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Juvenile dispersal affects straying behaviors of adults in a migratory population

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Abstract. The resilience of organisms to large-scale environmental and climatic change depends, in part, upon the ability to colonize and occupy new habitats. While previous efforts to describe homing, or natal site fidelity, of migratory organisms have been hindered by the confounding effects of fragmented landscapes and management practices, realistic conservation efforts must include considerations of the behavioral diversity represented by animal movements and dispersal. Herein, we quantify straying away from natal origins by adult chinook salmon (*Oncorhynchus tshawytscha*) in a wild population that inhabits a pristine wilderness basin. Using natural isotopic signatures ($^{87}Sr/^{86}Sr$) to reconstruct the migratory behaviors of unhandled individuals over their entire life cycle, we identified ecological and behavioral factors influencing the propensity to stray. Our results indicate that natal site fidelity is scale dependent, ranging from 55% at ~1-km distances to 87% at longer (>10-km scale) distances, and juvenile dispersal and sex highly influence straying occurrence. These findings lend support for the conservation of behavioral diversity for population persistence, and we propose straying as a mechanism for maintaining genetic diversity at low population densities.

Key words: behavior; chinook salmon; dispersal; life history diversity; migration; natal site fidelity; Oncorhynchus tshawytscha; *Sr isotopes; straying.*

Introduction

Homing to natal areas and the exploration of alternative habitats through straying jointly convey adaptive advantages to the evolutionary persistence of migratory organisms. While there has been significant progress in describing the mechanisms that contribute to successful homing across taxa (e.g., Bingman and Cheng 2005, Lohman et al. 2008), much less is understood concerning the ecological factors that impact individual homing success and their consequences for populations. On the one hand, natal site fidelity results in locally specialized life history adaptations and fitness characteristics that structure populations and increase reproductive success (Cury 1994, Dittman and Quinn 1996, Hendry et al. 2004, Quinn 2005). Alternatively, straying allows for the colonization of new habitats, provides the opportunity for genetic mixing among populations (Cury 1994, Hendry et al. 2004) and can serve as a buffer against variation in habitat quality (McDowall 2001). As expanding technologies suggest, there can be considerable within-population variation in the degree to which individuals repeat migratory routes and return to natal source habitats (Vardanis et al. 2011); however, unraveling the entire migration history of individuals has rarely been accomplished for any migratory species (Alerstam 2006).

Efforts at understanding the significance of homing in migratory populations have often overlooked the occurrence or significance of straying, as tagged individuals within a population are rarely recovered from straying destinations and untagged individuals in the focal population cannot definitively be called strays. Further, juvenile dispersal often cannot be measured, which precludes linking the scales at which homing and straying can be defined or are relevant. For migratory fishes, any insights into straying tendencies come from tagged hatchery populations, and this body of research implicates a number of individual condition and environmental factors as causes of adult salmon failing to return to natal rearing locations. While not thought to be consistently sex biased (Unwin and Quinn 1993, Hendry et al. 2004), males may stray more frequently in order to avoid inbreeding and kin/reproductive competition (Hard and Heard 1999, Hutchings and Gerber 2002, Garant et al. 2005). Both older (Quinn and Fresh 1984, Quinn et al. 1991, Labelle 1992, Unwin and Quinn 1993, Pascual et al. 1995) and younger fish (Hard and Heard 1999) have demonstrated increased straying rates. Spawner density could be a contributing factor as well, as increased adult returns to a spawning location causes decreased straying (Quinn and Fresh 1984, Hard and

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Heard 1999) or has no effect on straying (Labelle 1992, Schroeder et al. 2001).

Much less is known about the causes and consequences of straying behavior in wild populations (Quinn and Fresh 1984, Quinn 1997) due, in part, to the lack of methodologies that can track fish movements over large spatial scales with fine-scale resolution. Over the last decade, chemical and isotopic signatures have provided an emerging approach for studying the movements and migrations of organisms (Marra et al. 1998, Rubenstein and Hobson 2004). Within fish populations, the preservation of these signatures within otoliths (ear stones) has provided novel ways for distinguishing among stocks of fish, quantifying movements, and identifying homing tendencies of fish populations (Thorrold et al. 1998, Kennedy et al. 2000, Campana and Thorrold 2001). Otoliths grow by the daily accretion of calcium carbonate in thin (e.g., 2–5 μm), concentric rings throughout the entire lifetime of a fish. Variation in watershed geology contributes to differences in elemental and isotopic composition of water that, in turn, directly affects the otolith chemical composition of resident fish (Kennedy et al. 2000). Strontium (Sr) substitutes for calcium without isotopic fractionation in biological materials (Kennedy et al. 2000, Campana and Thorrold 2001); therefore, the spatial variation in Sr isotope ratios, $^{87}Sr/^{86}Sr$, experienced by fish is recorded daily in the otolith increments. Otolith chemistry remains unaltered following deposition, and thus, the geochemical signature can be used to reconstruct ontogenetic habitat shifts or to distinguish individuals that originated in different geographical areas (Kennedy et al. 1997, 2000, 2002, Thorrold et al. 1998). By collecting otoliths from adult carcasses at the salmon nests, the final intended spawning location for each fish is precisely known, and factors that can bias straying estimates using alternative methods are negated (Quinn et al. 1991).

We studied a salmon population in Big Creek, a fourth-order tributary of the Middle Fork Salmon River (MFSR) in central Idaho, USA, which has high geologic heterogeneity and, consequently, high variation in stream water Sr isotopic values. Spawning habitat is characteristically patchy here (Isaak et al. 2003), and adult salmon returning to Big Creek tend to aggregate in six distinct spawning clusters (Fig. 1a). Located almost entirely in designated wilderness area, this basin encompasses some of the most pristine aquatic habitat in the contiguous United States, and each spring and summer, threatened *Oncorhynchus tshawytscha* (chinook salmon) begin navigating over 1000 river kilometers to access these natal rearing sites. Considering that major alterations have occurred along the mainstem migratory corridor, the life history diversity related to juvenile and adult migration behaviors expressed in these remnant populations has likely contributed to species perseverance despite, at times, drastic declines from historical abundances.

Though extensive efforts have been made to describe and quantify the drivers of population dynamics within Big Creek, the spatial structuring of this salmon population is incompletely understood. Previous studies on juvenile growth and survival, spawning habitat availability, and genetic structure have suggested the existence of possible (and sometimes conflicting) subpopulation structure within Big Creek. For example, significant differences in juvenile survival between the upper and lower basin (Zabel and Achord 2004) and marked differences in the timing of adult returns to these two areas suggest a spring (upper basin) and summer (lower basin) population of fish. However, the patchiness of spawning habitat (Isaak et al. 2003) and juvenile demographics are in contrast to genetic data that show fairly low genetic structuring within the adult chinook population at this spatial scale (Neville et al. 2006, Neville et al. 2007). Understanding the factors that determine individual straying behavior is critical for interpreting information on genetic variation, identifying relevant scales of population delineation, and quantifying the spatial considerations of practical conservation measures.

The objectives of our study were (1) to quantify the frequency of straying in a wild chinook salmon population; (2) to examine how individual condition, environmental factors, and early life history decisions influence straying occurrence; and (3) to determine the spatial scale over which straying occurs. At the *fine* scale, we considered straying any movement away from natal emergence clusters (i.e., equal to adults spawning <1 km away from natal areas). Alternatively, at the *coarse* scale, we used more conventional designations of straying and quantified the occurrence of adults spawning at a distance of ≥ 10 km from natal areas.

Methods

To establish baseline signatures for the watershed, 47 water and whole juvenile otolith samples from the mainstem and all major tributaries of Big Creek were collected over four years at multiple time periods relevant to juvenile chinook growth and analyzed for Sr isotopic ratios (Appendix A). Additional samples from neighboring sites within the greater MFSR basin were analyzed to account for potential source locations of straying fish originating outside of the Big Creek watershed. Water was collected in acid-washed polyethylene (HDPE) bottles in riffle areas just below the water surface and refrigerated as soon as logistical considerations allowed. Stream water was centrifuged to remove ≥ 0.45-μm particles, and Sr was separated using standard column chemistry. Sr isotopes ($^{87}Sr/^{86}Sr$) were analyzed using a Finnigan MAT 262 multi-collector thermal ionization mass spectrometer (TIMS; Thermo Scientific, Bremen, Germany) (Kennedy et al. 2002), and $^{87}Sr/^{86}Sr$ were normalized to $^{86}Sr/^{88}Sr = 0.1194$. Eighteen analyses of a National Institute of Standards and Technology (NIST) standard reference material (NBS-987) were

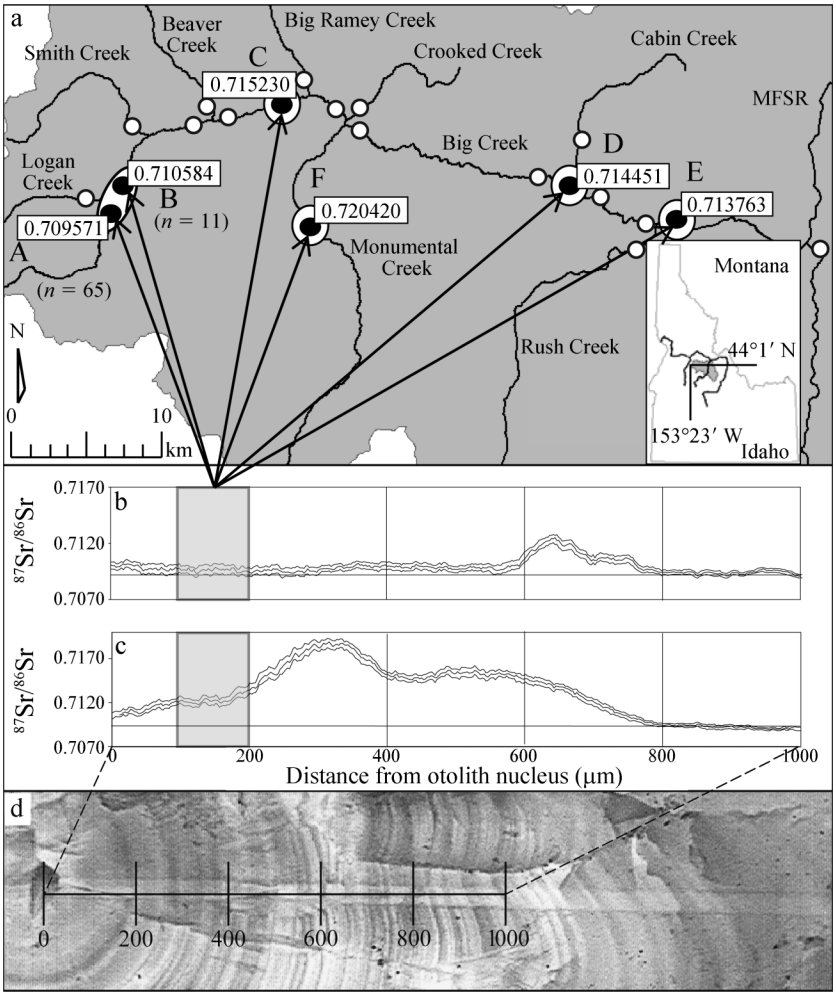

FIG. 1. Developing a baseline isotopic map for Big Creek, a fourth-order tributary of the Middle Fork Salmon River (MFSR) in central Idaho, USA, and determining natal origin of spawners (chinook salmon, *Oncorhynchus tshawytscha*) using otolith microchemistry. (a) Map of the Big Creek watershed. Water samples were collected seasonally and annually over three years from mainstem sites and major tributaries of Big Creek to establish baseline Sr isotopic ratios for the basin (small white circles; Appendix A). Circles (A–F) represent primary spawning clusters/potential natal source locations, with black depicting fine-scale analysis and white representing the coarse-scale analysis (corresponding mean $^{87}Sr/^{86}Sr$ values are shown in the boxes). All 76 carcasses were collected in sites A and B over four spawning seasons (sample sizes in parentheses), and all sites (A–F) represent possible natal source locations for spawning fish. (b, c) Otolith transect analysis output of an individual exhibiting (b) low and (c) high juvenile movement. The *x*-axis otolith measurement is representative of time in a fish's ontogeny, and the middle solid black line (mean ± SEM) depicts $^{87}Sr/^{86}Sr$ values. The shaded gray box overlays the ~100-μm window used to derive the mean $^{87}Sr/^{86}Sr$ value representing natal origin. The global marine value for modern seawater ($^{87}Sr/^{86}Sr = 0.70918$) is shown for reference, and Sr isotopic ratios stabilizing at this value indicate ocean residency. (d) Otoliths were polished until clear annuli were visible from the core to the outer edge.

completed during the duration of this study, yielding a $^{87}Sr/^{86}Sr$ ratio of 0.710240 ± 0.000014 (mean ± 2 SE). In order to compare water signatures to resident fish otolith values, juvenile chinook salmon were sampled during 2005 National Oceanic and Atmospheric Administration (NOAA) electrofishing surveys at the highest elevation salmon spawning region where the lack of juvenile immigration from other sites could be assured. TIMS analyses of these whole otoliths provided a high-resolution, temporally averaged confirmation of the otolith–water Sr isotope relationship for this spawning reach.

Otoliths were collected from adult chinook carcasses in the uppermost section of the watershed over four spawning seasons; during this time, salmon returns to Big Creek ranged from 127 to 628 spawners. The two adjacent spawning clusters in the upper basin have traditionally been considered and sampled as one continuous spawning group. However, significant geochemical variability between these nearly contiguous clusters allowed us to test whether factors that contributed to straying differed as a function of spatial scale, with fine scale (<1 km) quantifying straying between these sites and coarse scale (≥10 km) consid-

ering those straying events into this combined cluster from a greater distance. Sagittal otoliths were cleaned, mounted on glass microscope slides with thermoplastic resin, and polished on a lapping wheel using a series of alumina slurries. Polishing was stopped when clear growth rings were visible from the nucleus to the outer edge of each otolith (Fig. 1d).

We analyzed the $^{87}Sr/^{86}Sr$ ratios from the dorsal region of prepared otoliths using a Finnigan Neptune multi-collector (Thermo Scientific, Bremen, Germany) inductively coupled plasma mass spectrometer coupled with a New Wave UP-213 laser ablation sampling system (MC-LA-ICPMS; New Wave Research, Fremont, California, USA) (Outridge et al. 2002). A marine carbonate reference shell (assumed to be in isotopic equilibrium with modern seawater [$^{87}Sr/^{86}Sr = 0.70918$]) was used to evaluate the internal precision of our measurements. A daily correction factor was calculated based on deviations of the reference material from the global marine value, and $^{87}Sr/^{86}Sr$ values of each otolith sample were adjusted accordingly. The laser ablated material at a constant speed at a 90° angle from the sulcus beginning at the outer edge of the otolith and extending to the core. If clear rings were not present in this region, the area for analysis was adjusted to an area with increased resolution.

Natal origin of adult spawners was determined by calculating the mean value along each otolith transect that represented emergence and initial rearing location (Fig. 1b, c). The extent of this region was based on the location of hatch checks (dark bands on the otolith associated with embryonic hatching) of juvenile chinook salmon sampled in late summer from throughout the Salmon River and excluded areas that could potentially contribute maternally derived information to the analysis. Based on these values, we considered natal stream origin the area between 100 and 250 μm from the otolith core that remained stable over a ~100-μm window.

Analysis of variance (ANOVA, $\alpha \leq 0.05$) was used to compare mean Sr isotopic ratios of the six primary spawning/natal source locations. Tukey's honestly significant difference (HSD, $\alpha \leq 0.05$) was then used to determine where significant differences existed between sites (PROC GLM, SAS 9.2; SAS Institute 2008). Due to the relatively small sample size ($n = 30$), a single-factor linear discriminant function analysis (LDFA) with jackknife cross-validation was used to first create a calibration set from the water and juvenile otolith (where available) values and then assign posterior probability of group membership (natal origin) to each of the adult otolith samples based upon $^{87}Sr/^{86}Sr$ ratios (PROC DISCRIM, SAS 9.2; SAS Institute 2008). Differences between carcass locations and natal origins (as determined by the posterior discriminant function classifications) were used to determine the amount and spatial extent of straying in this system.

To discern the relative importance of individual condition and environmental variables and predict the probability of straying occurrence, we developed logistic regressions for a group of candidate models using R, including a global model and several reduced forms (R Development Core Team 2009). We evaluated each based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). Model variables included fish age (3, 4, or 5 years old), sex, and spawner density for the entire Big Creek Basin (low, medium, or high, where high densities can increase nest interactions but are likely to be a fraction of historic or saturated spawning levels) (Isaak et al. 2003; E. J. Hamann et al., *unpublished manuscript*). Additionally, the spatially explicit geochemical signatures recorded in otoliths allowed us to consider the effects of juvenile site fidelity (low vs. high) on straying occurrence, which was evaluated based on visual assessment of otolith transect outputs (see Fig. 1b, c, for an example of low and high juvenile movement). Dispersal was easily recognized as directional shifts in the isotopic signature, and we tested the hypothesis that high juvenile dispersal during the freshwater phase leads to increased straying occurrence as adults.

Results

Seasonal and annual variability in water signatures was minimal, and replicate samples did not deviate from the mean value for that site by more than 0.1%. Sr isotopic ratios varied significantly between the six primary spawning clusters (ANOVA, $F_{5,24} = 661.16$, $P < 0.0001$), and significant comparisons existed between all sites (Tukey's HSD, $\alpha \leq 0.05$; Appendix B).

The re-substitution and cross-validated error rate of the water data (the calibration set) using LDFA was 5.6%. Overall, our results show that at the fine scale, straying was relatively common in Big Creek (45%), but at the coarse scale, only 13% of the overall sampled population strayed into non-source locations. Fine-scale straying occurrence varied considerably between the two upper-basin sites, however, ranging from 40% in site A to 73% in site B (12% and 18% at the coarse scale at sites A and B, respectively; Table 1). The majority of straying salmon (71%) moved between the two upper-basin clusters, a minimum total distance of <1 km from natal emergence locations. Of the 34 fish that strayed into non-source locations to spawn, six originated in site E and strayed a total minimum distance of 26–29 km (depending on carcass location; Fig. 1a, Table 1).

Logistic regression indicated that at the fine scale, juvenile movement was the best predictor of straying occurrence followed by the model combining juvenile movement and sex. Likewise, at the coarse scale, juvenile movement and sex were the best predictors of straying occurrence, with male salmon 12 times as likely to stray as female fish (Table 2, Fig. 2, and Appendix C).

Discussion

Interest in the homing tendencies of organisms has historically focused on the sensory and behavioral

TABLE 1. Posterior classifications of adult chinook salmon, *Oncorhynchus tshawytscha*, to natal source habitat.

Parameter	Source location						Fine scale		Coarse scale	
	A	B	C	D	E	F	Salmon returning home (%)	Salmon straying (%)	Salmon returning home (%)	Salmon straying (%)
Carcass location A ($n = 65$)							*60*	40	88	12
Distance to source location (km)	0	<1	10	24	29	30				
No. carcasses	*39*	18	1	3	4	0				
Carcass location B ($n = 11$)							*27*	73	82	18
Distance to source location (km)	<1	0	7	21	26	27				
No. carcasses	6	*3*	0	0	2	0				
Total							55	45	87	13

Notes: Column headings A–F represent isotopically distinguishable juvenile source locations within Big Creek, Idaho, USA (see Fig. 1), and the row identifiers (A and B) are locations where adult carcasses were found in the stream with minimal postmortem movement. The fine spatial scale was defined as <1 km, and the coarse spatial scale was defined as distances >10 km. Fine-scale homing occurred when carcasses were found in the same location that was identified (via otolith microchemistry) as the juvenile natal rearing location (shown in italics).

mechanisms by which individuals find their way back to natal areas (Quinn 1997, Lohman et al. 2008). But, while salmon homing is thought to be guided by olfactory recognition of natal waters and sequential imprinting of waypoints learned during outmigration (Hasler et al. 1983), our results indicate that extensive juvenile movements potentially reduce the propensity of adult salmon to home accurately. Juvenile exploration and dispersal from natal areas can result in characteristic leptokurtic distributions of movement strategies, suggesting the existence of complex behavioral polymorphisms within populations (Paradis et al. 1998, Fraser et al. 2001, Selonen and Hanski 2006). For juvenile salmonids, a number of factors, including food availability, habitat quality, density, and competition contribute to whether individuals establish territories or explore multiple habitats during freshwater residency (Grant and Noakes 1987, Gowan et al. 1994, Achord et al. 2003). To the extent that juvenile movements may be density dependent (Steingrímsson and Grant 1999), our results suggest a mechanism to regulate the exploration of new habitats as adults. Further, as human-mediated changes to river landscapes impact the connectivity, movement strategies, and migratory timing of juvenile salmon, there are likely to be indirect effects on the propensity to stray at the adult stage. At the individual scale, strays may have lower reproductive success (Lin et al. 2008), potentially resulting from inadequate or inappropriate habitats for offspring survival, limited mating options, or missed reproductive synchrony. However, straying of individuals confers benefits at the population scale through the support of metapopulation structure (Hanski 1998), the maintenance of genetic diversity (Neville et al. 2006), and colonization of newly opened habitats (Hendry et al. 2004).

In addition to juvenile movement, sex was a key factor influencing straying occurrence in this population. The occurrence of sex-biased patterns of dispersal can be common and is often related to specific mating systems (e.g., Selonen and Hanski 2006). However, the effect of sex on straying of migratory individuals has received much less attention. Male-biased straying has been

TABLE 2. Model selection results for logistic regression analysis of factors affecting straying occurrence at two spatial scales.

Model number	Candidate model variables	p†	Log likelihood	AIC_c	ΔAIC_c‡	w_i
Fine scale						
1	juvenile movement	2	−43.5	91	0	0.47
2	sex, juvenile movement	3	−43.1	93	2	0.22
8	full (density, sex, age, juvenile movement)	5	−42.3	100	9	0.01
9	null	1	−51.4	105	14	0
Coarse scale						
1	sex, juvenile movement	3	−20.9	48	0	0.62
5	full (density, sex, age, juvenile movement)	5	−19.6	54	6	0.03
12	null	1	−29.5	61	13	0

Notes: Independent variables included in each candidate model are listed for both the fine and coarse scales. The ranking metric (ΔAIC_c) is the difference between the AIC_c of a candidate model and the one with the lowest AIC_c, and values between 0 and 2 indicate substantial support for a model being the best approximating model. Akaike weights (w_i) represent the strength of evidence in favor of model i being the best model.

† Number of parameters.

‡ Models are ranked from most plausible ($\Delta AIC_c = 0$) to least plausible.

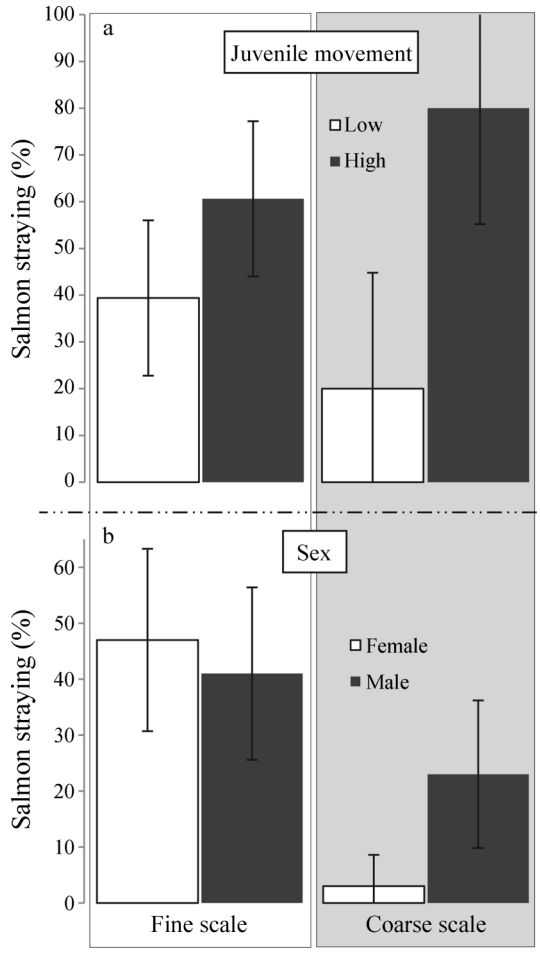

FIG. 2. The relative occurrence of adult chinook salmon straying in relation to (a) dispersive movements as juveniles and (b) sex at two spatial scales. Top logistic regression models indicated that both juvenile movement (high) and sex (male) were the best predictors of straying occurrence for salmon. Results at the fine spatial scale (straying at <1 km scales) are shown as the left-hand pair of histogram bars; results at the coarse spatial scale (>10 km) are shown as the right-hand pair of histogram bars. Straying results as a function of juvenile dispersal [panel (a)] represent all straying adults at each spatial scale in the study, whereas results as a function of sex [panel (b)] represent the percentage of either females or males within the study population that strayed at the two spatial scales. Error bars represent 95% confidence intervals.

documented by transplanted salmon (Hard and Heard 1999) and suggested for salmon in the MFSR basin based upon genetics (Neville et al. 2006). Females typically choose a single nesting location in the stream in which to lay their eggs (Quinn 2005), and subsequent movements may be constrained by their protection of those nests until death. In contrast, forays into non-source habitats by males may improve access to females, increase mating opportunities, and reduce competition (Hard and Heard 1999).

Our study design assumed that a basin-wide sampling regime was sufficient to identify strayers and the spatial scale at which straying occurs. The assertion that our methods represent an improvement over conventional tagging techniques assumes that extra-basin straying (beyond the chemical signatures in our training set) is minimal, otherwise our approach might significantly underestimate out-of-basin straying. However, the presence of undetected strays from outside the Big Creek basin would be unlikely, and none of the collected carcasses demonstrated evidence of hatchery origin (e.g., internal tags or clipped adipose fins). Previous work by Neville et al. (2006) identifies the existence of a within-basin genetic structure, which supports our findings of homing at the tributary (Big Creek) scale. The largest genetic differentiation in this system occurs between the lower and upper MFSR subbasins (Neville et al. 2006), and Big Creek salmon are less closely related to other salmon spawning in the tributary streams of the lower MFSR subbasin.

However, our data suggest that long-distance straying (>80 km) may occur in one out of our 76 study individuals. Upper Big Creek (site A) has the least radiogenic signature within the basin (lowest $^{87}Sr/^{86}Sr$), and a single carcass exhibited an otolith isotopic ratio that was significantly lower (i.e., greater than three standard deviations from the mean) than the other 38 fish assigned to this cluster. Classifying this fish as a stray does *not* significantly alter our straying rates, but it does significantly increase the spatial scale over which we contend rare straying events may occur for wild chinook salmon (80–200 km). This signature is consistent with Sr isotope values for streams draining predominantly Batholith geologies in the upper sections of the MFSR (Bear Valley ($^{87}Sr/^{86}Sr = 0.708231 \pm 0.00001$ [mean ± 2 SE]; >100 km) and Elk ($^{87}Sr/^{86}Sr = 0.708287 \pm 0.00001$; >100 km) or the South Fork of the Salmon River ($^{87}Sr/^{86}Sr = 0.708087 \pm 0.00004$; >180 km; see Table 1).

While knowledge of the spatial scale at which migratory fish populations home accurately is limited and unresolved (Quinn 2005, Quinn et al. 2006), our findings offer definitive support for the ability of wild chinook salmon to distinguish natal sites with high spatial precision while providing clearer definition to the scale at which straying occurs. Fine-scale straying was common in Big Creek, occurring with relatively high frequency between the adjacent spawning clusters in the upper basin. Further, the existence of straying varied between the two sites in the upper basin where carcasses were collected, with more fine-scale straying occurring from upstream origins to downstream spawning than the reverse pattern. At river reaches of increasingly fine scale, it is likely that final spawning decisions may be determined by local-scale site factors rather than precise homing ability, and it remains possible that salmon in this study accurately recognized natal scents but chose alternative sites in the nearby cluster based on physical habitat attributes conducive to reproductive success (Hendry et al. 1995, Quinn et al. 2006).

The maintenance of species-level life history diversity is essential for providing metapopulation stability, ecosystem integrity, and resilience against climate-based range shifts (Parmesan 2006, Schindler et al. 2010). Our results suggest that for migratory organisms, behavioral diversity expressed at the individual scale across life cycle stages may make an equally important contribution to species stability and provide an important mechanism by which portfolio effects can occur within metapopulations. Quantifying this diversity across broader spatial scales may serve as an integral piece of successful conservation efforts. Regardless of the spatial scale over which individuals strayed, each salmon in this study successfully returned to Big Creek and had the opportunity to reproduce. Although the significance of drawing from a diverse pool of juvenile movement strategies has been demonstrated for other taxa (Paradis et al. 1996, Fraser et al. 2001, Selonen and Hanski 2006), the link to potentially adaptive adult behaviors has not previously been established. For threatened and endangered species, understanding and preserving multiple behavioral life history strategies may be necessary to ensure species resilience in the face of continued anthropogenic threats. Ultimately, the viability of these extant migratory populations will be determined not only by whether current impacts fall within an acceptable range of historic physical and climatic conditions, but also by whether conservation and management practices have preserved enough behavioral diversity to adapt to changing environments (Waples et al. 2009).

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Supplemental Material

Appendix A

Site specific information on sample analysis and Sr isotope values (*Ecological Archives* E093-064-A1).

Appendix B

Cluster analysis and source site designation of individual chinook salmon (*Ecological Archives* E093-064-A2).

Appendix C

Parameter estimates (juvenile movement and sex) for models predicting straying occurrence for adult chinook salmon (*Ecological Archives* E093-064-A3).