

Ecology/Ecological Monographs/Ecological Applications

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Signals of climate, conspecific density, and watershed features in patterns of 1 homing and dispersal by Pacific salmon 2 3 Peter A. H. Westley^{1,2} Andrew H. Dittman³, Eric J. Ward⁴ and Thomas P. Quinn¹ 4 5 ¹School of Aquatic and Fishery Sciences, University of Washington, Seattle, USA. 6 ² Current address: School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 7 Fairbanks, Alaska, USA, 99775 8 9 ³Environmental and Fisheries Sciences Division, Northwest Fisheries Science Center, National 10 Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle WA, USA. 11 ⁴Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries 12 Service, National Oceanic and Atmospheric Administration, Seattle WA, USA. 13 14 *Corresponding author: pwestley@alaska.edu 15 16 Author contributions: A.H.D, T.P.Q, and P.A.H.W conceived the research. P.A.H.W compiled 17 the data and conducted analyses with E.J.W. All authors contributed to the writing. 18 19 Submission type: Article Running title: Dispersal plasticity in Chinook salmon 20 21 Keywords: Philopatry, dispersal, reaction norms, homing, straying, collective behavior,

migration. Pacific salmon. Columbia River

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Abstract

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It is widely assumed that rates of dispersal in animal populations are plastic in response to intrinsic and extrinsic cues, yet the factors influencing this plasticity are rarely known. This knowledge gap is surprising given the important role of dispersal in facilitating range shifts that may allow populations to persist in a rapidly changing global climate. We used two decades of tagging and recapture data from 19 hatchery populations of *Oncorhynchus tshawytscha* (Chinook salmon) in the Columbia River, USA, to quantify the effects of regional and local climate conditions, density-dependence, watershed features such as area and position on the landscape, and direct anthropogenic influence on dispersal rates by adult salmon during the breeding season. We found that the probability of dispersal, termed straying in salmon, is plastic in response to multiple factors and that populations showed varied responses that were largely idiosyncratic. A regional climate index (Pacific Decadal Oscillation), water temperatures in the mainstem Columbia River that was commonly experience by populations during migration, water temperatures in local sub-basins unique to each population during the breeding season, migration distance, and density- dependence had the strongest effects on dispersal. Patterns of dispersal plasticity in response to commonly experienced conditions were consistent with gene by environment interactions, though we are tentative about this interpretation given the domesticated history of these populations. Overall, our results warn against attempts to predict future range shifts of migratory species without considering population-specific dispersal plasticity, and also caution against the use of few populations to infer species-level patterns. Ultimately, our results provide evidence that analyses that examine the response of dispersal to single factors may be misleading.

Introduction

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Dispersal – defined as permanent movement away from natal areas – has profound influences on population demography and evolution (Clobert et al. 2001) and plays a key role in climate-induced species range shifts in terrestrial (Thuiller et al. 2008) and aquatic ecosystems (Perry et al. 2005, Pinsky et al. 2013). There is clear consensus that dispersal is important for populations to respond to changing environmental conditions (Thuiller et al. 2008, Bellard et al. 2012, Schloss et al. 2012, Leroux et al. 2013, Travis et al. 2013) and mounting evidence reveals that dispersal is a complex trait that varies in time and space (Clobert et al. 2009, Delattre et al. 2013, Buoro and Carlson 2014). However, little remains known about how dispersal may respond to changing climatic conditions (Massot et al. 2008, Travis et al. 2013), and it is largely unclear the extent to which dispersal plasticity has an underlying genetic basis (Ronce 2007). Moreover, a recent review of dispersal responses to climate change by Travis et al. (2013) reveals a clear lack of large-scale empirical studies from aquatic ecosystems. Taken together, these knowledge gaps impede our understanding of how dispersal of aquatic species is shaped by climatic factors and how it may evolve in response to natural or anthropogenic sources of selection. Reaction norms are a convenient heuristic framework for simultaneously exploring the strength and shape of plasticity, as well as determining whether plasticity is consistent with an underlying genetic basis (West-Eberhard 2003, Ghalambor et al. 2007). Simply put, reaction norms quantitatively describe phenotypic responses, such as dispersal probability, to environmental gradients exhibited by groups of related genotypes (Hutchings 2011). A phenotypic response to an environmental variable is interpreted as the presence of plasticity within groups. In contrast, variation in how groups respond to a shared environmental gradient

are referred to as gene by environment interactions, or G x E, and are considered integral inherited properties of related individuals (Via et al. 1995). If groups display significantly different shapes of plasticity when exposed to the same environmental factor, most often quantified as the slope between phenotype and environment (Bolker et al. 2009), then a G x E is suggested to be present.

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Here we quantify dispersal reaction norms of 19 populations of hatchery-produced Chinook salmon (Oncorhynchus tshawytscha) in response to multiple factors during 17 years of upstream migrations in the Columbia River, USA. The 673,400 km² Columbia River basin historically produced millions of migratory Pacific salmon (Oncorhynchus spp.) (Lichatowich 2001). However, an estimated 40% of salmon populations were extirpated by construction of impassable dams, which blocked upstream migrants from reaching natal spawning and rearing habitats (NRC 1996). Hatchery propagation to supplement lost production of salmon is pervasive in the basin with 178 hatchery programs in operation as of 2009 (HSRG 2009). Notwithstanding the conservation concerns of hatchery-produced fish interacting with wild counterparts (Hayes and Carmichael 2002), the Columbia River basin provides an unprecedented opportunity to examine the patterns of dispersal in Pacific salmon. For decades, millions of juvenile salmon have been produced in hatcheries and marked with ca. 1mm coded wire tags (CWTs) (Jefferts et al. 1963) that allow for quantification of dispersal rates by associating an individuals' release location to its final recovery location. Effort to recover CWTs is extensive throughout the basin and along the coast and is "double-blind" because the people in the field collecting tags do not know if the fish has dispersed (or is a 'stray') from a neighboring population or is a native fish, nor do those in the lab processing the tags (HSRG 2009, Nandor et al. 2010).

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Chinook salmon, like other Pacific salmon, are well known for their capacity to use recalled olfactory (Scholz et al. 1976) and geomagnetic cues (Putman et al. 2013) to return to natal locations for reproduction after extended periods of time foraging in the ocean (Quinn 2005). The majority of adult salmon surviving to return to freshwater 'home' to natal locations for reproduction, but a small and variable percentage of individuals disperse (termed 'straying' in the salmon literature and synonymously used with dispersal hereafter) to non-natal areas for reproduction (Hendry et al. 2004, Westley et al. 2013, Keefer and Caudill 2014). All migratory salmon are thought to have a sensitive window for imprinting to migratory cues during the parrsmolt transformation (PST), a development process that readies salmon for life at sea (Dittman and Quinn 1996). Therefore, most hatchery programs plan juvenile releases to coincide with the PST. Stream-type Chinook salmon (i.e., fish that spend a full year in freshwater as juveniles) in the wild often make extensive migrations away from their natal site prior to the PST suggesting that imprinting may also occur during earlier development periods (Dittman et al. 2010). Harden Jones (1968) hypothesized that juvenile salmon learn a series of olfactory waypoints during their downstream migration and then utilize these retained odor memories to guide their return migration. While the salmon olfactory system is extremely sensitive, it is unlikely that salmon can detect their natal site at extreme downstream locations but rather homing adults are thought to identify the series of learned olfactory waypoints sequentially as they migrate upstream. Consequently, transfer of young among hatchery and release sites may disrupt the imprinting process during the PST and is correlated with increased straying later in life (Candy and Beacham 2000, Ford et al. 2015).

In this paper we explore this potential disruption of imprinting processes, as well as the role of regional-scale climate and local-scale environmental factors on shaping reaction norms of

straying rates in hatchery-produced Chinook salmon populations. We test the hypothesis that population-specific straying rates are plastic against the predicted alternative that straying is constant in these populations and insensitive to external drivers. Specifically, we investigated abiotic factors related to a regional climate index, the Pacific Decadal Oscillation that describes anomalies in ocean surface temperature and correlates with salmon survival (Mantua et al. 1997) and local environmental conditions (e.g., stream flow and water temperature commonly experienced by populations and unique to each population), a biotic factor (population-specific abundance, referred to as 'run size' hereafter), and human disturbance during the juvenile rearing period in hatcheries prior to seaward migration (transfer to a different watershed for release) that might affect the process of imprinting to natal odors. Additionally, we tested the hypotheses that abiotic conditions encountered during the juvenile stage along with the magnitude of the discrepancy in conditions between years of outmigration vs. year of return would combine to influence straying at adulthood. Our approach allowed us to quantify the overall mean 'net' influence of each hypothesized factor on straying as well as population-specific responses. By doing so, we are able to test for the presence of plasticity in response to environmental gradients and determine whether responses are at least consistent with G x E interactions.

Materials and Methods

Definition of 'stray'

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We categorized recovered tagged individuals as strays if they were recovered in subbasins (tributary watersheds of the Columbia basin) that they had not experienced during hatchery rearing or release and hence should not have imprinted there. This definition avoids ambiguity in the cases where fish are displaced between sub-basins used for rearing and release. We assessed straying at the sub-basin spatial scale, which is in line with several previous studies

in the basin (Quinn and Fresh 1984, Pascual and Quinn 1994, Pascual et al. 1995, Westley et al. 2013) and generally conforms to the spatial scale designated as conservation units (HSRG 2009). Although we do not know the fate of fish recovered at each location, individuals that return to non-natal hatcheries are often used in breeding propagation without respect to origin, and all Chinook salmon die after their first bout of reproduction. As a consequence, we presume that individuals recovered on the spawning grounds of non-natal sites would have at least attempted to reproduce before dving. Thus, our definition of straving is equivalent to 'permanent straving' as used by Keefer and Caudill (2014) that provided an excellent review on the complications and caveats of definitions involving straying. Our analyses excluded recoveries that are ambiguous with regards to homing and straying (i.e., caught by anglers or recovered at mainstem dams within the Columbia River corridor as these fish may have homed if given the opportunity), opting only to use recoveries to hatchery facilities and on spawning grounds. Despite our conservative approach, there were nearly 450 sites where salmon could have been detected. The 154,620 tags were recovered from a subset of 164 unique locations, and all but 15 individuals were recovered within the Columbia Basin. The majority of recoveries (75%) were from hatcheries or their associated collection facilities (e.g., fish traps or weirs) and the remaining 25% were collected from spawning grounds.

CWT data

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Tagging and associated release and recovery data were downloaded from the Regional Mark Information System (RMIS, publicly available at: www.rmpc.org), which is maintained by the Regional Mark Processing Center of the Pacific States Marine Fisheries Commission. Each recovery was expanded to account for sampling fractions (i.e., the fraction of fish examined for tags in that recovery event) (Nandor et al. 2010). The median expansion factor in the dataset was

1.01, thus most recoveries reflect single individuals. Taken together, the database we constructed for analyses spanned 17 years of adult returns (1993-2009) and included 154, 620 tagged adult salmon recoveries from over 70 million individuals tagged as juveniles (Table 1) from 19 hatchery populations (Fig. 1A). These return years were chosen as they reflected the period of greatest temporal and spatial coverage in the database. Time series of straying were constructed by calculating the proportion of total number of individuals recovered from each population in each return year that strayed to foreign sub-basins.

Hypothesized predictors of straying

We tested 17 factors hypothesized to be influencing straying rates, and summarize those factors with associated hypotheses and predictions in Table 2. Prior to analyses, we examined pairwise correlation between covariates and when correlations were greater than 0.5 in magnitude, we regressed one against the other and used the subsequent residuals for analyses. This procedure was applied to two pairs of covariates; i) watershed area positively correlated with migration distance (r = 0.54), ii) mainstem flow disparity (absolute value of flow in year of return minus the discharge in year of release) was positively correlated with year of release, r = 0.74). We regressed watershed area against migration distance and return year mainstem flow against release year flow. By using residuals from these relationships, the correlations between all covariates were weak (p < 0.3). The strongest remaining correlation was r = -0.28 between discharge in the mainstem Columbia and PDO, consistent with observations over longer temporal scales (Hamlet and Lettenmaier 1999)

Modeling

To account for the variability in sample sizes and tag recoveries between years, we conducted a hierarchical logistic regression on the raw counts, instead of performing a simple

linear regression on the calculated straying rates. The hierarchical Bayesian logistic regression was estimated in R using the r2jags package (Sung Su and Yajima 2012) following the general form of:

$$logit(P_{z,t}) = \beta_{0,z} + \beta_{1,z} X_1 + \beta_{2,z} X_2 + \beta_{3,z} X_3 \dots \beta_{n,z} X_n + u_z * t$$
 Eq. (1)

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where $P_{z,t}$ is the probability of straying by population z in return year t, $\beta_{0,z}$ is the randomly varying intercept, X_1 to X_n are transformed and z-scored covariates (mean = 0, standard deviation = 1) and u_7 is a population specific trend term to capture any underlying non-stationary behavior in the data series of population z. Both the mean stray rate $\beta_{0,z}$ (intercept) and trend (u_z) were treated as population-specific random effects, $B_{0,z} \sim Normal(\overline{B_0}, \sigma_{B0})$ and $u_z \sim Normal(\bar{u}, \sigma_u)$, where the hyperparameters represent the global means and variances shared among all populations. To quantify population-level straying plasticity, we also treated all continuous covariates as population-specific random effects, e.g. $B_{1,z} \sim Normal(\overline{B_1}, \sigma_{B1})$. In other words, we estimated a mean net effect shared amongst all populations, as well as population-specific deviations from that mean. We treated the categorical 'displacement' parameter as a fixed effect for reasons of identifiability (most populations had the same value of displacement, which did not vary over time). For any combination of covariates, we had n fish recovered as strays from a known number of N total recoveries. To incorporate this variation in sample sizes between population and year, we treated the observed data $n_{z,t}$ as being drawn from a Binomial $(P_{z,t}, N_{z,t})$ distribution, which was appropriate given the raw level of the data (individuals were classified binomially as 'strays' or 'not strays'). Bayesian parameter estimation was done using Markov Chain Monte Carlo (MCMC) in the JAGS software (Plummer 2003), using 5 chains, with a burn-in of 50,000 draws (saving every 15th sample), resulting in 1670

saved samples for each parameter. We used normally distributed, uninformative priors with mean = 0, sd=1. The Gelman-Rubin diagnostic was used to assess parameter convergence (Gelman and Rubin 1992). The strength of effect of a given predictor was based on the absolute value of the median coefficient value and whether the 95% credible intervals included zero.

Results and Discussion

We were able to explain 87% of the observed inter-annual deviance in stray rates (Fig. 1B) using a single hierarchical Bayesian logistic regression simultaneously fit to population-specific time series of dispersal. The analysis revealed marked plasticity in dispersal at the species –level (interpreted as net effects of predictors) as well as population-specific patterns of dispersal (interpreted from population-specific random effects). These results provide evidence of gene by environment interactions, and that multiple factors had countervailing influences on dispersal. Therefore, analyses of single environmental factors to predict changes in dispersal should be viewed with caution, and future studies should account for variation in dispersal rates that differ markedly among populations and that is plastic to environmental forcing.

Model diagnostics indicated that our model adequately captured the biology of this system and was suitable for interpretation (Appendix A). All parameter estimates converged based on Gelman-Rubin diagnostic values of < 1.2. The effect sizes of factors related to straying are listed in ascending order in Fig. 2 and tabulated in Table 3. We focus our attention on 12 predictors that had net or population –specific effect sizes with credible intervals that did not include zero (Fig. 2, Table 3).

Counter to predictions (Table 2), straying was negatively correlated with values of the Pacific Decadal Oscillation (PDO) climate index in the return year of adult migration (standardized effect size, SES = -1.16). The PDO index is defined as the leading principal

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component of North Pacific monthly sea surface temperature variability and correlates with salmon survival and patterns of freshwater temperature and flow in the Columbia (Mantua et al. 1997, Hamlet and Lettenmaier 1999). Positive values of the PDO are associated with warm temperature anomalies in the ocean and freshwater, lower survival of salmon in this region, and lower flow in the Columbia. Although the net effect across all populations marginally included zero (and thus would not be interpreted as 'significant' in a traditional statistical approach), seven populations exhibited a negative response while the rest were neutral (Fig. 2, Table 3). In contrast the net and population-level effects of the PDO during the release year (assumed to be four year prior to the return year for most fish) overlapped zero. Again, counter to predictions the discrepancy in PDO values between years of outmigration from freshwater to the ocean by juveniles and return by adults was inversely associated with straying. While the mechanism underlying the influence of the PDO on straying is not clear, we suggest that its role is not a result of simple correlations with other predictors, (e.g. water flow, water temperature, or salmon run size) given the direction of the associations with these factors summarized in Table 3, and overall weak correlations (r < 0.3) among covariates. The influence of the PDO on straying is consistent with the observation that large-scale climate forcing is sometimes a better predictor of ecological dynamics compared to local-scale environmental conditions (Hallett et al. 2004). We detected evidence of inverse density-dependence, consistent with our predictions (Table 2) and findings elsewhere (Hendry et al. 2004). The net effect of run size on rates of

(Table 2) and findings elsewhere (Hendry et al. 2004). The net effect of run size on rates of straying was negative SES = -1.03 (and intervals did not include zero) and 12 of 19 populations exhibited this response (the remaining were neutral). Although an inverse relationship between density and straying is counter to typical simple assumptions about density-dependence and dispersal (Hansson 1991), we interpret the reduced straying rates during years of high abundance

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as an emergent property of collective migratory behavior in salmon groups (Couzin et al. 2005, Berdahl et al. 2013, Pettit et al. 2013). This newly articulated collective navigation hypothesis with specific regards to salmon has recently been reviewed Berdahl et al. (2014) and warrants future scrutiny as collective behavior could have clear adaptive benefits to both individual salmon and populations. In addition, the potential for straying to increase during periods of low abundance adds further to the consequences of habitat loss and population declines observed throughout the southern range of Pacific salmon (NRC 1996).

Increasing migration distance was negatively associated with a net effect of straying, but the mean response of all populations included zero in the parameter estimates (all populationspecific SES included zero, Table 3). While the mean was estimated precisely, the individual deviations were not, because unlike the other covariates (which were time varying), migration distance (and watershed area) was static for each population. This finding is counter to our prediction and may result from watersheds in the lower part of the basin sharing greater similarity in local water chemistry than basins in the upper watershed, which may reduce the fitness costs of straying (Lin et al. 2008, Peterson et al. 2014). Alternatively, greater straying may reflect a greater historical legacy of among-basin hatchery transfers in populations of the lower Columbia basin (HSRG 2009) or from other factors that are unquantified and ultimately unknowable. Regardless, our analysis provided no evidence that populations from natal subbasins in the upper Columbia basin lack the energy to complete such long distance migrations or are victim of the presumed cumulative probability of a navigational error as fish migrate upstream. In general this result of little straying of upriver populations would help preserve locally adapted traits that may aid in their arduous migrations (Eliason et al. 2011). It is important to note that the effect of migration distance was independent of the correlative effect

of watershed size, which we analyzed as residuals between variables (Table 2). That is, positive residuals reflected large watershed for their distance upstream and vice versa, and overall we detected a neutral net effect on straying and variable population-effects (Table 3, Fig. 2). Reverse analyses done with area as the covariate and distance as residuals revealed no significant effect, suggesting a true influence of migration distance independent of watershed size.

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The average May water temperature of the mainstem Columbia River that was commonly experienced by the populations during a time of year corresponding to upstream migration by adults, and average August water temperature in local sub-basins near the breeding season both had strong net positive effects on straying rates (Table 3, Fig 2). Moreover, straying rates of six populations were positive in response to maintem Columbia River temperature and four populations responded positively to sub-basin temperatures (all others were neutral). In contrast, the average August water temperature at the last major confluence that upstream migrating populations would have experienced before reaching their natal sub-basins did not have an effect. Overall, the finding of maintsem and sub-basin temperatures is consistent with observations that migrating fall Chinook salmon will enter non-natal tributaries, especially when water temperatures exceeded 20° C (Goniea et al. 2006). The strong effect of water temperatures on straying we detected occurred at temperatures (min = 11.5, max = 13.8) being well below the thermal optima of 16°C for spring Chinook salmon migration (Torgersen et al. 1999). The strong effect of temperature in local sub-basins suggests that the 'decision' to stray may be influenced during both the period in the mainstem river corridor and during the breeding season. Given the nature of CWT recoveries, we are unable to quantify the proportion of fish that strayed from local sub-basins after first returning there and then subsequently strayed elsewhere.

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Counter to hypotheses and predictions, the remaining factors had no significant net effects on straying. However, 10 of the 13 predictors with a neutral net effect revealed at least one population that exhibited a positive or negative response (Table 3), suggesting caution when interpreting species-level or population-level dispersal rates from few populations. We highlight that our analysis did not find evidence to suggest that displacing juvenile fish from one location and then releasing them in another sub-basin increased rates of straying (as we have defined it) at the sub-basin spatial scale, counter to findings elsewhere (Pascual et al. 1995, Candy and Beacham 2000). Pooled across all years and populations, 2.5% of the 154,620 recovered fish strayed to non-natal sub-basins and 0.4% of the total recoveries returned to sub-basins of early rearing despite being displaced and released elsewhere. While these fish may be considered a stray from a management perspective, given that fish are released in locations with the intention they will imprint and return there, the return to sites of early life exposure is consistent with the sequential imprinting hypothesis (Harden Jones 1968). It was also noteworthy that there was no evidence to support an underlying net temporal trend in straying rates, independent from the effects of the covariates in the model. However, for reasons that are not clear, four populations showed negative trends while the rest were neutral (Table 3, Fig. 2).

Population-specific plasticity in straying rates in response to commonly experienced environmental variables, such as the PDO index and mainstem Columbia River water temperature is consistent with expectations if G x E interactions and underlying heritability of dispersal reaction norms were present. Across taxa, natural selection acting on heritable dispersal reaction norms is often invoked to explain observations that the rate of dispersal can evolve rapidly in response to external forcing (Phillips et al. 2006, Ronce 2007). With regards to salmon in the Columbia River, our results suggest that trans-generational rates of straying may be altered

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in response to natural or anthropogenic sources of selection, a critical insight in predicting how salmon populations may respond to future environmental change (Hutchings 2011) or human disturbance (Keefer et al. 2008). We are cautious in this interpretation of a heritable basis to the patterns in dispersal observed here as the role of genetics is confounded by unknown environmental and hatchery-specific practices that may influence these populations. Additionally, although we treat each hatchery as distinct populations it is likely that at least some of the fish that strayed to non-natal hatcheries were used in breeding programs as fish are often spawned blind with respect to their population of origin. Given this, we are tentative in assuming that hatchery-populations are genetically distinct groups for interpreting G x E reaction norms. With that caveat, the use of non-natal strays in breeding programs could alter the patterns of dispersal reaction norms in these hatchery populations, to the extent that a heritable basis to dispersal is indeed present. It is impossible to know whether artificial selection has already shifted patterns of plasticity in these populations given that the strength of selection acting on dispersal is rarely clear in salmonid populations (Peterson et al. 2014) and the value of heritability is unknown (Carlson and Seamons 2008). We do caution against transferring the results gleaned here from hatchery-produced salmon to wild populations as multiple lines of evidence suggest that hatchery fish are likely to stray at different rates than wild fish (Quinn 1993, Dittman and Quinn 1996, Keefer and Caudill 2014). In a recent paper using genetic parentage assignments, Ford et al. (2015) provide evidence that hatchery-produced fish stray at markedly higher rates among tributaries within the Wenatchee River (the Leavenworth hatchery in our analysis located in this sub-basin) than wild fish, and stray to other Columbia sub-basins at higher rates than wild fish. Whether the patterns of dispersal reaction norms reported in our analysis fundamentally differ from wild populations remains unknown.

Conclusions

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Understanding the factors that shape reaction norms of dispersal is necessary in order to accurately predict metapopulation dynamics (Hanski 1998), gene flow and the maintenance of locally adapted populations (Hendry et al. 2000), range shifts and the rate of biological invasion (Phillips et al. 2006), or potential for adaptation to environmental change (Carlson et al. 2014). The results presented in this paper contribute to the rapidly mounting evidence that dispersal is plastic in response to regional-scale and local-scale external forcing, population density, and is highly variable in time and space across populations within species. Evidence assembled from across a range of taxa, including insects (O'Neil et al. 2014), amphibians (Phillips et al. 2010). fish (this study), birds (Walls et al. 2005), and mammals (Schloss et al. 2012) now make it obvious that treating dispersal as a fixed quantity within species or populations is invalid. Moreover, attempts to understand the response of dispersal to anthropogenic sources of disturbance must account for the additional influence of population-specific responses to environmental factors. We echo the warning of Travis et al. (2013) that the continued failure to account for biologically realistic variation in dispersal rates is likely to mislead our predictions of how species may respond to a rapidly changing climate.

Acknowledgements

This project was funded by the US Army Corps of Engineers, and the H. Mason Keeler Professorship at the University of Washington, and made possible by the massive behind-scenes efforts by individuals and organizations involved in recovery, reading, and processing of codedwire tag data. We are deeply indebted to D. Isaak, D. Horan, D. Nagel, and J. Verhoef for their help providing sub-basin and confluence junction water temperatures. This manuscript was

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533	Ecological Archives
534	Appendix A. Model diagnostics and adequacy
535	

Table 1. Table 1. Summary of coded-wire tagged, released, and recovered stream-type Chinook salmon that returned to the Columbia River in 1993-2009. Populations are listed in ascending distance from the mouth of the Columbia River, superscripts correspond to numbers in Fig 1A. Data compiled from the Regional Mark Information System (RMIS, freely available at: www.rmpc.org), which is maintained by the Regional Mark Processing Center of the Pacific States Marine Fisheries Commission.

Hatchery population	Number tagged	Number released	Total recovered	Total stray
Cowlitz Salmon Hatchery ¹	5,825,928	12,316,141	18,953	43
Fallert Creek Hatchery ^{2,A}	3,059,341	5,581,164	8,570	466
Lewis River Hatchery ³	4,206,582	10,470,231	9,477	292
Clackamas Hatchery ⁴	2,238,913	13,652,035	12,555	81
Marion Forks Hatchery ⁵	2,206,015	11,496,768	5,047	40
South Santiam Fish Hatchery ⁶	868,762	5,900,296	1,820	154
McKenzie Hatchery ⁷	4,633,270	14,705,124	14,345	169
Willamette Hatchery ⁸	3,629,797	13,573,134	5,813	769
Carson National Fish Hatchery ⁹	3,965,160	23,221,399	5,117	516
Little White Salmon National Fish Hatchery ¹⁰	1,501,350	16,096,349	2,926	119

Grand Totals	70,872,179	213,291,332	154,620	3,884
Lookingglass Hatchery ¹⁹	6,829,497	9,220,046	5,735	241
Kooskia National Fish Hatchery ¹⁸	2,274,485	6,138,926	2,388	261
Dworshak National Fish Hatchery ¹⁷	4,038,340	12,597,479	4,988	412
Methow Hatchery ¹⁶	4,156,119	4,255,237	7,445	52
Winthrop National Fish Hatchery ¹⁵	4,513,164	5,768,281	6,058	41
Entiat National Fish Hatchery ¹⁴	2,677,376	7,115,008	4,287	53
Leavenworth National Fish Hatchery ¹³	6,665,903	29,141,868	8,586	61
Round Butte Hatchery ¹²	6,069,246	6,642,545	25,660	86
Klickitat State Fish Hatchery ¹¹	1,512,931	5,399,301	4,851	27

Aincludes values of fish tagged and released from Kalama Falls Hatchery within the same sub-basin

Table 2. Hypotheses and predictions for each of 17 covariates included in mixed-effect Bayesian logistic regression model to explain straying rates in 19 stream-type Chinook salmon populations during return years 1993-2009. Some covariates were commonly experienced by populations (shared) while others were unique to specific populations. All (except the displacement rearing variable) were continuous and standardized. Columbia flow discrepancy and watershed area were transformed to control for collinearity with other covariates. See main text for details.

Predictor in model	Hypothesis & Prediction
Regional and local-scale predictors of straying	
(shared)	
Pacific Decadal Oscillation (return year ¹)	Conditions in freshwater and ocean affect migrations. PDO inversely related to survival and streamflow,
Pacific Decadar Oscillation (feturii year)	and positively related to water temperature in this region. Positive correlation with straying.
Pacific Decadal Oscillation (release year ²)*	Same as above
Pacific Decadal Oscillation discrepancy(return -	Abrupt climate change in freshwater and ocean may alter cues used for homing and increase straying.
release)	Positive correlation with straying.
Columbia flow (return year ^{1,3})	The amount of water experienced by upstream migrants may delay migration and dilute olfactory cues.
Columbia now (return year 1)	Positive correlation
	The amount of water experienced by downstream migrants may accelerate migration, dilute odorants used for
Columbia flow (release year ^{2,3})*	imprinting.
	Positive correlation with straying.

Columbia flow discrepancy (return - release⁴)*

Abrupt change in freshwater conditions may alter cues making them more difficult to detect. Positive correlation with straying.

Columbia water temperature (return year¹)*

Warm water temperatures will encourage individuals to seek thermal refugia. Positive correlation with straying.

Local-scale environmental predictors of straying

(unique)

Run size⁵

Confluence water temperature (return year⁶)

Migration distance⁷

Sub-basin flow (release year²)*

Sub-basin flow (return year¹)

Sub-basin flow discrepancy (return - release)*

Sub-basin water temperature (return year⁸)

Sub-basin watershed area⁹

Previous studies suggest an inverse density-dependent relationship. Negative correlation with straying.

Individuals that experience warm temperature en route to natal sub-basins will seek thermal refugia.

Positive correlation with straying.

Individuals from populations further upstream have a greater likelihood of encountering adverse conditions at

some point during their migration in the mainstem en route, or making a navigational error. Positive

correlation with straying

Same as Columbia flow (release year)

Same as Columbia flow (return year)

Same as Columbia flow discrepancy (return-release)

Warmer temperatures during the spawning season will encourage individuals to seek thermal refugia in

foreign sub-basins.

Positive correlation with straying.

Despite acute sensory capacity in salmon, larger watersheds should be easier to detect and less prone to

adverse conditions such as low flow and warm temperatures. Negative correlation with straying

Anthropogenic and temporal predictors of straying

Displacement rearing in hatcheries¹⁰ (shared) Displacing fish between locations will disrupt the imprinting process and influence straying.

Straying will increase with displacement (negative correlations given coding of covariate in the model)

Temporal trend¹¹ (unique)

Straying may be responding to factors not included in model. No a priori prediction

http://waterdata.usgs.gov/WA/nwis/current/?type=flow

PDO data from: http://jisao.washington.edu/pdo/PDO.latest, flow data from: http://waterdata.usgs.gov/WA/nwis/current/?type=flow

¹ Values for May, corresponding to peak of upriver migration. PDO data from: http://jisao.washington.edu/pdo/PDO.latest, flow data from:

² Values for April, corresponding to peak downstream migration.

³ As measured at the Dalles Dam, data from: http://waterdata.usgs.gov/WA/nwis/current/?type=flow

⁴ Included in model as residuals between the discrepancy (return-release year) vs. release year to control for correlations with release year or return year flows

⁵ run size calculated by expanding recoveries to account for sampling and tagging proportions, data from: www.rmpc.org

⁶August average water temperature at first downstream confluence junction from rearing hatchery associated with each population, data provided by D. Isaak, personal communication

⁷ Measured in (km) using the path tool in Google Earth. The distance was measured from each hatchery location (latitude and longitude from www.rmpc.org) to Astoria bridge in the estuary

⁸August average water temperature at point adjacent to rearing hatchery associated with each population, data provided by D. Isaak, personal communication, http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html

⁹ Included in model as residuals between watershed area (km²) vs. migration distance to control for the observation that watershed size increases with distance upstream,

data from: http://water.usgs.gov/osw/



¹⁰ Data from: www.rmpc.org, coded 1 if reared and released in same sub-basin, 0 if otherwise

¹¹Derived quantity from the model

^{*}Covariates for the release year were four years prior to the return year, assuming that the majority of the fish mature and total age of 5.

Table 3. Estimated net effects of hypothesized predictors on straying of Chinook salmon in the Columbia River inferred from mixed-effect Bayesian logistic regression. 'Significant' predictors (non-zero overlapping 95% credible interval) are denoted in bold. Populations exhibiting significant (shown in bold) positive and negative responses are listed by number corresponding to locations in Table 1 and Fig 1A. Displacement rearing was treated as a fixed effect, thus population-specific responses are not applicable.

	Median net	- N		
Predictor of straying	effect	95% credible interval	Positive	Negative
PDO (return year)	-1.16	-2.06, 0.033	i	3, 4, 9, 10, 11, 14, 19
Run size (density-dependence)	-1.03	-1.59, -0.47		4, 5, 8, 9, 11-19
Migration distance	-0.79	-1.46, -0.16		
Columbia flow discrepancy (return - release)	-0.47	-1.39, 0.41		1, 9, 12
Sub-basin flow (return year)	-0.46	-1.27, 0.32	13, 18	2, 6, 19
Sub-basin flow discrepancy (return - release)	-0.38	-1.28, 0.30	18	9, 4, 17
PDO discrepancy (return - release)	-0.36	-1.16, 0.20		3, 6, 17, 18, 19
Columbia flow (release year)	-0.19	-1.30, 0.90		

Confluence water temperature (return year)	-0.19	-1.09, 0.67	18, 19	1, 9, 17
Temporal trend	-0.17	-0.36, 0.09		3, 6, 15, 19
Displacement rearing in hatcheries	-0.14	-0.60, 0.39	Treated as fixed	Treated as fixed
PDO (release year)	0.04	-0.71, 0.83		
Sub-basin watershed area	0.10	-0.25, 0.47	2, 4, 6, 8, 11, 17	9, 12, 15, 16, 18
Sub-basin flow (release year)	0.17	-1.46, 2.42	19	
Columbia flow (return year)	0.23	-0.59, 1.26		
Columbia water temperature (return year)	0.67	0.016, 1.90	1, 2, 4, 5, 12, 17	
Sub-basin water temperature (return year)	0.91	0.12, 1.42	5, 10, 18, 19	



1 Figure Legends

2

- 3 Figure 1. Map of the Columbia River Basin, USA (A) showing hatchery populations of stream-
- 4 type Chinook salmon used for analyses.1 = Cowlitz Salmon Hatchery, 2 = Fallert Creek
- 5 Hatchery, 3 = Lewis River Hatchery, 4 = Clackamas Hatchery, 5 = Marion Forks Hatchery, 6 =
- 6 South Santiam Fish Hatchery, 7 = McKenzie Hatchery, 8 = Willamette Hatchery, 9 = Carson
- 7 National Fish Hatchery, 10 = Little White Salmon National Fish Hatchery, 11= Klickitat State
- 8 Fish Hatchery, 12 = Round Butte Hatchery, 13 = Leavenworth National Fish Hatchery, 14 =
- 9 Entiat National Fish Hatchery, 15 = Methow Hatchery, 16 = Winthrop National Fish Hatchery,
- 10 17 = Dworshak National Fish Hatchery, 18 = Kooskia National Fish Hatchery, 19 =
- Lookingglass Hatchery. Major dams are shown as white wedges. Time series of observed
- proportion of total recovered tags for each population in each year that were recovered as strays
- 13 (B) where the color of lines corresponds to the hatcheries in (A).
- 14 Figure 2. Effect sizes for standardized predictors hypothesized to influence stray rates of
- 15 Chinook salmon in the Columbia River, ranked in ascending order. Box plots represent the
- posterior distribution of estimated net effects of predictors on straying, and the points are 19
- population median estimates of each predictor's influence. Significant (determined by non-zero
- overlapping 95% credible intervals) effects are coded in red for negative, grey for neutral, and
- 19 blue for positive.

20



