast Alaska using stream characteristics known to attract hatchery strays, as a first step towards development of an applied management tool. Estimating numbers of hatchery-origin strays on the spatial scale of the stream throughout the region could better inform hatchery and fishery management goals such as improved estimates of wild spawner escapement and could benefit hatchery release site planning, whereby hatchery managers could assess the extent of straying by returning adults around existing or proposed hatchery release sites. As such, our specific objectives were to 1) describe the current and future landscape of stream attractiveness to stray hatchery-origin chum salmon in Southeast Alaska by quantifying the magnitude and distribution of straying based on stream characteristics, and 2) explore the potential utility of our predictive framework for use as a management tool to predict stream attractiveness given changes to hatchery release sites.

Materials and Methods

Study system

Southeast Alaska comprises 135,000 km^2 of temperate terrestrial and aquatic habitat that has been sustainably stewarded for millennia by the Eyak, Łingít, Haida, and Tsimshian peoples. Small, mountainous watersheds with short streams characterize the region and provide excellent habitat for anadromous fish species, particularly pink salmon (*O. gorbuscha*, cháas' in Łingít language), chum salmon (téel'), and coho salmon (*O. kisutch*, l'ook, Giefer and Blossom 2020). There are currently 7,118 documented streams that support spawning populations of natural-origin (i.e., "wild") chum salmon (Giefer and Blossom 2020). Beyond production in nature, 12 chum salmon enhancement hatcheries with 28 release sites currently operate in Southeast Alaska with the goal of augmenting harvest in common-property commercial fisheries (Wilson 2021).

Predictive model development

A model to predict stream attractiveness to stray hatchery-origin chum salmon was developed as a function of stream characteristics for 57 streams in Southeast Alaska 2008–2019.

Detailed methods for data collection and model development are included in Chapter 1, thus we only briefly describe them here.

We defined the model response variable as the *attractiveness index*. The attractiveness index (A_{iy}) was calculated for each stream and year as the effective number of hatchery-origin strays detected across multiple sampling events, divided by the number of carcass surveys conducted in stream i in year y, in order to account for variable effort among sites. The effective number of hatchery strays accounts for bias in the number of strays detected among streams with variable numbers of dead chum salmon and is calculated as the total number of hatchery strays divided by the proportion of carcasses sampled. Thus, our model response variable may be interpreted as the average abundance of hatchery-origin chum salmon in a stream across sampling events. Data used to calculate the attractiveness index were derived directly from Piston and Heinl (2012) and Josephson et al. (2021), the latter of which summarized results from the Alaska Hatchery Research Project, a multi-year project that assesses the extent and impact of straying by hatchery-origin chum salmon in Southeast Alaska (Alaska Department of Fish and Game n.d.). Hatchery-origin spawners were identified by thermally marked otoliths retrieved by survey crews. Stream surveyors collected chum salmon carcasses along the entire length of the stream up until the spatial point where chum salmon were no longer observed to be spawning. Thus, the identity of individuals as hatchery-origin is assumed to be known without error and the effective number of hatchery-origin strays identified in a survey is assumed to be a representative sample of the total number of hatchery-origin strays that spawned in the stream in that year. The data indicating the number of hatchery-origin spawners in the 57 streams in Southeast Alaska were available 2008–2019, excluding 2012 and 2016. All surveys took place at the peak, or near the peak of chum salmon spawning for each stream in each year.

We tested a suite of stream characteristics as model covariates to predict the attractiveness index of each stream. These included 1) subregion-level fishery harvest, 2) the weighted moving average of the number of hatchery chum salmon juveniles released within 40 km of the stream 3, 4, and 5 years prior to the survey year based on the age distribution of hatchery strays in the stream, 3) natural-origin chum salmon and 4) pink salmon abundance in the stream, 5) mean long-term stream discharge, and 6) the coefficient of variation of long-term stream discharge, along with a random effect of year. We fit the data with a generalized linear mixed effects model using a negative binomial distribution and log link. The final model was selected as the most parsimonious model that was within 2 AIC_c of the model with the lowest AIC_c. The final model accounted for 36% of the total AIC_c weight and predicted the attractiveness index of a stream as:

(1)

$$\log(A_{iy}) = 0.481 + 0.364X_1 + 0.463X_2 + 0.800X_3^2 + a_y$$

where X_1 is the number of hatchery fish released within 40 km of the stream, X_2 and X_3 are the coefficient of variation (CV) of streamflow, and $a_y \sim Normal(0, \sigma^2)$ is the random effect of year (Table S2.1).

We cross-validated the model in chapter 1 by randomly removing 30% of the original stream-year observations, refitting the model, and using the remaining 70% of observations to predict the omitted values. We repeated this removal and refitting process over 500 iterations and calculated the mean absolute error (MAE) for each retained observation. The MAE error was 10.98 strays for a given prediction, thus the model was modestly accurate in predicting the actual number of strays (Table S2.1). However, we found that the final model robustly predicted the rank, or relative attractiveness of streams to hatchery-origin strays (Fig. 2.1). Thus, we felt confident scaling up the model to predict out-of-sample stream attractiveness and we discuss stream attractiveness primarily in the context of other streams' predicted indices (relative number of strays).

To successfully implement the model across streams in Southeast Alaska, we adjusted our methodology for weighting the number of fish released within 40 km of a stream due to the age distribution of hatchery-origin strays in unsampled streams being unknown. Instead of weighting by the age distribution in the stream and year, the weighting for a given stream was based on the overall age distribution of hatchery strays in the 2008–2019 dataset.

Predicting out-of-sample stream attractiveness

Across Southeast Alaska, we predicted the annual attractiveness indices of 640 streams with documented chum salmon usage in the Anadromous Waters Catalog (Giefer and Blossom 2020) that also had matching metadata across covariate datasets. Covariate data for the 640 streams came from the same sources as those used to fit the models (Table S2.2). Data were missing in 2012 and 2016, so our predictions were for 2008–2011, 2013–2015, and 2017–2019.

To estimate uncertainty around each prediction, we bootstrapped prediction intervals around each model prediction. The prediction intervals were estimated by generating a random normal distribution around each model coefficient estimate, based on the model-estimated mean and standard error, and randomly sampling a single value, with replacement, from each distribution to use as a basis for prediction. This was repeated 1000 times to generate 1000 predictions for each of the initial 640 predictions. We then took each simulated attractiveness value and generated a negative binomially distributed deviate. Simulations were conditional on the estimates for annual random effects. We calculated a coefficient of variation around each individual prediction by taking the mean (μ) and standard deviation (σ) of each set of 1000 predictions. Since each stream had 10 years of predictions (2008–2019 excluding 2012 and 2016), we primarily discuss the mean prediction and mean CV of the 10 predictions for each stream in our results and discussion section.

In addition to predicting attractiveness indices for 2008–2019 streams, we also predicted stream attractiveness for all sites in 2020 and 2021 using updated data on the number of fish released within 40 km of each stream reported in the most recent Alaska salmon fisheries enhancement report (Wilson 2021). The CV of flow values for 2020–2021 predictions came from the same source (Sergeant et al. 2020; Table S2.2) as our original model because those data are static over time, i.e., the CV was calculated as a single value from the entire distribution of modeled daily stream discharge values from 1979 to 2012 and thus cannot be updated for future years.

Finally, we also predicted future stream attractiveness for three arbitrary, hypothetical new release site scenarios. The first scenario was the creation of a new release site in Freshwater Bay (57.93313, -135.18000), a location where a hatchery release site has never existed. The second and third hypothetical scenarios included increasing the number of hatchery chum salmon released at two existing release sites; Crawfish Inlet (56.77120, -135.13760); and Port Asumcion (55.37382, -133.5536). For each of these hypothetical scenarios, we increased the number of fish released by 20.8 million, which was the standard deviation around the mean number of fish released within 40 km of all sites in Southeast Alaska from 2020 to 2021. We held the CV of streamflow values constant at their previous values for these predictions, as these data are static over time. Finally, because random effects do not exist for hypothetical future years or for the 2020 and 2021 predictions, we sampled random deviates from the estimated normal distribution describing common among-year variation in attractiveness and incorporated these into our bootstrapped coefficient of variation estimates of uncertainty (described above) for the 2020–2021 and hypothetical release site predictions. This distribution was based on the mean and standard deviation (σ^2) of the normal random effects distribution $a_y \sim Normal(0, \sigma^2)$ estimated to describe the 2008–2019 random year-specific intercepts. Thus, our 2020–2021 model predictions are unconditional on the 2008–2019 random year effects.

Results

Stream attractiveness across Southeast Alaska

Across Southeast Alaska, we predicted the relative attractiveness of 640 streams to stray hatchery-origin chum salmon using historical (2008–2019) data (Fig. 2.2). The top 10%, or most attractive, streams had a predicted attractiveness index of 57 hatchery-origin strays (range: 9–600) on average, while the remaining 90% were predicted to have < 5 strays on average (Table 2.1). Coefficients of variation were 0.21–0.62 for these predictions (Fig. 2.2). It should be noted that these simulations are conditional on our estimated year effects, and thus reflect expected attractiveness in those specific years rather than any year with similar environmental and hatchery release conditions.

The majority of attractive streams were located in the northern part of Southeast Alaska (Fig. 2.2). These streams were near a group of hatcheries and release sites concentrated in that part of the region. On average, attractive streams such as those in the northern region were located within 40 km of releases of > 24 million hatchery-origin juvenile chum salmon (range: 0–107 million; Table 2.1). Streams predicted to be moderately attractive and unattractive were located near release sites releasing < 15 million hatchery juveniles or were not near release sites at all.

The attractive streams had the highest intra-annual streamflow variability (Table 2.1), but several attractive sites also had low CV of streamflow, as evidenced by the lower end of the range of values of streamflow CV associated with the attractive sites (Table 2.1). CV of streamflow could make a stream attractive independent of proximity to hatchery release sites. For example, Dry Bay Creek was predicted to be attractive with 13 predicted hatchery-origin strays (Fig. 2.2). Further, relative to all other historical (2008–2019) predictions (n = 640), Dry Bay Creek was predicted to be 39th most attractive stream in all Southeast Alaska. This high degree of relative attractiveness was confirmed by a single 2010 survey in Dry Bay Creek which detected an observed attractiveness index of 24 hatchery-origin strays, relative to the average attractiveness index of 10 strays in the entire dataset used to fit the model. Dry Bay Creek was not within 75 km of any hatchery release sites 2008–2019 but had a high CV of streamflow of 0.61.

Future predictions of stream attractiveness

The number of hatchery-origin chum salmon released within 40 km of streams decreased slightly in 2020 and 2021 relative to 2008–2019, but generally the distribution of (un)attractive streams and the degree of stream attractiveness remained similar across the two time periods (Table 2.2). For all 2020–2021 predictions, coefficients of variation were 0.70–1.50. It should be noted that these forward simulations were unconditional on random year effects, and thus uncertainty estimates reflect both uncertainty in covariate effects and that of random year effects. Under the future hypothetical release site scenarios in Freshwater Bay, Crawfish Inlet, and Port

Asumcion, we predicted negligible increases in stream attractiveness for streams within 40 km of the release sites and coefficients of variation ranging 0.70–1.15 (Fig. 2.3).

Discussion

Here we describe the occurrence and distribution of streams predicted to be (un)attractive to stray hatchery-origin chum salmon in Southeast Alaska. We further demonstrate the extent to which modeling stream attractiveness may address data gaps in the distribution of hatchery-origin strays across a landscape. We show that most streams across the landscape were predicted to be unattractive, but there was a subset of highly attractive sites predicted to have large numbers of hatchery-origin strays. Our model outputs can be useful for gaining insight into straying beyond the spatial extent of the observed data but may have less utility in forecasting stream attractiveness beyond the temporal range of the data. Taken together, our findings provide an example of how a basic understanding of factors influencing stream attractiveness to hatchery-origin strays can be applied in a hatchery and fishery management context.

Understanding the current stream attractiveness landscape

We predicted that across Southeast Alaska from 2008 to 2019, most streams would be unattractive to stray hatchery-origin chum salmon. 90% of sites were predicted to have fewer than five hatchery-origin strays on average, with an estimated error of approximately ±11 strays based on model cross validation (Table S2.1). Although we emphasize that the models are best suited to predict relative stream attractiveness, their predictions of the number of hatchery strays are not wholly uninformative. Indeed, among the original 57 streams used to fit the model, there was a small subset of sites with large observed numbers of hatchery strays for which the model also predicted significantly above average indices of attractiveness (Fig. 2.1). Therefore, we assume that model predicted indices that are significantly above average correspond to actual indices of attractiveness that are above average as well. Thus, we show that fewer than 10% of all sites across the landscape are predicted to attract large numbers of hatchery-origin strays (Table 2.1). Using the proportion of hatchery-origin spawners (pHOS) as a measure of comparison, Knudsen and colleagues (2021) similarly found that most of the streams they sampled in Prince William Sound, Alaska were also unattractive to stray hatchery-origin chum salmon; two sites consistently had a pHOS of 0.60–0.90 over three years, while the other 15 sites had a mean pHOS of < 0.05 (range: 0.00–0.33).

Nonetheless, the attractiveness of the subset of attractive sites should not be discounted due to their potential to obstruct hatchery, fishery management, and conservation objectives. For example, Fish Creek was the stream with the highest predicted attractiveness index (115 strays) of the original 57 streams and it also had the highest observed attractiveness index across time (115 strays). An attractiveness index of 115 strays translates to a potentially enormous number of hatchery-origin spawners in a stream over the course of a spawning season. To provide some context, in 2015 in Fish Creek, 486 hatchery-origin chum salmon in total were detected out of 608 sampled fish. Four hundred and eighty-six hatchery-origin spawners represent a significant contribution to Fish Creek's total proportion of spawners, which 1) is not accounted for in sub-district-level escapement estimates by the state management agency, and 2) complicates conservation objectives around protecting the natural-origin chum salmon population from interactions with hatchery-origin conspecifics. Several other streams are predicted to be equally or more attractive than Fish Creek (Fig. 2.2), so the effects of such levels of straying by hatchery-origin chum salmon are not unique to Fish Creek and likely not inconsequential either.

Like Knudsen and colleagues' (2021) study of hatchery chum salmon straying in Prince William Sound, we found that Fish Creek and other attractive streams were overwhelmingly proximate to release sites for juvenile hatchery chum salmon. In other systems, donor (Jonsson et al. 2003) and recipient stray rates (Hard and Heard 1999, Josephson et al. 2021) were higher when streams were closer to hatchery release sites, indicating that creating targeted locations for the return of adult hatchery fish increases the apparent attractiveness of nearby spawning streams. We further reveal that the larger the potential source of hatchery strays, the higher the predicted attractiveness index of nearby sites. Attractive streams in our study were predicted to be within 40 km of releases 2–5 years earlier of at least 24 million hatchery fish on average, while moderately attractive and unattractive streams were near release sites releasing < 15 million fish or were not near release sites at all. Thus, the attractiveness of a stream is predicted to scale directly with the number of adult hatchery fish returning to the area.

As the results of chapter 1 revealed, proximity to hatchery release sites is an important factor in dictating the attractiveness of a site, but ecological factors (intra-annual streamflow variability) may also influence predicted stream attractiveness. For instance, there were many streams across the region that were only moderately attractive or unattractive despite being near large hatchery release sites (Fig. 2.2). Admiralty Creek, a site close to the large release sites in northern Southeast Alaska (and to Fish Creek), was only moderately attractive with a predicted index of four hatchery-origin strays and an observed index of 7.6, which is attributable to an unattractive intermediate CV of streamflow (0.56). Similarly, there are streams distant from hatchery release sites that are predicted to be attractive. For example, Dry Bay Creek was an attractive site with 13 predicted strays and an observed index from a single survey of 24 hatchery-origin strays (Fig. 2.2). Dry Bay Creek was located > 75 km away from any hatchery release site but had an extremely flashy stream hydrograph (0.61), confirming the importance of streamflow observed in other studies (Unwin and Quinn 1993, Anderson and Quinn 2007, Mahlum et al. 2020) in influencing the distribution of hatchery-origin strays. Finally, we found that for 2008–2019 predictions, coefficients of variation were 0.21–0.62 (Fig. 2.2), indicating modest uncertainty in predicting stream attractiveness to streams outside of the spatial range of the observed data.

Exploring future stream attractiveness

The models predicted little overall change in the attractiveness landscape across Southeast Alaska in 2020–2021 compared to the previous period (Table 2.2) and elevated coefficients of variation (range: 0.70–1.50). This is indicative of greater uncertainty in model predictions when predicting outside of the temporal range of the observed data. Since the CV of streamflow is static over time for all sites, the lack of noticeable change in attractiveness is directly attributable to minimal change in the number of fish released within 40 km of sites.

Beyond 2021, we find that results for predicted stream attractiveness of sites near increased hypothetical hatchery releases are less conclusive. Increases in predicted stream attractiveness are negligible despite proximity to increased hatchery releases. Furthermore, the coefficients of variation around all future predictions are high, both in 2020–2021 and for the hypothetical release site scenarios (Fig. 2.3), indicating greatly increased uncertainty in the predictions largely attributable to the unknown random intercept. We conclude that for the models to be used as a tool to predict stream attractiveness beyond the 2008–2021 timeframe, and to improve and verify the predictive accuracy of the 2020–2021 predictions, additional straying data to determine observed attractiveness indices need be collected throughout the region. It is not clear at this time if the random intercepts for 2008–2019 years accurately account for uncontrolled factors in 2020–2021 and beyond. Observed data would allow for verification of model predicted indices at relevant sites and could also be used to update the predictive models to include a random intercept for the relevant year if model predictions using 2008–2019 random intercepts consistently mis-predict observed indices. Attempting to predict stream attractiveness in a future year, which by default means that the random intercept is unknown, is not likely to be very accurate or informative. Given the likelihood that ongoing climate change may facilitate altered straying patterns (Dunmall et al. 2022) and possibly even increased straying by salmon (Horreo et al. 2011), it is essential that we continue to collect straying data into the future to evaluate how the influence of attractive stream characteristics may change.

Several caveats and limitations warrant mention in our study. First, we assumed that the coefficient of variation of streamflow was unchanging in the development of our model and in making predictions of stream attractiveness. This likely does not reflect the hydrographic reality of these streams, especially given increasing frequency of heatwaves which may affect streamflow conditions now and into the future (von Biela et al. 2022). We urge that future research endeavors incorporate temporally finer scale flow data into model development to better predict stream attractiveness to hatchery-origin strays, as streamflow conditions clearly influence the choice of spawning stream by hatchery strays (Unwin and Quinn 1993, Hard and Heard 1999, Mahlum et al. 2020), or at least serve as a potential proxy for other important stream characteristics (Chapter 1). Second, we have merely estimated uncertainty around our model predictions of stream attractiveness based on our covariate and random effect estimates from

2008–2019 data. Model predictions would ideally be verified with observed data, especially for the sites that were only sampled once or twice and identified as unattractive.

Finally, we recognize that there are a multitude of other factors which likely influence stream attractiveness to hatchery-origin strays beyond the handful we have analyzed in our study. Future research may also address such factors with the availability of a larger straying dataset for Southeast Alaska to allow for model convergence with added covariates. Our work simply seeks to take a first step in demonstrating that 1) ecological characteristics of streams beyond distance to hatchery release sites influence attractiveness to hatchery-origin strays, and 2) this understanding has some applicability in predicting stream attractiveness to other streams in the region within the same time period.

Thus, despite the limitations discussed, our results indicate how understanding stream attractiveness to hatchery-origin strays may be used for landscape scale hatchery and fishery management. With current stream characteristic data and updated straying data for a subset of sites in hand, our two predictive models can provide insight into the magnitude of straying and the distribution of hatchery-origin strays beyond sites with on-the-ground data. Such information would aid in accurately estimating natural-origin chum salmon escapement, quantifying the lost fishery yield from hatchery strays, and understanding the extent of potential interactions between hatchery and wild chum salmon, particularly in expansive regions like Southeast Alaska where it is logistically unfeasible to sample all streams.

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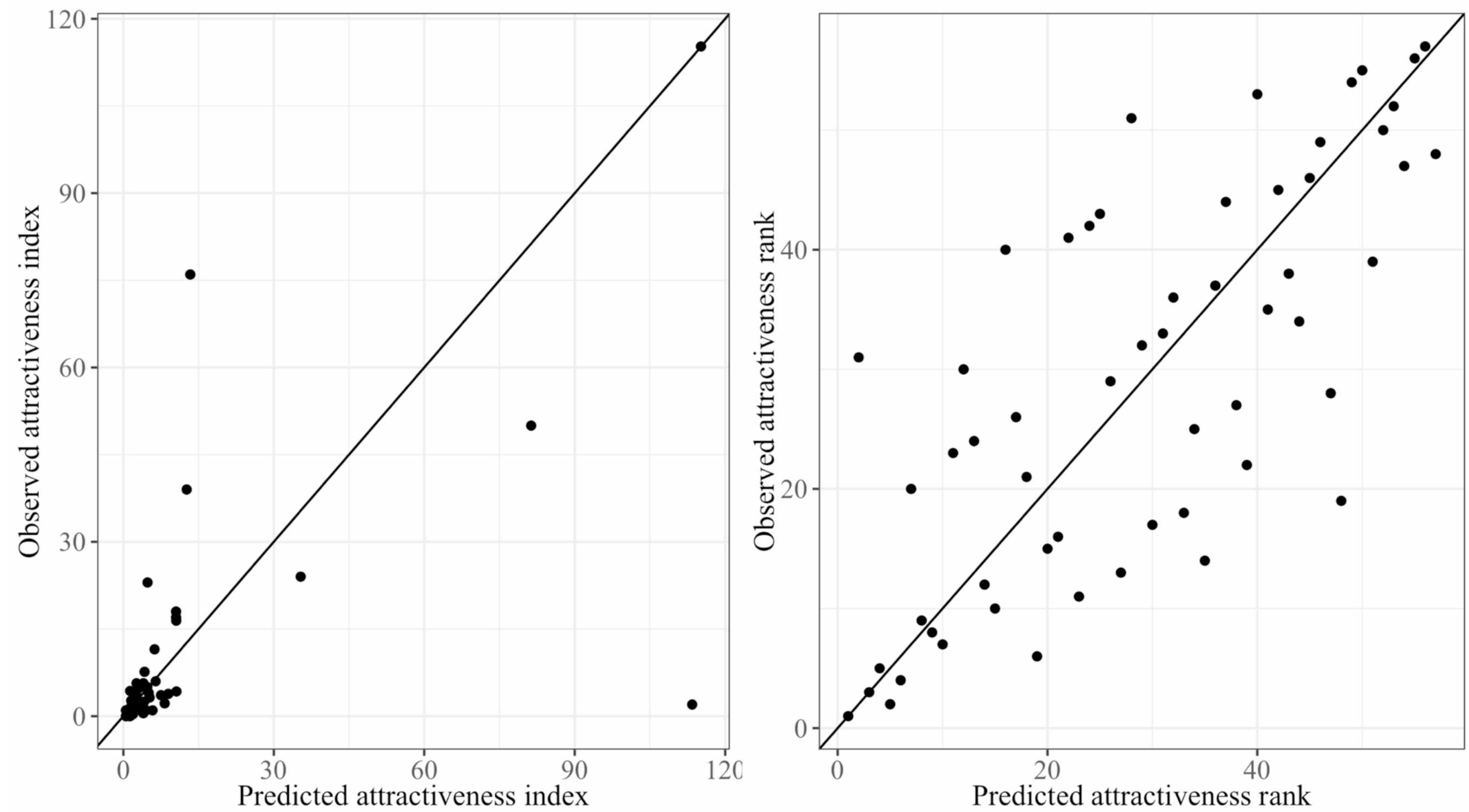

Figure 2.1 Left panel: the observed attractiveness indices for the 57 streams in Southeast Alaska used to fit the model plotted as a function of the model-predicted attractiveness indices. Right panel: the observed relative attractiveness indices, or ranks, of the 57 streams plotted as a function of the model predicted relative attractiveness indices. The solid black line in both plots is a 1:1 line.

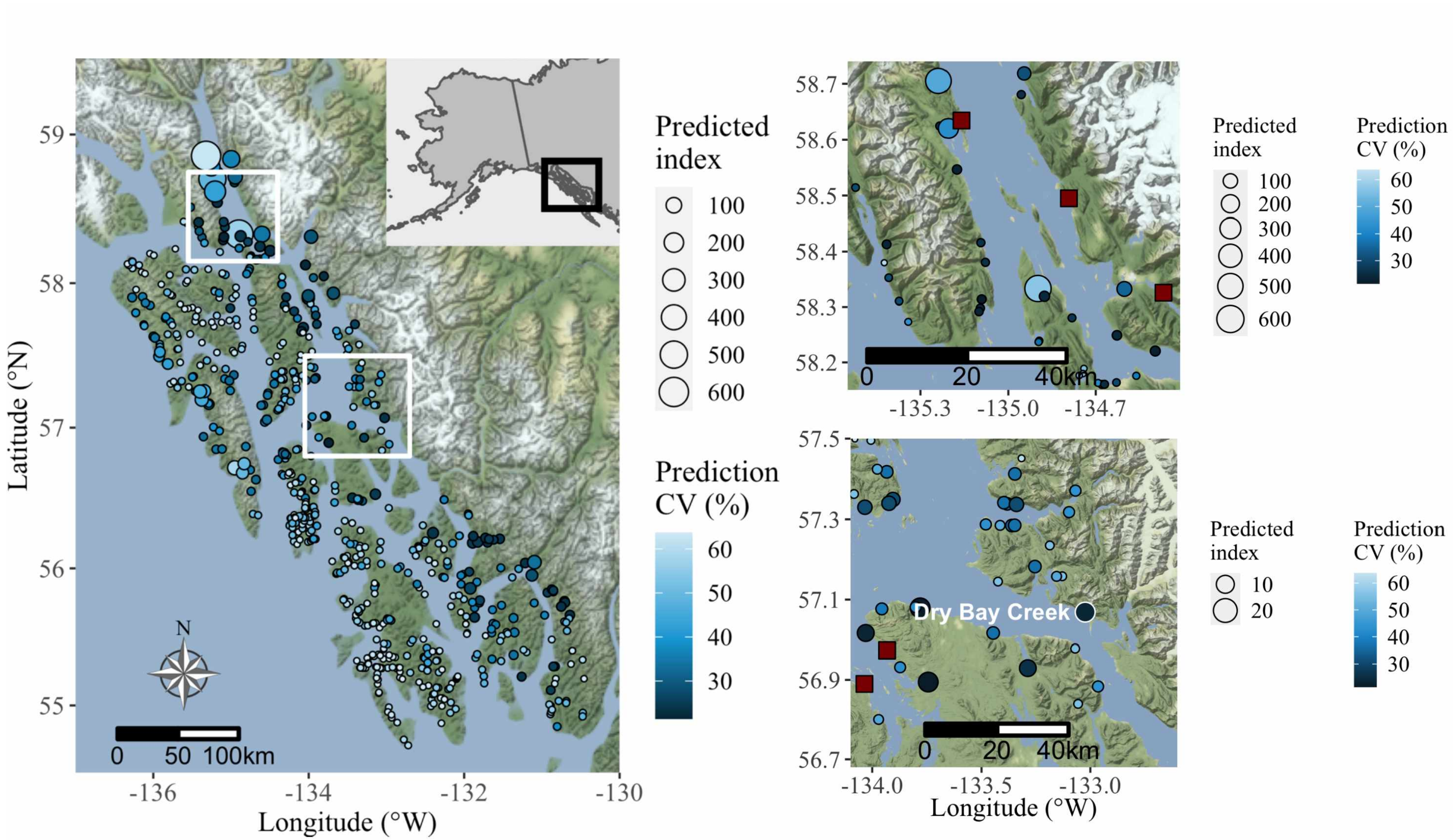

Figure 2.2 Predictions (n = 640) of stream attractiveness across Southeast Alaska using 2008–2019 data for all streams. The locations of the two panels on the right are shown in the white inset boxes on the panel on the left in order of north to south. Note that the bottom right panel has a different predicted index scale to show contrast between streams with smaller predicted attractiveness indices. Red squares indicate hatchery release site locations. This map was created using the R package ‘ggmap’ (Kahle and Wickham 2013).

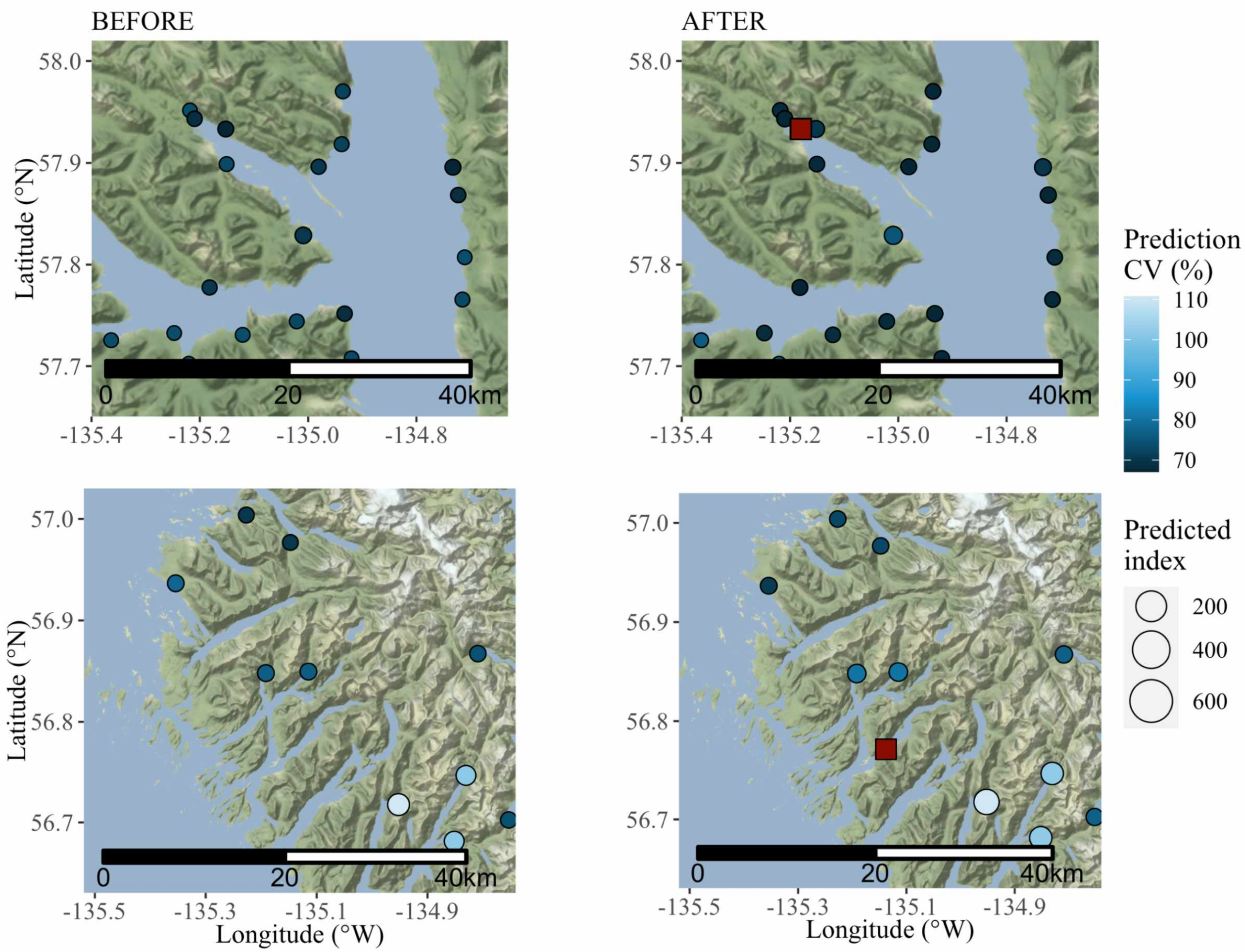

Figure 2.3 Top row: Predicted attractiveness indices for streams in Freshwater Bay, Alaska before (left) and after (right) the addition of a hypothetical new release site releasing 20.8 million hatchery-origin juvenile chum salmon per year. Bottom row: Predicted indices for streams in Crawfish Inlet, Alaska before and after the hypothetical increase of 20.8 million hatchery-origin juvenile chum salmon released at the Crawfish Inlet release site. The red square in both right-hand plots shows the location of each respective release site. The left-hand "before" plots for both areas depict the 2020–2021 stream attractiveness predictions. This map was created using the R package 'ggmap' (Kahle and Wickham 2013)

Table 2.1 Summary of 2008–2019 predicted attractiveness indices in Southeast Alaska and the stream characteristics associated with them. The mean of each metric for each attractiveness percentile category is presented, followed by the range in parentheses.

Stream Percentile	n	Predicted attractiveness index	Number of fish released within 40 km in millions	Coefficient of variation (CV) of streamflow
Top 10%	64	57.2 (9.4–600.0)	24.3 (0–107.5)	0.57 (0.39–0.68)
Middle 40%	256	4.1 (2.1–9.4)	14.7 (0–107.5)	0.54 (0.43–0.60)
Bottom 50%	320	1.8 (1.5–2.1)	0.6 (0–21.1)	0.52 (0.48–0.55)

Table 2.2 Summary of 2020–2021 predicted attractiveness indices in Southeast Alaska and the stream characteristics associated with them. The mean of each metric for each attractiveness percentile category is presented, followed by the range in parentheses.

Stream Percentile	n	Predicted attractiveness index	Number of fish released within 40 km in millions	Coefficient of variation (CV) of streamflow
Top 10%	64	64.0 (11.0–700)	24.8 (0–105.6)	0.56 (0.39–0.68)
Middle 40%	256	5.2 (3.4–10.8)	17.8 (0–105.6)	0.53 (0.44–0.60)
Bottom 50%	320	2.8 (2.2.5–3.4)	1.4 (0–30.1)	0.52 (0.48–0.56)

Supplemental Material

Table S2.1 Coefficient estimates for the top two candidate models (in ranked order) to predict the number of stray hatchery-origin chum salmon in a stream in Southeast Alaska. The approximate 95% confidence interval for each estimate is included in the parentheses. AICc criteria used for model selection, model weights, cross validation results (MAE; mean absolute error), and pseudo-R2 values are shown in the bottom half of the table for both models as well as the null model.

	Model 1	Model 2	Null model (Year random effect only)
40km_release	0.345 (0.163, 0.527)	0.364 (0.182, 0.546)	NA
Cons_Abundance	-0.178 (-0.413, 0.057)	NA	NA
CV_flow	0.416 (0.234, 0.598)	0.463 (0.291, 0.635)	NA
CV_flow^2	0.769 (0.612, 0.926)	0.800 (0.641, 0.959)	NA
df	7	6	3
$\log(L_i)$	-468.42	-469.50	-548.54
ΔAIC_c	0.00	0.00	151.71
$w_i(AIC_c)$	0.36	0.36	< 0.01
MAE (all values)	10.51	10.98	14.89
MAE (x < 40)	6.18	6.31	8.27
Marginal R^2	0.38	0.37	0.00
Conditional R^2	0.52	0.52	0.04
Intercept (SD)	0.48 (0.73)	0.48 (0.75)	0.41 (0.64)

Table S2.2 Definitions and data sources of the covariates used to predict stream attractiveness indices.

Covariate	Description	Varied by year	Data source(s)
Number of fish released within 40 km of the stream	Weighted moving average of number of hatchery chum salmon released within 40 km of stream 2–4 years prior to stream sampling	Yes	Chum salmon age distribution: Alaska Hatchery Research Project (AHRP) data, i.e., Josephson et al. 2021 **Hatchery release site data**
Coefficient of variation (CV) of flow	Long-term average coefficient of variation of discharge from all freshwater channels in the surrounding watershed of stream	No	Sergeant et al. 2020

Conclusions

In this thesis, I sought to understand how stream characteristics mediate stream attractiveness to stray hatchery-origin salmon. Using data on the number of hatchery-origin chum salmon spawning in streams throughout Southeast Alaska over a 10-year period, I identified attractive stream characteristics and quantified the extent to which those characteristics increased the number of hatchery strays received by a stream. With this information in hand, I predicted the distribution and magnitude of straying by hatchery-origin chum salmon throughout Southeast Alaska, inclusive of sites where the number of hatchery strays was unknown. The most salient findings of this research were as follows:

- The characteristics that shaped stream attractiveness to hatchery-origin strays included proximity to large releases of hatchery juveniles and the intra-annual variability in stream discharge. These results confirm that distance to a hatchery release site influences patterns of straying, but that additional ecological factors also play a role.
- Attractiveness of individual streams to hatchery-origin salmon relative to other streams was accurately predicted using a model that incorporated the influential stream characteristics. The absolute stream attractiveness, or the average number of strays in a stream and year, was predicted with modest accuracy.
- The model was able to effectively predict stream attractiveness for streams without observed straying data beyond the spatial extent of the observed data, but predictions were less reliable beyond the temporal range of the observed data due to the lack of known model random effects in future years.
- In general, most streams (~90%) are predicted to be relatively unattractive to stray hatchery-origin chum salmon. However, the potential for extensive hatchery-wild

interactions in the subset of attractive sites and their consequences for the wild population are not to be ignored. Even within the less attractive sites, a couple of hatchery-origin spawners sharing a stream with an equal or lesser number of wild salmon can still substantially negatively impact the genetic integrity and/or reproductive success of that wild population.

- Altogether, my results indicate that the distribution of hatchery strays across a landscape is not random, but rather is at least partially driven by spatial and ecological factors. This information can be used to estimate the impact of hatchery-origin strays spawning in streams on the wild chum salmon population and the extent to which hatchery release site practices may either improve or exacerbate these effects.

In Southeast Alaska, most hatchery-produced chum salmon are released at remote release sites in the open estuary to increase survival of the juvenile salmon and to create terminal fisheries at those locations (Wilson 2021). Because of remote nature of the release sites, returning adult hatchery salmon that escape fishery capture are functionally set up to stray into a stream instead of returning to a hatchery that may be tens of kilometers away and therefore undetectable from the release site. As such, my results may not be applicable in other regions where hatchery salmon are released in river tributaries to which they are expected to return in order to supplement wild salmon populations (Quinn and Fresh 1984). Nevertheless, despite the specificity of the estimated relationships between stream attractiveness and stream characteristics to Southeast Alaska in this study, the methodology for consideration of attractive stream characteristics and predictive model development could be readily applied elsewhere.

The results of my research confirm the importance of proximity to hatchery release sites in increasing the number of hatchery strays in recipient streams; this effect has been identified in numerous studies on straying by other species of salmon in other locations (Pascual and Quinn 1994, Hard and Heard 1999, Jonsson et al. 2003). My results also underscore the importance of ecological characteristics of streams in influencing the number of hatchery strays beyond spatial distance to hatchery release sites. The importance of ecological characteristics, such as stream discharge and vegetative cover, in driving patterns of dispersal has been tested in a wild sockeye salmon population in western Alaska (Peterson et al. 2016) and mentioned but not explored in isolated studies on hatchery salmon straying (Unwin and Quinn 1993, Hard and Heard 1999). My research represents one of the first attempts to identify causal links between ecological characteristics, in this case streamflow variability, of recipient streams and patterns of straying by hatchery-origin salmon. These results can be useful in estimating the extent of hatchery straying in expansive regions like Southeast Alaska where it is logistically impossible to survey and document straying in all streams.

Given the potential for profound genetic (Christie et al. 2014) and competitive (Grant 2012, Anderson et al. 2020) consequences of hatchery straying for wild salmon populations, organizations interested in conserving wild salmon need to understand what drives straying by hatchery salmon in order to identify successful mitigation strategies. I recommend that the model developed in my study be used by hatchery and fishery managers alike for the purposes of chum salmon hatchery planning and fishery management in Southeast Alaska. First, prospective hatchery release sites could be placed in locations distant from streams with ecological characteristics known to be attractive to hatchery-origin strays to potentially reduce the number of strays received by proximate streams, or to avoid streams with especially vulnerable wild populations. From a fishery management standpoint, landscape-scale predictions of stream attractiveness could be used to update wild salmon spawner escapement estimates, which at present do not incorporate hatchery contribution within streams.

I strongly recommend that future research expand upon the work I have done in several important ways. Undoubtably there are additional ecological factors that influence stream attractiveness to hatchery-origin strays beyond the small set of covariates that I explored. For instance, there is evidence in the Columbia River that temporary and permanent straying of hatchery-produced Chinook salmon increases with elevated temperatures in the mainstem river (Goniea et al. 2006, Bond et al. 2017). It would be beneficial to know what additional factors are attractive to strays and at what point during the migration the decision to stray is made to better understand the extent to which hatchery salmon might be deciding to stray into streams they encounter. This modeling framework did not include spatial information beyond the incorporation of hatchery releases within 40 km of a stream. A logical first step would be to include a covariate of watershed size and to consider the location of streams along the main migratory pathways used by adult chum salmon as they return to the estuary. Moreover, a similar predictive modeling framework for stream attractiveness should be developed in other regions to verify whether predictions of stream attractiveness to hatchery strays might be applicable beyond chum salmon in Southeast Alaska. Finally, for the conclusions and the model developed here to truly be usable as a management tool, I urge interested parties to continue to collect data on the number of hatchery-origin strays spawning in a subset of streams throughout the region to validate model predictions. Such data could also be used to re-parameterize the model further into the future. Current coefficient estimates were based on straying patterns documented 2008–2019 and it is unclear if those same straying patterns would continue to be observed far into the future, especially in an era of rapid climate change.

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