

Tidal gradients, fine-scale homing and a potential cryptic ecotype of wild spawning pink salmon (*Oncorhynchus gorbuscha*)

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Funding information

Alaska Fisheries Science Center, Grant/Award Number: NA16NMF4270251; Cooperative Institute for Climate, Ocean, and Ecosystem Studies (CICOES), Grant/Award Number: 2023#x2010;1265; NOAA Cooperative Agreement, Grant/Award Number: NA20OAR4320271; North Pacific Research Board, Grant/Award Number: 1619

Handling Editor: Maren Wellenreuther

Abstract

The homing behaviour of salmon is a remarkable natural phenomenon, critical for shaping the ecology and evolution of populations yet the spatial scale at which it occurs is poorly understood. This study investigated the spatial scale and mechanisms driving homing as depicted by spawning site-choice behaviour in pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Molecular pedigree analyses of over 30,000 adult spawners in four streams revealed that pink salmon exhibit fine-scale site fidelity within a stream, returning to within <100m of their parents. Homing behaviours were driven in part by a salinity gradient between intertidal and freshwater environments, with individuals incubated in freshwater environments more than twice as likely to spawn upstream of tidal influence than those incubated in the intertidal. Our findings challenge the traditional view that pink salmon populations are genetically and phenotypically homogenous due to their short freshwater residency as juveniles and high rates of dispersal as returning adults (i.e. straying). This study has important implications for rates of inbreeding, local adaptation and gene flow within populations, and is particularly relevant to the management of salmon hatcheries, given the high incidence of hatchery-origin pink salmon, reared in freshwater hatchery environments, that stray into wild populations of Prince William Sound.

KEYWORDS

ecotype, natal homing, pedigree, population structure, reproductive behaviour, Salmon

1 | INTRODUCTION

The natal homing of Pacific salmon (genus *Oncorhynchus*) with high fidelity to the rivers, streams and lakes of their birth is one of the great wonders of the natural world (Hasler & Scholz, 2012; Quinn, 2018). Across migratory taxa, homing behaviours facilitate the formation and maintenance of structured metapopulations, reduce gene flow among habitat patches, and contribute to local adaptation to site-specific regimes of natural selection (Hanski, 1999;

Xu, 2018). Ultimately, homing behaviour underpins the emergent property of increased intraspecific diversity that buffers metapopulations against perturbations in any one subunit (i.e. portfolio effects; Schindler et al., 2010, 2015). Despite the importance of homing in ecological and evolutionary processes, the spatial scale at which homing occurs is poorly understood in nature.

Salmonid fishes have long served as model species in ecological and evolutionary studies. It is increasingly recognized that salmon function as spatially structured metapopulations, where locally

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adapted populations exist in a dynamic balance of extinction and (re)colonization, mediated by behaviours of philopatry and dispersal (Hendry et al., 2004). Understanding the spatial structure of salmon metapopulations requires knowledge as to what scales Pacific salmon home (Neville et al., 2006). For example, sockeye salmon (*O. nerka*) are not only predicted to have among the highest rates of homing to natal streams of the Pacific salmonids, but have also been shown to exhibit remarkable fine-scale spatial and temporal fidelity, where individuals are known to return within <50m of their natal incubation sites (Lin et al., 2008; May, 2022; Quinn et al., 2006) and within <5 days from the day they were fertilized as eggs several years prior (Barnett et al., 2019; May, 2022). Such behaviours may increase the chances of mating between fish who share ancestry (i.e. inbreeding) or traits (i.e. assortative mating), and subsequently may contribute to within-population genetic structure (May et al., 2023). Furthermore, this fine-scale structure can have fitness consequences and result in local adaptation within populations if gene flow is sufficiently limited and selection sufficiently variable within continuous habitats (i.e. microgeographic adaptation; Torres Dowdall et al., 2012; Richardson et al., 2014). Recent simulation efforts have demonstrated how such fine-scale population dynamics can positively influence recruitment and resilience to perturbations compared to unstructured or randomly mating populations (Godineau et al., 2022; May et al., 2023; Yeakel et al., 2018).

In contrast to sockeye salmon, pink salmon (*O. gorbuscha*) are thought to have the lowest rate and least precision of homing, inferred from largely homogenous population genetic structure and high rates of straying between habitat patches (Bett et al., 2017; Salmenkova, 2017). Although Pacific salmon are known to be able to home to fully marine waters (Hauser et al., 2017), low homing rates are often attributed to reduced juvenile imprinting on freshwater natal sites. Unlike congeners that rely heavily on freshwater for juvenile rearing, pink salmon use freshwater only for spawning and embryonic development and spend the rest of their life history in coastal, estuarine habitats and at sea (Keefer & Caudill, 2014; Quinn, 2018). Instead of spatial-genetic structure, pink salmon populations are known for particularly strong temporal-genetic structure resulting from a fixed 2-year life cycle, such that there is near zero gene flow between odd- and even-year lineages, even those spawning in the same spatial habitats (Christensen et al., 2021; Tarpey et al., 2017). Pink salmon, and in some regions chum salmon, are the only species of Pacific salmon that frequently spawn in intertidal (i.e. intermittently saline) environments at the marine outlets of freshwater creeks (Groot, 1989; Quinn, 2018). In fact, empirical evidence demonstrates that as much as 75% of wild pink salmon spawning within coastal streams may occur in intertidal areas (Roys, 1971). Though little about this unique life history has been published in peer-reviewed literature, empirical work suggests that pink salmon can imprint natal site characteristics as early as the embryonic stage, suggesting that even limited lifecycle dependence on freshwater may be sufficient to home on fine scales (Bett et al., 2016). Freshwater and intertidal spawners can also be segregated in both time and space (Helle, 1970), which

could lead to the creation of genetically distinct population segments (Gharrett et al., 2013; Seeb et al., 1999).

Although separated by very short spatial distances on the order of 10s to 100s of meters, the spawning habitat and subsequent environment of embryonic development varies markedly between freshwater and intertidal areas, particularly with regards to salinity and temperature regimes (Beacham & Murray, 1993; Sergeant et al., 2017). There may exist important bioenergetic trade-offs associated with spawning and incubating in these different environments. For example, freshwater migration is an energetically costly life-history feature of most anadromous salmonids (Fleming & Gross, 1989; Jonsson et al., 1997), whereas energy may instead be allocated to increase fecundity or reproductive lifespan of individuals spawning in the intertidal (Heard, 1991; Helle et al., 1964). Additionally, moderate exposure to salt water during incubation could reduce fungal infection and increase egg survival (Taylor & Bailey, 1979). However, the more variable intertidal environment could reduce survival of incubating eggs or fry and may have selected for specific adaptations to this environment. Alternatively, upstream sections may be at higher risk of dewatering during winter months, so intertidal environments are less variable in this respect. Because of these potential differences, pink salmon donor stocks for the Armin F. Koernig Hatchery, which supplied Walley Noerenberg and Main Bay Hatcheries in Prince William Sound, Alaska, were chosen in the 1970s because 75% of the spawning occurred above high tide (Habicht et al., 2000). More broadly, the potential for fine-scale population structure represented by freshwater and intertidal spawning pink salmon may represent an understudied ecotype on par with ecotypes of sockeye salmon spawning in deep lakes and shallow rivers or streams that have resulted from divergent selection on body size (Larson et al., 2017, 2019). These phenotypic differences in sockeye salmon limit gene flow between adjacent habitats (Peterson et al., 2014), and we hypothesize that similar ecotypic patterns of divergence may exist in pink salmon populations due to differences in salinity regimes between incubation environments. Such a finding may suggest underlying adaptive genetic architecture that could contribute to increased population diversity and stability in the face of climate change, hatchery supplementation and harvest.

This study aimed to investigate the fine-scale population structure of wild pink salmon populations in Prince William Sound, Alaska (PWS) using molecular-based pedigrees of four intensively sampled populations as part of a larger project to understand the interactions between wild and hatchery salmon (Knudsen et al., 2021; Shedd et al., 2022). Specifically, we tested the hypotheses that pink salmon offspring return to specific spawning locations used by their parents and that the emergent population structure is driven by a salinity gradient at the estuarine intersection of marine and freshwaters. We discuss results in the context of implications for gene flow, local adaptation and hatchery-wild interactions within populations. This work is particularly relevant given the high incidence of hatchery-origin pink salmon, incubated in artificial freshwater hatcheries from wild donor stocks that

spawned and reared in freshwater, that stray into wild populations in PWS (i.e. >5–15% of wild spawners are hatchery origin; Brenner et al., 2012; Knudsen et al., 2021) and on-going conservation concerns about effects of these hatchery-origin strays on the phenotypic and genetic diversity of wild populations (Naish et al., 2008; Rand et al., 2012; Shedd et al., 2022).

2 | MATERIALS AND METHODS

2.1 | Study sites and data collection

Samples were collected as a part of the Alaska Hatchery Research Program (AHRP), a long-term, industry-agency led sampling program of selected salmon spawning streams in PWS. Returning adult pink salmon were sampled during the spawning season from four representative streams (Figure 1) from early August through late September from 2013 through 2020, although this study specifically used samples from 2014 and 2016: Erb Creek (60.3768305 N, -148.153307 W), Gilmour Creek (60.27245823 N, -147.1846866 W), Hogan Bay Creek (hereafter Hogan Creek; 60.20866485 N, -147.7616643 W) and Stockdale Creek (60.3034497 N, -147.1831793 W). Streams varied in length from approximately 300–1500 m (Figure 1), with a large portion of available spawning habitat influenced by tidal saltwater intrusion. The upper extent of tidal influence (i.e. areas affected by saltwater)

were measured in river meters: 198, 273, 429 and 368 m in Erb, Gilmour, Hogan and Stockdale Creeks, respectively.

Methodology for sampling, genotyping and pedigree reconstruction was described in detail in a previous publication (Shedd et al., 2022). Briefly, tissue samples (i.e. heart tissue) for genetic analysis and otoliths for identification of hatchery-origin fish (hatchery fish otoliths are thermally marked) were concurrently collected from carcasses during daily stream surveys. Although, sampling was limited on some days due to high bear activity or weather events. The proportion of sampled days was 0.61, 0.42, 0.41 and 0.48 in 2014 and 0.83, 0.40, 0.75 and 0.73 in 2016, in Erb, Gilmour, Hogan and Stockdale, respectively. A GPS location was associated with each sampled fish, marking the location the carcass was processed in the stream, typically within <100 m of true sampling locations. To quantify a sampling location for each fish, the distance between each GPS point (recorded in the middle of the sampled reach) and the mouth of the stream was measured in river meters using the R package *riverdist* (v0.15.5). For each fish, sex (male or female) was determined visually (pink salmon exhibit extreme sexual dimorphism when spawning and are readily distinguishable externally), body length was measured from mid-eye to hypural plate (in mm) and sample date was recorded. Sample day (measured as day of year; DOY) was used to approximate spawn timing, as pink salmon are known to spawn within just a few days of entering spawning habitats (McMahon, 2021).

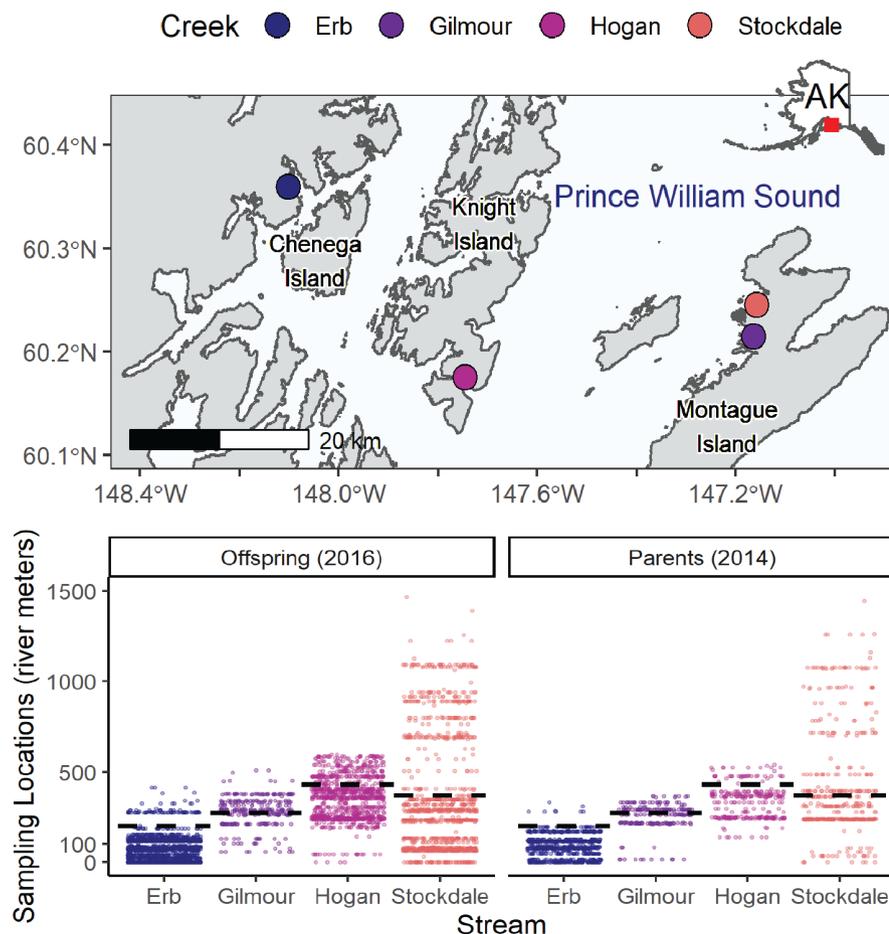


FIGURE 1 (Top) Map of sampled pink salmon spawning streams (colours) in Prince William Sound, AK. (Bottom) In-stream sampling locations (y-axis) of adult salmon carcasses returning to spawn in 2016 (left) and 2014 (right). Dashed lines represent the upper extent of tidal influence in each stream. [Colour figure can be viewed at wileyonlinelibrary.com]

DNA was extracted from tissue samples and genotyped following the methods of Campbell et al. (2015) using a panel of 298 single nucleotide polymorphism amplicons (SNPs) comprising 210 singleton SNPs and 88 microhaplotypes, specifically designed for pedigree reconstruction in PWS (Dann et al., *in prep*; Shedd et al., 2022). A description of genotyping, data filtering steps and power of this panel to assign parentage can be found in Shedd et al. (2022). Briefly, individuals were removed from subsequent analyses if they had $\geq 20\%$ missing genotypes or an excess of heterozygous genotypes indicating cross-contaminated samples. One individual per pair of duplicated samples was removed, defined as identical at $\geq 95\%$ of loci. To assign offspring sampled in 2014 to parents sampled in 2016 (pink salmon are all 2 years old at maturity and die after spawning), pedigree reconstruction was performed in FRANZ (Riester et al., 2009) on data from all streams in a single analysis. A detailed description of pedigree reconstruction methods including simulation results is provided in Shedd et al. (2022). Dispersers were removed from further analyses, identified as parent-offspring pairs sampled in different streams.

We were interested in the spatial resolution of sampling, as fish carcasses were carried from 'true' sampling locations to bulk processing areas. Field teams were instructed to limit the length of a given processing area stream reach to no more than 200m and to process samples approximately in the middle of each stream reach, such that fish were transported both upstream and downstream to processing areas (2015 PWSSC contractor report, Appendix C). We quantified a 'sampling interval' for each stream on each day, defined as half the mean distance between a sampling location '*i*' and sampling location *i*+1. The 'mean sampling interval' and standard deviation among days for each stream and year was estimated and reported. We assumed that this mean sampling interval was the mean maximum distance that fish were transported between 'true' sampling sites and processing areas (hereafter, 'sampling locations'); therefore, this distance provided the approximate resolution for which homing behaviours could be detected in later analyses.

2.2 | Inference of natal incubation locations from sampling location of parents

Sampling locations for each fish were used to approximate individual spawning locations, and the spawning location of parents (sampled in 2014) were used to approximate the natal redd location for each offspring (sampled in 2016), as natal incubation locations (i.e. redd locations) for each fish were not recorded in the field. To test whether sampling locations of carcasses were a reasonable approximation for true spawning locations, we examined whether the inferred spawning locations of parents were correlated. We assumed that if sample locations of mating parent-pairs were correlated, then we could conclude that in-stream carcass locations were not random and would provide information about their spawning locations. Carcasses were expected to drift downstream post-senescence in most cases, so we expected some error in this quantification (Strobel et al., 2009). However, meandering and shallow stream banks,

woody debris, bears translocating carcasses to the stream bank or riparian areas, and receding flood waters also frequently stranded carcasses and prevented downstream drift.

To test whether the sampling locations of dams and sires were correlated, we built a simple generalized linear model (GLM) with a Gaussian error distribution, where sire sample location (the response variable, in river meters) was a function of a fixed effect for dam sample location. Additional fixed effects were included for stream and an interaction term between stream and sample location to allow the estimation of stream-specific slopes and intercepts for these relationships. Only offspring assigned both a dam and a sire were included in this analysis.

Inference for all models in this study was performed using a model selection procedure, where a best-fit model was selected from a suite of nested sub-models, constructed by iteratively omitting different fixed effects. Comparisons between sub-models were made using a second-order Akaike Information Criterion (AICc) by quantifying the difference between each model's AICc score and that of the model with the lowest AICc score (ΔAICc). A given sub-model was considered as significantly better fit than another if the difference in AICc values between models was ≥ 2 . Best-fit models were selected from among sub-models if their ΔAICc was less than 2. The effects of fixed effects on response variables were interpreted in the most parsimonious best-fit model.

2.3 | Detection of fine-scale homing behaviours within populations

The second objective of this study was to examine whether individuals returned to their specific natal incubation locations within streams, after accounting for other variables that might affect choice of spawning location. To accomplish this objective, we built a global GLM with a Gaussian error distribution, where inferred spawning location of adults returning in 2016 (i.e. offspring) was the response variable and a function of inferred natal incubation location (i.e. inferred spawning location of parents returning in 2014), body length, sex, stream and DOY (day of year), which were fixed effects. An interaction term between inferred natal incubation location and stream was also included to allow for stream-specific intercepts and slopes for this variable of interest. Only one parent per offspring was included in this analysis; most offspring were only assigned one parent, but in the case of individuals with two parents assigned, the parent with the more upstream sampling location was included to account for expected downstream drift of carcasses post-senescence. Offspring body length (mid-eye to hypural plate in mm), sex (male or female) and DOY sampled were included following evidence in previous studies that these variables may affect salmon spawning location within streams (i.e. Hendry et al., 2001; Rich Jr et al., 2006; Neville et al., 2006). Again, for all models in this study, a best-fit model was selected from a suite of simpler sub-models following an AICc model selection procedure.

While regression analysis was an appropriate statistical approach to determine correlations between parent and offspring locations,

this analysis did not provide an interpretable estimate of the actual scale of homing. To examine the scale of homing, boxplots were used to visualize the median and quartile ranges of the difference between parent and offspring inferred spawning locations. Means and standard deviations were also reported for each stream.

The final objective of this study was to examine whether fine-scale homing behaviours may be driven by tidally influenced habitat gradients within streams. To examine the extent to which this ecological gradient might affect homing behaviours, we constructed a global GLM similar to that used to examine choice of spawning location from the mouth of the stream, but with a binomial error distribution. Spawning and natal environments were binary variables (i.e. either 'intertidal' or 'upstream'), depending on whether these locations fell below (intertidal) or above (upstream) the mean high tide line. Length, sex, stream and sample date of offspring were again included to account for additional behavioural variation in choice of spawning location. Inferred natal location was also included as a fixed effect, as in objective two, to account for homing behaviours explained by distance from the mouth of the stream. Additionally, interaction terms were included between stream and natal environment and between stream and parent location to account for differences between streams and to allow for estimation of stream-specific intercepts and slopes. If both natal environment (intertidal or upstream) and parent location (distance from stream mouth) were included in the best fit model, we concluded that natal habitats (differentiated by salinity) explained significant variation in choice of spawning location, beyond that explained by distance alone.

3 | RESULTS

3.1 | Data collection

From all four sampled streams, 4107 putative parents and 29,747 putative offspring were genotyped from tissue samples collected in 2014 and 2016, respectively. Of these, individuals were removed from the 2014 and 2016 datasets, respectively: 436 and 3460 fish

were removed for missing $\geq 20\%$ of genotypes, 24 and 166 fish were removed as duplicated samples and 157 and 1076 were removed due to excess heterozygosity. Of the remaining 3490 putative parents and 25,045 offspring, 1859 parents were assigned at least one offspring and 5982 offspring were assigned at least one parent. After removing parent-offspring pairs sampled in different streams, 1838 parents and 5804 offspring remained. Of these offspring, 4684 were assigned one parent and 1120 were assigned two parents. After removing individuals with missing data for variables used in this study (i.e. offspring or parent locations, offspring sex, body length or DOY sampled), 5459 offspring remained. Of the remaining offspring, 4414 were assigned one parent and 1045 were assigned both parents. Our final dataset thus comprised 1045 offspring-dam-sire trios used in our first GLM and 5459 parent-offspring pairs used in objectives two and three (Table 1). Among streams, the mean proportion of individuals spawning in intertidal environments was 0.71 (± 0.19), and specific estimates for each stream, sex and year are provided in Table 1.

A sampling interval was estimated as the maximum distance an individual fish would have been carried from 'true' sampling locations in the stream to the location where it was processed and a GPS location taken, averaged among days within streams. In 2014, sampling intervals were 58.50 m (± 21.61 m), 24.63 m (± 6.93 m), 46.57 m (± 18.58 m) and 73.94 m (± 20.61 m) in Erb, Gilmour, Hogan and Stockdale Creeks, respectively. These values in 2016 were 53.78 m (± 26.67 m), 39.94 m (± 14.91 m), 39.42 m (± 19.82 m) and 114.17 m (± 81.29 m). Averaged among all days and streams, the overall sampling interval was 61.11 m (± 48.98 m). From these results, we concluded that site choice behaviours could be examined on the spatial scale of approximately 100 m or less.

3.2 | Inference of natal incubation locations from sampling location of parents

We examined the relationship between the sampling locations of dam-sire pairs known to have produced offspring and found that

TABLE 1 Sample sizes of pedigreed pink salmon used in this study and the proportion spawning in the intertidal by sample stream and sex.

Stream	AWC	Offspring sex	Proportion intertidal	One parent	Both parents	Total offspring	Total parents
Erb	226-20-16040	Female	0.91	1036	298	1334	1632
		Male	0.98	840	276	1116	1392
Gilmour	227-20-17480	Female	0.51	324	119	443	562
		Male	0.47	325	132	457	589
Hogan	226-30-16810	Female	0.68	497	21	518	539
		Male	0.81	459	26	485	511
Stockdale	227-20-17520	Female	0.70	483	96	579	675
		Male	0.75	450	77	527	604

Note: Anadromous Waters Catalogue (AWC) stream identification numbers are also provided. Sample sizes are given for offspring sampled as returning adults in 2016 and assigned to either one or both parents sampled in 2014. Offspring assigned to no parents were excluded from this study.

sire sampling location was best explained by dam sampling location, stream and an interaction term between these two variables ($AICc=8297.00$, $wAICc=0.81$, $R^2_{Adj}=0.49$, Table S1). For all GLMs in this study, model selection results for the full suite of submodels are provided in Table S1, and all model coefficients for best-fit models are provided in Table S2. Model results indicated a positive correlation between dam and sire sampling areas ($\beta_{\text{dam location}}=0.27$), although the intercept and slope of this relationship varied among streams (Figure 2, Middle Panel; Table S2). The mean difference between dam and sire sampling locations was -1.09 m ($\pm 73.3\text{ m}$) in Erb Creek, 32.6 m ($\pm 88.6\text{ m}$) in Gilmour Creek, 36.8 m ($\pm 88.0\text{ m}$) in Hogan Creek and 55.2 m ($\pm 229.0\text{ m}$) in Stockdale Creek (Figure 2, Top Panel). These results indicated that offspring with dams that spawned further upstream were likely to also have sires who spawned further upstream. From these results we concluded that sampling locations within streams were reasonable proxies for spawning locations. In addition, we assumed the spawning locations of parents were representative of the natal incubation locations of their offspring, given that pink salmon embryos develop for months submerged in gravel prior to emergence the following spring.

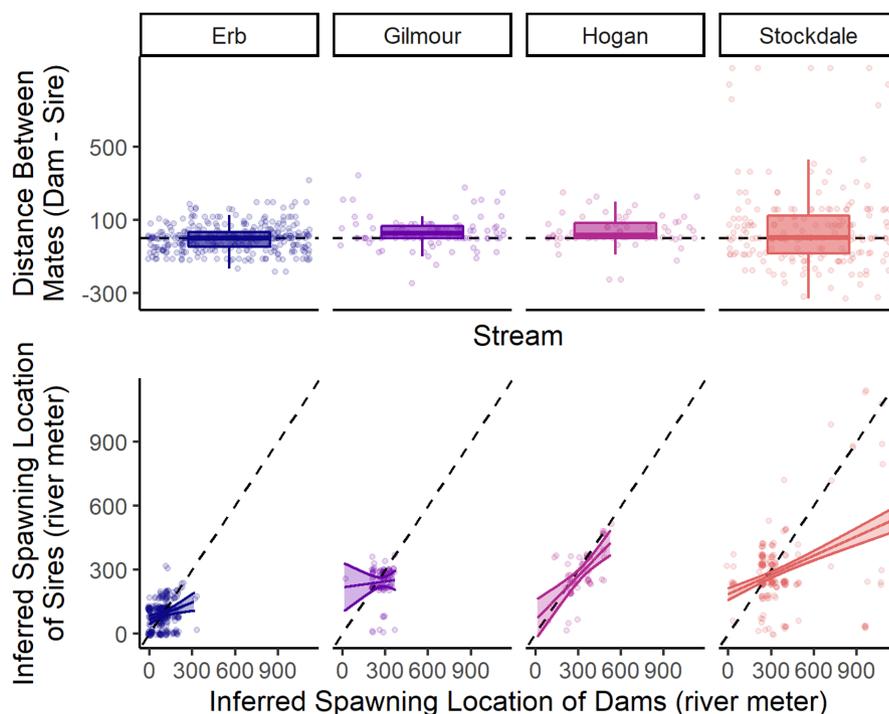
3.3 | Detection of fine-scale homing behaviours within populations

We quantified the phenotypic and behavioural factors associated with choice of spawning location within streams. We found that spawning location of offspring was best explained by inferred spawning location of parents, sex, DOY sampled, body length, stream and an interaction between spawning location of parents and stream ($\beta_{\text{parent location}}=0.22$, $AICc=71315.53$, $wAICc=0.40$, $R^2_{Adj}=0.38$,

Table S1). These results indicated that individuals tended to spawn nearby their parent's spawning location and their own natal incubation locations; although, the intercept and slope of these relationships varied among streams (Figure 3, Middle Panel; Table S2). The mean difference between parent and offspring sampling locations was 4.00 m (± 86.84) in Erb Creek, -12.27 m (± 116.44) in Gilmour Creek, -22.40 m (± 133.71) in Hogan Creek and 5.20 m (± 366.76) in Stockdale Creek (Figure 3, Top Panel). The magnitude and variance of fine-scale homing appeared to be correlated with stream length, possibly due to greater carcass displacement because of greater discharge in larger streams. However, we did not examine this relationship further because our sample size comprised only four streams.

Regressions also highlighted other factors influencing site selection behaviour. For example, females were sampled upstream more often than males ($\beta_{\text{sex males}}=-22.40$). This finding suggested that dam sampling locations may have been more representative of offspring natal locations than sires, as male salmon are thought to move more on spawning grounds in search of multiple mates and in avoidance of predators, whereas females tend to remain near redds (Quinn, 2018). Upon further investigation, we found that the mean difference between dam and offspring locations was smaller than the mean difference between sire and offspring locations ($\mu_{\text{dam-offspring}}=0.2 \pm 203.32$; $\mu_{\text{sire-offspring}}=-23 \pm 215.95$). Although this difference was small and variable, the trend was consistent across all four streams (Table S3). Regression results also indicated that early returning individuals also tended to spawn closer to stream mouths, while later returning individuals tended to spawn further upstream ($\beta_{\text{DOY}}=2.70$). In addition, body length had a negative effect on spawning distance from the mouth of the creek, indicating that smaller bodied fish tended to spawn further upstream than larger bodied fish ($\beta_{\text{Length}}=-0.15$).

FIGURE 2 (Top) Boxplots of distances between the inferred spawning locations of dams and sires (y-axis) for all detected pairs of mating adults returning in 2014 (points) to four pink salmon spawning streams (colours). Dashed lines at zero indicate that dams and sires were sampled at the same in-stream location. Spawning locations were inferred from the location of sampling areas where groups of carcasses were sampled, in river meters from the mouth of the stream (see 2. Materials and Methods). (Bottom) Regression of inferred spawning location of sires (y-axis) as a function of inferred spawning location of dams (x-axis). Empirical estimates (points) are coloured by sample stream; solid lines give significant fitted values for each stream, bounded by 95% confidence intervals. Dashed lines represent $y=x$. [Colour figure can be viewed at wileyonlinelibrary.com]



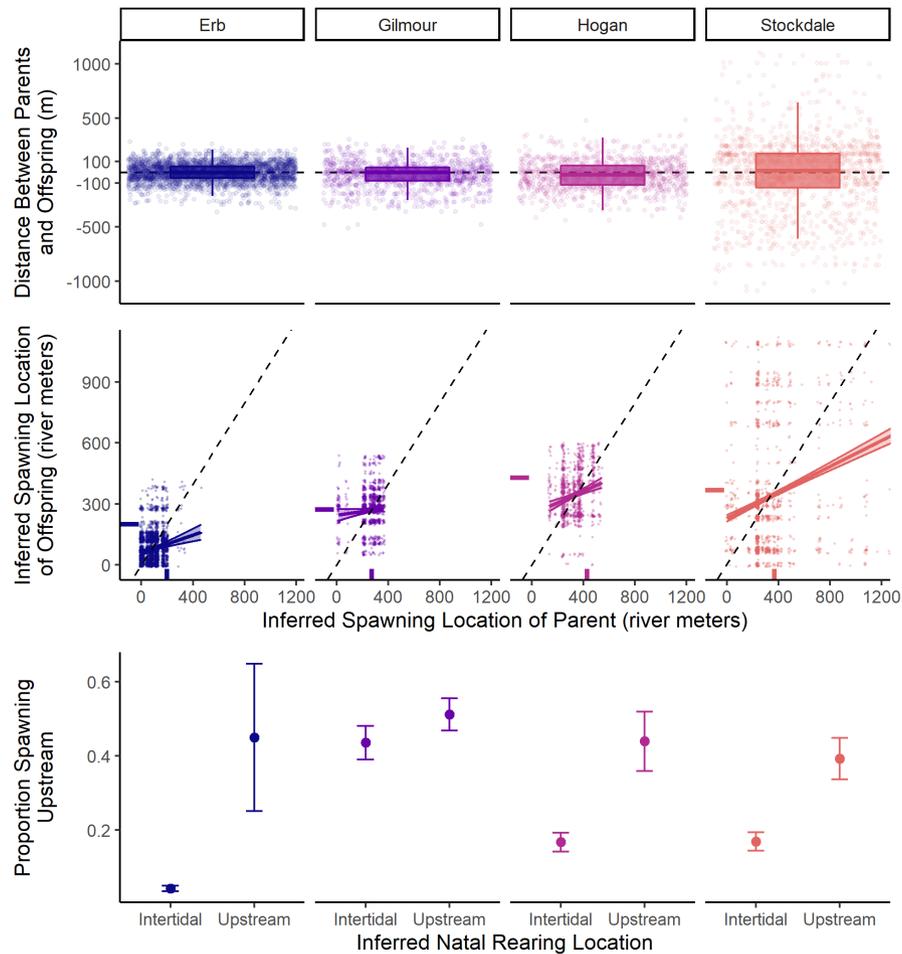


FIGURE 3 (Top) Boxplots of the distance between the inferred spawning locations of parents and offspring (y-axis), for all detected parent-offspring pairs (points) in four pink salmon spawning streams (colours). Dashed lines at zero indicate that parents and offspring were sampled at the same in-stream location. Spawning locations were inferred from the location of sampling areas where groups of carcasses were sampled, in river meters from the mouth of the stream (see 2. Materials and Methods). (Middle) Regression of inferred spawning locations of offspring (y-axis) as a function of inferred spawning locations of parents (x-axis). Empirical estimates (points) were removed above 1100 m in Stockdale to aid in visualization. Coloured lines give significant fitted values across sample locations in each stream, bounded by 95% confidence intervals. Dashed lines represent $y=x$. The upper extent of tidal influence in each stream is represented by coloured axis ticks. Only one parent was included per offspring; in the case of offspring with two pedigreed parents, the more upstream parent was used to account for carcass drift. (Bottom) Proportion of offspring spawning upstream of the high-tide line (y-axis) for individuals who were reared in the intertidal or upstream environments, inferred from spawning location of parents (x-axis). Points give model-predicted values from the best-fit model, bounded by 95% confidence intervals. [Colour figure can be viewed at wileyonlinelibrary.com]

Next, we examined whether observed fine-scale homing behaviours may have been driven by tidally influenced habitat gradients within streams. Results of a binomial regression revealed that spawning environment (a binary trait: intertidal or upstream) was best explained by both incubation environment (also a binary trait: intertidal or upstream) and parent sampling location (distance from mouth of stream), as well as offspring sex, DOY sampled, body length, stream and interaction terms between parent sampling location and stream and incubation location and stream ($\beta_{\text{Incubation Env. Upstream}}=0.50$, $\beta_{\text{Parent Location}}=0.01$, $\text{AICc}=4660.78$, $w\text{AICc}=0.47$, $R^2_{\text{Adj}}=0.20$, Table S1). These results indicated that individuals assumed to have incubated in saltwater environments returned to spawn in freshwater environments less often than those incubated in freshwater, after accounting for other variables that influence choice of spawning habitat (Figure 3, Bottom Panel).

Compared to individuals incubated in the intertidal, fish incubated above the high tide line were more likely to return above the high tide line by a factor of 9.86, 1.13, 2.44 and 2.07 in Erb, Gilmour, Hogan and Stockdale Creeks, respectively. These values are likely reduced compared to true values due to the effects of carcasses drifting downstream prior to sampling.

4 | DISCUSSION

Here, we revealed through molecular pedigree analysis that pink salmon in Alaska return to the same fine-scale areas within streams as their parents, on the scale of tens of meters. Potential behavioural, environmental and temporal mechanisms driving these patterns of fine-scale site fidelity were investigated, and we detected that

homing behaviours were associated in part with a salinity gradient between intertidal and freshwater environments. We also detected phenotypic stratification between intertidal and freshwater spawning habitats, with a higher proportion of males and early returning fish sampled in the intertidal, while a higher proportion of females and later returning fish were sampled further upstream. Taken together, these results suggest that mating in pink salmon populations may be assortative with regards to tidal boundaries, spatial distance, temporal distance and phenotypic traits, thereby limiting gene flow between distinct populations segments.

A primary finding of this work is that pink salmon appear to be homing at small spatial scales, inferred from molecular pedigrees and the positive correlation between parent and offspring spawning locations. We acknowledge, however, that several key assumptions have the potential to influence interpretations of results. Firstly, it was assumed that carcass sampling locations accurately represented true spawning locations within streams. It should be noted that carcasses were sampled only once per day in the field, with some limitations due to harsh weather or bear presence. Carcasses were also transported to large stream banks for bulk processing (generally <100m from sampling locations), and there was a possibility that they drifted downstream of true spawning locations due to normal stream flow or flooding from tidal influences or precipitation events, particularly in larger streams like Stockdale. Seemingly against many odds, the sampling locations of dam-sire pairs were still significantly correlated, suggesting that sampling locations were a reasonable approximation of true spawning locations. It is also likely that the sampling locations of females were more representative of true spawning locations, as males are thought to traverse the spawning grounds more readily in search of multiple mates, whereas females tend to remain near their redds once eggs have been laid (Esteve, 2005). Secondly, it was assumed that the inferred spawning locations of parents represented the true natal development location of their offspring, although patterns of carcass drift, sampling or individual movement within the streams may have influenced these estimates. These factors may have increased the risk of type II error and made it difficult to detect correlations between parent and offspring locations even if they were genuinely occurring in nature. Yet, we still detected a significant correlation between parent and offspring locations, providing evidence that individuals were homing to fine-scale locations within the streams. Third, it was assumed that the sampling date of individuals was representative of spawn timing within cohorts, which could limit mating opportunities between individuals returning at different times if reproductive lifespans were shorter than the length of the spawning season. Previous research has shown that the mean reproductive lifespan of natural-origin fish in Paddy and Erb Creeks is 7.5–14 days, indicating substantial temporal segregation between early and late returning individuals (Fried et al., 1998; McMahon, 2021). While the present study did not measure reproductive lifespan directly, this short reproductive lifespan reported in the literature supports the assumption that sampling dates were a reasonable approximation of spawning timing, especially given that the spawning season in these streams is approximately 45 days long. These patterns may lead to assortative mating for different

phenotypes, if phenotypes are stratified throughout the season (May et al., 2023). Despite the possibility of these assumptions impacting the interpretation of results, the correlations observed in this study still imply genetic and phenotypic structure on smaller spatial scales than usually assumed in pink salmon.

Our results provide evidence for fine-scale homing behaviours in pink salmon and shed light on the factors influencing their spawning site selection. Specifically, we found a preference for intertidal environments, with 72.2% of offspring being sampled in the intertidal across streams in 2016. This preference is consistent with previous findings by Roys (1971) reporting >75% intertidal spawning in pink salmon streams. The preference for intertidal habitats may be due to poor habitat characteristics in the upstream environment, such as winter scouring events, high predation risk or unsuitable gravel size, although the underlying biotic or abiotic mechanisms are unknown. Consistent with presumed habitat quality, lifetime reproductive success has been reported as being significantly higher in intertidal than in upstream environments, implying a distinct fitness benefit associated with intertidal preference (Shedd et al., 2022). We also showed that early returning fish spawned in the intertidal more often than late returns. Several non-mutually exclusive mechanisms may underpin this pattern. First, these temporal differences in spawning site preference may be in part due to the influence of nearby pink salmon hatcheries, as hatchery-origin fish straying into these wild populations tend to spawn further upstream than natural-origin fish (Shedd et al., 2022). Hatchery-origin juveniles are incubated entirely in freshwater, whereas in our study streams and most PWS pink salmon populations, individuals in natural populations predominantly spawn in intertidal habitats. Furthermore, hatchery-origin fish in PWS are known to return later in the spawning season than natural-origin fish (McMahon, 2021; Shedd et al., 2022), and high heritability values have been reported for phenological traits in salmon such as return timing (Carlson & Seamons, 2008; Smoker et al., 1998). Thus, individuals are likely to return at the same time during the spawning season as when their parents returned (Smoker et al., 1998). Furthermore, original hatchery broodstock were taken in the 1970–80s from freshwater spawning, late-returning wild individuals, deliberately intending to temporally segregate the wild and hatchery runs (Habicht et al., 2000). If the upstream portion of these populations have been consistently influenced by hatchery-origin fish and if individuals are returning to natal incubation sites and times, hatchery selection on run timing and potential preference for freshwater spawning areas may be driving spatiotemporal stratification within these streams. An alternative explanation may be that higher-quality intertidal habitats are selected by early returning fish, and competition forces later returning individuals to spawn in the less desirable upstream habitats. Importantly, these explanations are not mutually exclusive, and our study provides a basis for further investigation into the complex mechanisms underlying pink salmon spawning site selection.

This study revealed conditions seemingly plausible for fine-scale adaptation to freshwater or intertidal areas to evolve; however, we are presently unable to test for evidence of microgeographic adaptation to intertidal or upstream habitats. We can conclude that spatial

and temporal segregation is likely driving an assortative mating system in these populations with regards to incubation environment, return timing and body size, which may be controlled by underlying genetic (co)variation and increase adaptive capacity, recruitment, and resilience in these populations (Godineau et al., 2022; May et al., 2023). Assortative mating systems may lead to microgeographic adaptation or adaptation-by-time if there exists heterogeneous selection regimes in different incubation environments or spawn times and genetic variation for these traits (Hendry et al., 1995; Hendry & Day, 2005; Richardson et al., 2014; Torres Dowdall et al., 2012). Beyond obvious differences in salinity, intertidal areas likely differ from freshwater in temperature regimes, substrate size and pathogen risk. One avenue for future research will be to explicitly test for adaptive differences by reciprocally comparing the reproductive success of individuals who were reared and spawned in each habitat (Kawecki & Ebert, 2004). This would require additional generations of pedigree data, or a common-garden style experimental approach, but would provide insights to important adaptive variation in these populations. Our study provides justification for this future work, as characterizing adaptive, ecotypic variation has been a key priority in recent years. For example, ecotypic variation attributed to large bodied 'lake-type' and small bodied 'stream-type' sockeye salmon has stemmed a large body of work to characterize genetic divergence (i.e. Lin et al., 2008), local adaptation (i.e. Peterson et al., 2014) and underlying genomic architecture (i.e. Larson et al., 2017, 2019), with the goal of understanding how life-history variation influences recruitment, resilience and persistence. Although not as visually striking as the body size ecotype in sockeye salmon, our results suggest that a cryptic saltwater-freshwater ecotype may exist on a similar scale in pink salmon.

Possible deleterious effects of production hatcheries on wild populations are an on-going management concern for many wild salmon populations (Naish et al., 2008; Rand et al., 2012). One major concern is the introgression of maladapted alleles that might erode local adaptation in natural populations (Knudsen et al., 2021; Shedd et al., 2022), particularly for populations with similar life-history traits such as spawn timing and location (Jasper et al., 2013). Our results suggest that hatcheries may be driving spatiotemporal stratification between early-returning natural-origin individuals spawning in the intertidal and late-returning hatchery-origin fish spawning upstream. An important conclusion that may be drawn from our results is that there appears to be more stratification between natural and hatchery-origin populations than previously thought, despite hatchery-origin spawners comprising >30% of returning adults in some pink salmon spawning streams (Knudsen et al., 2021; Shedd et al., 2022). Such stratification and subsequent assortative mating would likely slow the introgression of hatchery-origin alleles compared to a random mating system (May et al., 2023). However, if important adaptive differences between upstream and downstream population segments existed before hatchery programs began, maladapted alleles selected for in hatchery settings would likely have rapidly introgressed into the upstream population segment and may have already severely eroded natural genetic diversity. Somewhat surprisingly in the face of nearly 25 generations of large-scale hatchery releases in Prince William

Sound, recent work by the Alaska Department of Fish and Game is showing that at least some wild-type population structure has persisted since pre-hatchery times (Wei Cheng, Alaska Department of Fish and Game, unpublished results), and our study provides a potential spatiotemporal mechanism which may have helped maintain this diversity. While our study has shown that pink salmon are homing on the scale of tens of meters and that these homing behaviours are likely driving an assortative mating system, future studies should incorporate direct measurements of adaptive differentiation and habitat choice through reciprocal transplant experiments, fitness comparisons and genomic approaches to further explore the potential impacts of hatcheries to wild populations. Future studies should also investigate additional ecological drivers influencing the scale of homing within populations such as stream morphology, temperature regimes, or population density. By better understanding the mechanisms driving spatiotemporal stratification, this work can inform management strategies to maintain or increase segregation with the goal of mitigating negative impacts to wild salmon populations.

AUTHOR CONTRIBUTIONS

S. May designed the study, performed analyses and wrote the paper. K. Shedd led laboratory work, genotyping, pedigree reconstruction and edited the paper. P. Rand aided in project design, organized field collections and edited the paper. P. Westley aided in study design and edited the paper.

ACKNOWLEDGEMENTS

The authors would like to thank the Alaska Hatchery Research Program (AHRP) for securing funding and overseeing data collection for this study, which involved enormous efforts by innumerable field technicians, crew leaders and boat captains. The statements, findings, conclusions and recommendations are those of the author(s) and do not necessarily reflect the views of NOAA Fisheries. We specifically thank E. Knudsen with Prince William Sound Science Center (PWSSC) for establishing the field protocol for collection of spatial data; field crew leaders and field technicians from PWSSC for collecting field samples and data; R. Busch with Resource Data Inc. for developing software for field sampling and record keeping; the ADF&G GCL for genotyping, archiving, database development and GT-seq pipeline optimization; the Seeb Lab at the University of Washington for GT-seq panel development; C. Jalbert for GIS help with calculating stream distances; and L. Turner for assistance with data visualization and mapping. We thank two anonymous reviewers for their constructive feedback, which greatly improved the manuscript. Finally, we respectfully acknowledge that all fieldwork was conducted on the traditional homelands of Alaska's Alutiiq/Sugpiaq people who have stewarded these lands and waters for millennia.

FUNDING INFORMATION

Funding for the AHRP has been provided by seven of Alaska's largest private non-profit hatchery corporations, Seafood Processors Association and the State of Alaska. Funding for the genetic analysis for Hogan Creek was provided by a subaward through the North Pacific

Research Board (project number 1619) and funding for the Stockdale even lineage analysis was provided by funding under award (NA16NMF4270251) from NOAA Fisheries Service, in cooperation with the Saltonstall-Kennedy Grant Program. This publication was partially funded by the Cooperative Institute for Climate, Ocean, & Ecosystem Studies (CIOCES) under NOAA Cooperative Agreement NA20OAR4320271, Contribution No. 2023-1265.

CONFLICT OF INTEREST STATEMENT

The authors report no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and scripts used in this study are publicly available at github.com/SMay1/Pink_Salmon_Fine-Scale_Homing.

BENEFIT-SHARING STATEMENT

This work is a part of a larger effort by the Alaska Hatchery Research Program to examine the impacts of hatchery releases to wild salmon populations, which is a priority concern. The results of this work have been shared with stakeholders and the broader scientific community. As described above, data utilized in this study has been shared publicly via Github.

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SUPPORTING INFORMATION

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How to cite this article: May, S. A., Shedd, K. R., Rand, P. S., & Westley, P. A. H. (2023). Tidal gradients, fine-scale homing and a potential cryptic ecotype of wild spawning pink salmon (*Oncorhynchus gorbuscha*). *Molecular Ecology*, 32, 5838–5848. <https://doi.org/10.1111/mec.17154>