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Rates of straying by hatchery-produced Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) differ among species, life history types, and populations

Peter A.H. Westley, Thomas P. Quinn, and Andrew H. Dittman

Abstract: Here we ask whether straying differs among species, life history types, and populations of adult hatchery-produced Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) in the Columbia River basin. Previous estimates of straying have been confounded by various factors influencing the probability of individuals returning to non-natal sites (e.g., off-station releases), whereas analyses undertaken here of nearly a quarter million coded-wire tag recoveries control for these factors. Our results revealed large and generally consistent differences in the propensity to stray among species, life history types within species, and populations. Paired releases indicated that (*i*) Chinook salmon (*Oncorhynchus tshawytscha*) strayed more (mean population range 0.11%–34.6%) than coho salmon (*Oncorhynchus kisutch*) (0.08%–0.94%); (*ii*) ocean-type Chinook (5.2%–18.6%) strayed more than stream-type Chinook (0.11%–10%); and Chinook salmon (0.90%–54.9%) strayed more than steelhead (0.30%–2.3%). We conclude these patterns are largely the result of species-specific behavioral and endocrine factors during the juvenile life stages, but analyses also suggest that environmental factors can influence straying during the adult upstream migration.

Résumé : Nous voulions savoir si l'égarement varie selon l'espèce, le type de cycle biologique et la population chez des saumons du Pacifique (*Oncorhynchus* spp.) et des truites arc-en-ciel (*Oncorhynchus mykiss*) adultes issus d'écloseries, dans le bassin du fleuve Columbia. Des estimations antérieures de l'égarement étaient limitées par plusieurs facteurs de confusion ayant une incidence sur la probabilité que les individus retournent à des sites non natals (p. ex. lâchers hors station), alors que les analyses que nous avons menées de près d'un quart de million de micromarques codées récupérées tiennent compte de ces facteurs. Nos résultats révèlent d'importantes différences généralement cohérentes entre espèces, types de cycle biologique au sein d'une même espèce et populations sur le plan de la propension à l'égarement. Des lâchers appariés ont indiqué que (*i*) les saumons quinnats (*Oncorhynchus tshawytscha*) s'égaraient plus (fourchette des moyennes par population : 0,11 % – 34,6 %) que les saumons coho (*Oncorhynchus kisutch*) (0,08 % – 0,94 %), (*ii*) que les saumons quinnats de type océanique s'égaraient plus (5,2 % – 18,6 %) que ceux de type dulcicole (0,11 % – 10 %) et (*iii*) que les saumons quinnats (0,90 % – 54,9 %) s'égaraient plus que les truites arc-en-ciel (0,30 % – 2,3 %). Nous concluons que, si ces distributions découlent en bonne partie de facteurs comportementaux et endocriniens propres à chaque espèce durant les stades juvéniles du cycle biologique, les analyses suggèrent également que des facteurs environnementaux peuvent influer sur l'égarement durant la montaison des adultes. [Traduit par la Rédaction]

Introduction

The ecology, evolution, and management of salmonid fishes are inextricably shaped by homing to natal sites by adults for reproduction, though some individuals stray and spawn in non-natal areas (Klemetsen et al. 2003; Quinn 2005; Jonsson and Jonsson 2011). Theory predicts that variation in homing and straying should reflect the dynamic balance of interacting fitness costs and benefits (Hendry et al. 2004). Homing is beneficial to the extent that it increases the likelihood of finding suitable habitat or mates, familiarizes individuals with local breeding conditions, returns locally adapted individuals to well-suited environments, improves access to parental resources, and minimizes costs of movement. In contrast, straying facilitates colonization of newly accessible habitats (Anderson and Quinn 2007; Milner et al. 2008; Pess et al. 2012) and buffers against the loss of all progeny in the case of catastrophic events in the home river (Leider 1989; Quinn et al. 1991).

There are two general views of straying (reviewed by Quinn 1984, 2005; Hendry et al. 2004). Homing to the natal site is mediated by olfactory recognition of home stream odors learned by juveniles prior to seaward migration (Hasler and Scholz 1983). Straying may reflect "proximate" mechanisms such as a failure to home resulting from incomplete learning of odors during juvenile stages, inability to retain the odor memories, failure to detect or respond to odors as adults, or physical incapacity to reach the home site. An alternative "ultimate" view is that straying may represent adaptive behavior patterns, allowing colonization and buffering against environmental change. Moreover, straying occurs both into and out from populations and can thus be viewed from the perspective of the recipient and donor populations (reviewed by Keefer and Caudill 2012). Mechanisms and subtleties of definitions notwithstanding, straying of hatchery-produced fish and the subsequent ecological and genetic interactions with wild individuals on the spawning grounds are mounting conservation challenges (Araki et al. 2008; Kostow 2009; Brenner et al. 2012).

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Evidence suggests that rates of straying can be "anomalously" high in heavily modified watersheds (Keefer et al. 2008b; Johnson et al. 2012), yet uncertainty in what constitutes "normal" rates of straying severely impedes the ability to assess how disturbances may affect straying.

Reviews of straying report marked variation both within and among species (e.g., Quinn 1993; Hendry et al. 2004; Keefer and Caudill 2012), but these data are confounded by many sources of variation, including, but not limited to, the use of different tagging methods, comparisons of population amalgamations rather than discrete units, the incorporation of experimental groups (e.g., fish reared at one site and released elsewhere), transported and volitionally migrating individuals, and the comparison of local to nonlocal populations. Thus, the extent to which straying varies within and among species remains unclear, which underscores fundamental knowledge gaps in the understanding of straying as a biological phenomenon. Here we address this knowledge gap by testing predictions rooted in species-specific life histories with analyses of hundreds of paired hatchery releases that control for factors that influence straying.

In this paper we asked — if all else is equal — do species of Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) stray from natal sites at different rates, and to what extent do juvenile or adult life history patterns contribute to straying? Our specific objectives were to (i) quantify the relative rates of straying among species and life history types within species released in the same year from the same locations, (ii) quantify the extent to which straying varies across populations and identify hatcheries that produce consistently high or low rates of straying, (iii) assess the correlation in straying between species and life history types within years, based on comparisons from groups released in the same year as smolts (indicative of juvenile life history effects or environmental conditions during the seaward journey) or groups that returned as adults in the same year (evidence for adult life history effects or environmental conditions during the return journey).

Species descriptions and predictions

Here we briefly highlight life history differences used to derive our predictions concerning straying, but for more comprehensive reviews see Groot and Margolis (1991), Busby et al. (1996), and Quinn (2005). Chinook salmon (*Oncorhynchus tshawytscha*) exhibits two distinct life histories based on the age at which juveniles migrate to sea (Healey 1991): "ocean-type" (subyearling migrants) and "stream-type" (yearling migrants). These life history types correlate with growth opportunity; the ocean-type dominates in the southern part of the range and the stream-type to the north and in higher elevations and greater distances from the mouths of watersheds (Taylor 1990). Coho salmon (*Oncorhynchus kisutch*) and steelhead, like stream-type Chinook salmon, typically spend at least one full year in fresh water before transitioning to smolts (Sandercock 1991; Busby et al. 1996).

The patterns of juvenile migratory behavior and corresponding timing of imprinting differ among species and life history types (Quinn 2005). Increases in the levels of the hormone thyroxine have been mechanistically linked to the process of olfactory imprinting (Hasler and Scholz 1983; Dittman et al. 1996). We compiled data from the literature reporting seasonal changes in the levels of plasma T4 (Supplementary Table S1[1]), along with data on the seasonal use of estuaries by juvenile salmonids (Rich 1920; Dawley et al. 1986; Healey 1991; Fig. 1). The general patterns revealed from this literature review were (i) ocean-type Chinook salmon exhibit a relatively prolonged temporal period of physiological changes associated with smolting (Zaugg et al. 1985; Whitman 1987) compared with the condensed parr–smolt transition in stream-type Chinook salmon (Beckman et al. 1999), coho

salmon (Dickhoff and Sullivan 1987), and steelhead (Dickhoff et al. 1982), and (ii) greater use of estuaries by juvenile ocean-type Chinook salmon (suggesting slower migration to sea) compared with stream-type Chinook salmon, coho salmon, and steelhead smolts (Fig. 1).

In addition to differences in aspects of the juvenile life history, these species also differ in timing of adult migrations back to fresh water, maturation status upon freshwater entry, and in age at maturity. Most stream-type Chinook salmon (spring Chinook) in the central and southern part of their North American range and steelhead (summer-run) enter fresh water in an early state of maturation, whereas ocean-type Chinook salmon (fall Chinook), winter-run steelhead, and coho salmon enter in a more advanced maturation state. An additional consideration is that both types of Chinook salmon and steelhead exhibit more variation in age at maturity than do coho salmon, which was hypothesized to vary inversely with straying (Quinn 1984).

Given these life history differences, we predicted that ocean-type Chinook salmon would stray at relatively higher rates than stream-type Chinook salmon, coho salmon, or steelhead if sharp spring peaks in plasma T4 and rapid migration are linked to imprinting. In contrast, if straying is more associated with aspects of the adult life history, then one might expect differences to reflect timing of upstream migration (ocean-type Chinook salmon should be more similar to coho salmon, and summer-run steelhead more similar to stream-type Chinook salmon), stage of maturation upon freshwater entry (ocean-type Chinook = coho salmon, summer-run steelhead = stream-type Chinook), and variation in age of maturity (coho salmon < ocean-type and stream-type Chinook salmon and summer-run steelhead).

Methods

Coded-wire tag (CWT) data

We assembled tagging data from the Regional Mark Information System (RMIS, available from http://www.rmpc.org), which is maintained by the Regional Mark Processing Center of the Pacific States Marine Fisheries Commission. Since their invention in the 1960s (Jefferts et al. 1963), CWTs (~1 mm sections of coded magnetized wire that are inserted into the cranial cartilage of juveniles) have revealed stock structure, marine distributions, and smolt–adult survival in salmonids (Quinn 2005). Because the locations of release and subsequent recovery are recorded, CWT data have also played a prominent role in studies of homing and straying (among the first examples, see Quinn and Fresh 1984). We systematically searched the RMIS database for hatcheries that produced multiple species or life history types within the Columbia River basin. Our focus on the Columbia River was motivated by the extensive hatchery production and long-term data in the region (reviewed by Hatchery Reform Group 2009), as well as widespread recovery efforts in hatcheries and spawning grounds. Prior to filtering the tag codes for specific criteria (see below), there were 445 recovery locations in the database we assembled (285 hatchery sites and facilities and 160 spawning ground sites). Such an extensive recovery effort would be impossible in more remote areas and is critical because the ability to detect strays depends on the search effort in non-natal sites.

We utilized freshwater recoveries in hatcheries and on spawning grounds and excluded individuals recovered at sea or harvested in-river, as these fish were intercepted while still en route to breeding areas. We combined associated release data for recovered tag codes and retained releases for analyses that met all the following criteria:

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[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2012-0536.

Fig. 1. Patterns of migration and endocrine processes (plasma thyroxine level) associated with imprinting in generalized cohorts of hatchery-produced ocean-type and stream-type Chinook salmon, coho salmon, and steelhead. Patterns characterize trends observed at the aggregate species or life history level and are not intended to imply that individual fish necessarily demonstrate these patterns. The trends depicted here were populated with migration data from Dawley et al. (1986) and plasma T4 data from references in the online supplementary data[1].
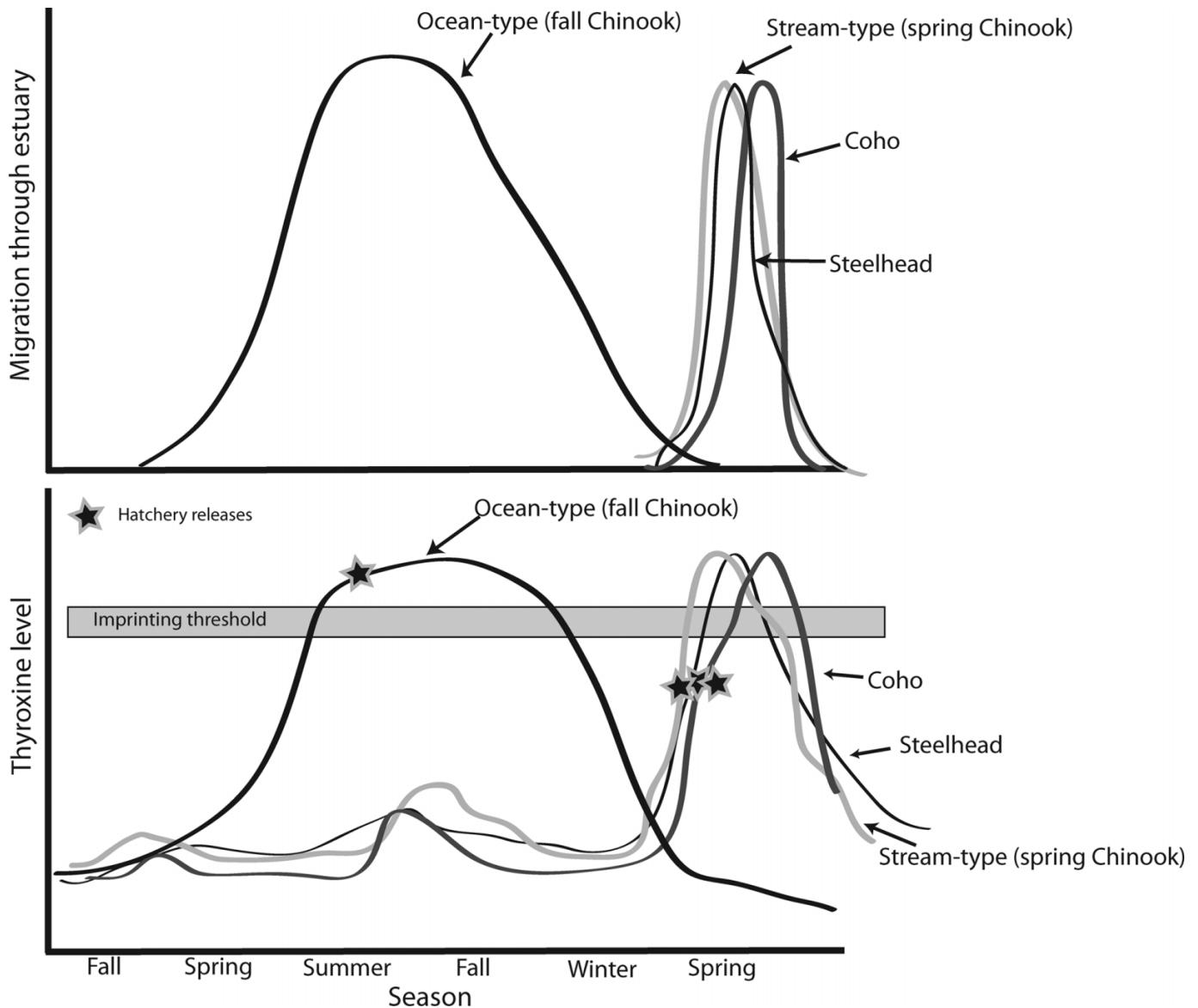
(1) **Paired releases of species or life histories in the same years**, as straying varies year-to-year within a location (Shapovalov and Taft 1954; Quinn and Fresh 1984; Quinn et al. 1991; Labelle 1992). Locations that yielded at least 2 years of common releases for different species or life history types (ending in release year 2006 to allow return of dominant age classes for all species) were considered for analyses.

(2) **Station rearing and release**, because individuals reared in one location and released at another tend to stray at higher rates than individuals reared and released on site (Solazzi et al. 1991; Pascual et al. 1995; Candy and Beacham 2000; Dittman et al. 2010).

(3) **"Local" broodstock only**, as the genetic control of straying is not well known (Carlson and Seamons 2008), and transplanted individuals, in some cases, continue to home to ancestral locations despite being spawned, reared, and released elsewhere (McIsaac and Quinn 1988). We acknowledge that "local" broodstock may in some cases be genetic amalgama- tions resulting from historical hatchery transfers or may contain strays from other areas because individuals are typically spawned without knowledge of their origin (http://www.hatcheryreform.us/hrp/reports/appendixe/welcome_show.action).

(4) **No experimental releases**, as experimental manipulation can artificially increase straying (e.g., Dittman et al. 1996). All releases that were designated as "experimental" in the RMIS database were excluded from analysis.

Operational definition of "stray"

There is considerable debate on how to define straying (reviewed by Keefer and Caudill 2012), resulting in part from variation in temporal and spatial scales used in different studies (e.g., compare scales of examination between Labelle 1992 and Hamann and Kennedy 2012). Additionally, migrating adults — especially in species with complex life histories — may spend substantial amounts of time in non-natal locations (e.g., Chinook salmon or

steelhead holding in a thermal refuge), before moving to a breeding site (e.g., Berman and Quinn 1991; Keefer et al. 2009). These "temporary strays" differ from "permanent strays" that are last detected and presumed to have spawned in non-natal areas. Our estimates of straying constitute permanent straying because CWT data only provides information on the final recovery location and because individuals in hatcheries are likely spawned. Thus, for each recovery we defined individuals as strays if they were recaptured outside the river basin of their release, a spatial scale that generally conforms to the local population level and scale for conservation (http://www.hatcheryreform.us). This definition is consistent with previous studies using CWT data in the Columbia River basin (e.g., Quinn and Fresh 1984; Pascual et al. 1995) and reduces ambiguity between fine-scale straying from habitat and spawning site selection (Dittman et al. 2010; Cram et al. 2012). We note, however, that salmon entering a hatchery often have no opportunity to leave, as would be the case for fish entering a non-natal tributary as part of the migration process. This may result in some elevation in straying estimates from hatcheries relative to spawning grounds, though the extent of this bias is unclear (Quinn et al. 1991; Griffith et al. 1999).

Data analysis

For each hatchery, we calculated the stray rate (r) of individuals released in the same year and same rivers as

$$(1) \quad \frac{\sum \text{tags recovered as strays from hatchery } (i) \text{ and release year } (j)}{\sum \text{all tags recovered from hatchery } (i) \text{ and release year } (j)}$$

where tag recoveries represent expanded estimates to account for sampling effort. These estimates, provided in the RMIS database, were calculated as aR_0, where a is the sampling expansion factor (total sample/sample examined for tags), and R_0 is the observed number of tags in the sample (Nandor et al. 2010). As our focus was on rates per se, it was not necessary to expand recoveries for variation in the proportion of released individuals tagged with CWTs, though efforts to quantify the total number of strays produced from a given year of release would need to take this into account (e.g., Clarke et al. 2011).

To test the hypotheses that rates of straying differ (i) among species, (ii) between life history types within species, and (iii) among populations, we fit a series of logistic regression models where the response variable (r) was weighted by total number of tag recoveries. Combinations of explanatory variables were then used to assess the support for each model in a selection framework. Our general approach was to compare the performance of models that included species, life history, and hatchery population predictors (categorical) versus those that did not. We also explored annual variation in straying by including the year of release as a fixed factor. Additionally, we explored the consistency of species or life history patterns among years by including year interactions. To account for overdispersion common in proportional data, we fit models with quasibinomial error structure and logit link. Model selection with QAICc was conducted with the AICcmodavg package (Mazerolle 2012) in R 2.15. Based on data structure and availability, we conducted separate analyses for comparisons between Chinook salmon and coho salmon, ocean-type and stream-type Chinook salmon, and Chinook salmon and steelhead.

Spearman rank correlations (to account for nonparametric data) were used to test the association of stray rates between species and life history types produced by given hatcheries and to test whether rates of straying, paired by release year or return year, were correlated among species or life history types. For correlational analyses, we based our interpretation of significance on $\alpha = 0.05$.

We modified eq. 1 above and calculated r based on recoveries returning as adults in the same year ("run year" in the RMIS database) to explore the potential for factors during the return migration to influence straying. The weight of other predictions concerning the adult life history (e.g., influence of variation in age at maturity) was assessed qualitatively given patterns in the data.

Results

No hatchery was identified that produced both life history types of Chinook salmon, as well as coho salmon and steelhead. However, seven hatcheries (Cowlitz River, Elochoman River, Fallert Creek, Kalama Falls, Lewis River, Toutle River, and Washougal River) in the lower Columbia River reared and released Chinook salmon and coho salmon, and three of those (Cowlitz, Fallert, and Kalama) produced both stream- and ocean-type Chinook salmon (Fig. 2). The release of Chinook salmon (an ocean-type lineage) as yearlings and subyearlings from the Lyons Ferry hatchery provided another opportunity to compare straying among life histories within Chinook salmon. Releases from Dworshak National Fish Hatchery, Lyons Ferry Fish Hatchery, and the Umatilla Hatchery provided comparisons between summer-run steelhead (freshwater maturing) and Chinook salmon (Fig. 2).

Species-specific straying

Chinook versus coho

Our compiled database of stray rates between Chinook salmon and coho salmon yielded 186 870 recoveries of 34 207 055 tagged individuals (62% coho, 8% ocean-type Chinook salmon, and 30% stream-type Chinook salmon; Table S2[1]). These releases also included many untagged fish (an additional 71 652 252 coho, 163 810 931 ocean-type Chinook salmon, and 8 478 773 stream-type Chinook salmon; Table 1). Data pooled across years and hatcheries revealed the highest straying in ocean-type Chinook salmon (grand mean 15.3%), intermediate in stream-type Chinook salmon (4.4%), and lowest in coho (0.52%), with the rank pattern consistent within locations (i.e., ocean-type Chinook salmon > stream-type Chinook salmon > coho salmon; Table 1). Model selection provided clear support for differences between species (Table 2a), which were generally evident in paired releases. Coho salmon strayed less than stream-type Chinook salmon or ocean-type Chinook salmon in 75% ($n = 52$) and 95% ($n = 66$) of paired releases, respectively.

Chinook versus steelhead

A higher percentage of Chinook salmon strayed than steelhead (15.9% versus 1.2%, based on recoveries of 11 181 530 and 3 843 108 tagged individuals, respectively; Table 3; Table S3[1]). However, stream-type Chinook salmon released in the Umatilla River strayed at exceedingly high levels (mean = 54.9%). Given the potential for data from this hatchery to drive interpretation, we conducted parallel analyses with only data from Dworshak and Lyons Ferry facilities (Table 2c), but still reached similar conclusions (Table 2d). Model selection, with or without the Umatilla data, indicated that Chinook salmon strayed more often than did steelhead (Tables 2c, 2d). Chinook salmon strayed at higher rates than steelhead in 66% of the 39 releases within a year (including Umatilla data). After excluding the Umatilla releases, 59% of 32 release year comparisons still indicated higher straying by Chinook salmon.

Life history specific straying

Ocean-type versus stream-type Chinook salmon

Patterns of recovery from 5 678 241 and 8 766 144 tagged ocean-type and stream-type Chinook salmon, respectively, from the Cowlitz River, Fallert Creek, and Kalama Falls hatcheries indicated consistently higher straying by ocean-type Chinook salmon than stream-type Chinook salmon (Table 4; Supplementary Table S4[1]). In

Fig. 2. Map of study region showing locations of release hatcheries used in analyses. In ascending distance from the mouth of the Columbia River: 1, Elochoman River; 2, Cowlitz River; 3, Toutle River; 4, Fallert Creek; 5, Kalama Falls; 6, Lewis River; 7, Washougal River; 8, Umatilla River; 9, Lyons Ferry; 10, Dworshak NFH. Adapted from Quinn (2005) and reprinted by permission of the University of Washington Press.
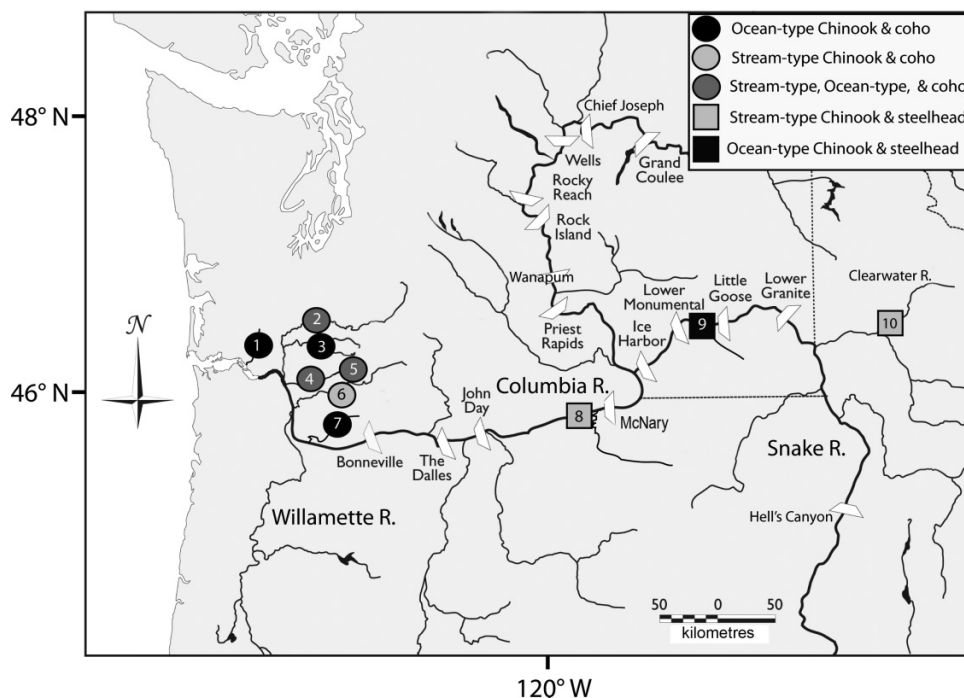

Table 1. Paired comparisons of Chinook salmon versus coho salmon stray rates (%) from individuals reared and released at the Cowlitz, Elochoman, Fallert Creek, Kalama, Lewis, Toutle, and Washougal hatcheries in the Columbia River basin, USA.

			Release data				Tag Recoveries				
Location	Species	Release years	Day of year	Length	Mass	Total released	Total tagged	Home	Stray	Avg. % stray	CV
Cowlitz	Ocean-type Chinook	1982–1984, 1986–1995, 1999–2006	172 (39)	82 (5)	8.1 (5.4)	130 406 609	5 368 258	6 577	248	5.2	0.9
	Stream-type Chinook	1974, 1982–1989, 1991–1996, 1999–2006	92 (44)	172 (25)	69.9 (23.2)	14 868 644	7 478 055	39 010	56	0.11	1.6
	Coho	1974, 1982–1989, 1991–1996, 1999–2006	125 (8)	177 (25)	27.9 (4.5)	46 662 790	3 672 665	28 240	27	0.08	1.7
Elochoman	Ocean-type Chinook	1997–2006	166 (9)	84 (4)	6.7 (0.9)	20 275 004	1 643 337	1 011	509	34.6	0.3
	Coho	1997–2006	114 (12)	138 (5)	31.6 (2.9)	2 327 080	694 673	2 371	21	0.94	0.9
Fallert	Ocean-type Chinook	1995–2006	174 (8)	78 (4)	5.9 (0.91)	10 805 332	1 152 336	1 581	347	18.6	0.6
	Stream-type Chinook	1995–2006	82 (13)	153 (27)	63.2 (15.2)	2 661 138	1 655 146	2 992	211	10.0	1.4
	Coho	1995–2006	114 (8)	141 (15)	33.1 (4.1)	1 371 485	415 407	3 400	21	0.73	1.4
Kalama	Ocean-type Chinook	2000–2006	176 (8)	80 (1)	6.4 (1)	2 510 852	627 702	1 335	266	13.9	0.4
	Stream-type Chinook	2000–2003, 2005–2006	67 (2)	160 (8)	53.0 (6.8)	1 463 627	1 419 872	4 167	167	4.6	1.0
	Coho	2000–2006	104 (5)	136 (3)	31.4 (4.4)	461 767	459 925	3 726	15	0.93	1.1
Lewis	Stream-type Chinook	1994–2006	73 (12)	139 (15)	34.7 (17.2)	2 246 671	2 208 234	8 283	280	2.8	0.9
	Coho	1994–2006	122 (22)	139 (15)	31.5 (14.1)	20 028 008	3 513 722	66 513	117	0.21	1.4
Toutle	Ocean-type Chinook	1997–1999, 2002–2006	185 (11)	83 (5)	5.9 (0.68)	5 464 243	897 403	927	56	5.8	1.0
	Coho	1997–1999, 2002–2006	131 (10)	142 (3)	31.9 (2.6)	11 398 390	1 842 672	8 618	28	0.4	1.8
Washougal	Ocean-type Chinook	1998–1999, 2001–2006	184 (13)	86 (2)	8.8 (0.95)	4 950 738	912 811	1 915	370	13.9	0.6
	Coho	1998–1999, 2001–2006	114 (8)	134 (4)	33.59 (2.5)	246 843	245 047	3 412	53	0.4	0.9

Note: Release years, day of year (SD in parentheses), average length (mm, SD), average mass (g, SD), total released, and total tagged are shown. The number of tags recovered at home and as strays was expanded to account for sampling. Average stray rate was calculated for each paired release year comparison and shown with the coefficient of variation (CV).

Table 2. Logistic regression models comparing rates of straying between (*a*) Chinook salmon and coho salmon, (*b*) ocean-type and stream-type Chinook salmon, and (*c*) Chinook salmon and summer steelhead (including data from the Umatilla River) or (*d*) excluding data from the Umatilla.

Predictors	K	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	Log-likelihood
(*a*) Chinook versus coho					
Year, location, species, life history	34	559	0	1	−239
Year, location, species	33	722	163	0	−322
Year, species	27	1 336	777	0	−637
Year × species	51	1 336	807	0	−618
Year, location, life history	33	1 544	985	0	−733
Location	8	1 614	1 054	0	−738
Species	3	1 770	1 211	0	−882
Year	26	2 492	1 933	0	−1 217
Life history	3	2 758	2 199	0	−1 376
Null	1	60 959	60 399	0	−30 478
(*b*) Ocean-type versus stream-type Chinook					
Location, life history	5	275	0	1	−132
Year, location, life history	27	315	40	0	−116
Year, location	26	471	195	0	−196
Location	4	477	201	0	−264
Year, life history	25	500	225	0	−213
Year × life history	47	569	294	0	−167
Life history	3	590	315	0	−292
Year	24	777	502	0	−353
Null	1	14 089	3 814	0	−7 043
(*c*) Chinook versus steelhead (including Umatilla)					
Year, location, species, smolt age	23	233	0	1	−82
Year, location, species	21	295	62	0	−117
Location	4	444	210	0	−217
Year, species	19	755	521	0	−351
Year × species	35	799	556	0	−412
Smolt age	4	891	657	0	−441
Species	3	1 002	768	0	−497
Year	18	1096	782	0	−523
Null	1	12 364	12 131	0	−6 181
(*d*) Chinook versus steelhead (excluding Umatilla)					
Year, location, species, smolt age	22	185	0	1	−56
Year, location, species	20	224	38	0	−80
Year, species	19	248	63	0	−81
Year	18	263	78	0	−105
Species	3	318	133	0	−156
Location	3	319	134	0	−156
Smolt age	4	322	136	0	−157
Year × species	35	349	163	0	−82
Null	1	11 987	11 766	0	−5 992

Note: Models are listed in descending order from most to least parsimonious.

83% of 40 paired comparisons, stream-type Chinook salmon straying rates were lower than ocean-type Chinook salmon released in the same location in the same year.

Subyearling versus yearling smolt age in ocean-type Chinook salmon

Stray rates of yearling groups (modified life history) were 2.5 times the rate of straying by groups released as typical subyearlings (Table 4) from the Lyons Ferry location (the only location in our database to release ocean-type Chinook as yearlings). Models that included a categorical predictor for smolt age (yearling or subyearling) were heavily favored (Tables 2*c*, 2*d*), indicating a difference among groups.

Population-specific straying and correlations among populations

Populations of coho salmon (Fig. 3*a*), Chinook salmon (Figs. 3*b*, 3*c*, 4*a*, 5*a*), and steelhead (Fig. 5*a*) differed significantly in the rate of straying, evidenced by stronger support of models that included a population term (Table 2). The average rate of straying

was positively correlated among populations of Chinook salmon and coho salmon (Fig. 3*d*); some locations tended to produce more strays than others irrespective of species. The Spearman rank correlation coefficient was statistically significant between hatcheries producing ocean-type Chinook salmon and coho salmon (*n* = 6, Spearman's ρ = 0.94, *p* = 0.01), but despite a high correlation coefficient, this was not significant between hatcheries producing stream-type Chinook salmon and coho salmon (*n* = 4, ρ = 0.8, *p* = 0.33). The average rates of straying from hatcheries producing Chinook salmon and steelhead were inversely related (Fig. 4*b*), but not statistically significant (*n* = 3, ρ = −0.5, *p* = 1). Similarly, the correlation between mean rates of straying among the three locations that produce ocean-type and stream-type Chinook was high (ρ = 1), but not statistically significant (Fig. 5*b*, *p* = 0.3).

Correlations between species and life histories within years

We detected significant positive correlations in straying based on paired comparisons of ocean-type Chinook salmon and coho salmon (*n* = 66, ρ = 0.33, *p* < 0.05) and stream-type Chinook salmon

Table 3. Paired comparisons of Chinook salmon and steelhead stray rates (%) from individuals reared and released at the Dworshak, Lyons Ferry, and Umatilla hatcheries in the Columbia River basin, USA.

| Location | Species | Release years | Release data | | | | Tag Recoveries | | | | |
			Day of year	Length	Mass	Total released	Total tagged	Home	Stray	Avg. % stray	CV
Dworshak	Stream-type Chinook	1988, 1990, 1991, 1994–2006	110 (47)	NA	27.8 (9. 5)	13 162 132	3 778 733	4 899	335	5.30	0.97
	Summer steelhead		116 (6.2)	NA	69.9 (23.4)	25 680 325	2 712 929	5 228	18	0.30	1.14
Lyons Ferry	Ocean-type Chinook Yearlings	1995–2000, 2002–2004	103 (9)	164 (2)	48 (2.6)	4 718 791	4 671 578	23 420	439	2.30	1.14
	Subyearlings	1995, 1999–2004	159 (21)	81 (32)	9.5 (0.98)	1 797 989	1 774 440	2 815	35	0.90	1.55
	Summer steelhead	1995–2000, 2002–2004	109 (4)	208 (3.7)	104.5 (14.5)	1 461 085	732 065	3 242	74	2.30	0.96
Umatilla	Stream-type Chinook	1997–2006	69 (41)	NA	34 (4.9)	2 679 070	956 779	715	663	54.9	0.21
	Summer steelhead		113 (8.67)	NA	94.9 (11.1)	893 953	398 114	372	5	0.88	2.64

Note: Release years, day of year (SD in parentheses), average length (mm, SD), average mass (g, SD), total released, and total tagged are shown. The number of tags recovered at home and as strays was expanded to account for sampling. Average stray rate was calculated for each paired release year comparison and shown with the coefficient of variation (CV). Length data were not available (NA) for releases from Dworshak and Umatilla.

Table 4. Paired comparisons of ocean-type and stream-type salmon stray rates (%) from individuals reared and released at the Cowlitz, Fallert Creek, and Kalama hatcheries in the Columbia River basin, USA.

| Location | Life history | Release years | Release data | | | | Tag Recoveries | | | | |
			Day of year	Length	Mass	Total released	Total tagged	Home	Stray	Avg. % stray	CV
Cowlitz	Ocean-type Chinook	1982–1983, 1986–1988	180 (28)	84 (3)	6.9 (1.3)	112 452 397	4 397 186	3 524	151	5.20	1.00
	Stream-type Chinook	1991–2006	86 (20)	164 (35)	77.1 (20.9)	14 671 202	6 983 834	26 866	48	0.15	1.40
Fallert	Ocean-type Chinook		173 (7)	77 (3)	6.1 (0.54)	9 497 375	1 064 409	1 621	399	27.8	0.72
	Stream-type Chinook	1995–2006	82 (13)	153 (27)	63.2 (15.2)	2 661 138	1 655 146	2 992	211	10.00	1.44
Kalama	Ocean-type Chinook	1999–2003	186 (39)	84 (17)	8.3 (4.7)	8 878 693	216 646	1 511	295	17.60	0.37
	Stream-type Chinook	2005–2006	67 (27)	166 (24)	65.1 (17.7)	347 386	127 164	5 125	244	5.20	0.91

Note: Release years, day of year (SD in parentheses), average length (mm, SD), average mass (g, SD), total released, and total tagged are shown. The number of tags recovered at home and as strays was expanded to account for sampling. Average stray rate was calculated for each paired release year comparison and shown with the coefficient of variation (CV).

and coho salmon ($n = 52$, $\rho = 0.26$, $p < 0.05$) released in the same years in the same locations. In contrast, correlations between Chinook salmon and steelhead straying paired by year of release were negative but only significantly so when Umatilla releases were included (including Umatilla: $n = 39$, $\rho = -0.44$, $p < 0.001$; excluding Umatilla: $n = 32$, $\rho = -0.34$, $p = 0.053$). The straying rates of the two Chinook salmon life history types within a paired release year and location were significantly and positively correlated ($n = 40$ $\rho = 0.41$, $p < 0.01$).

We conducted a parallel analysis with comparisons paired by return year to examine the potential influence of conditions during the adult migration on straying. Similar to comparisons paired by year of release, we found significant positive correlations in straying between ocean-type Chinook salmon and coho salmon ($n = 87$, $\rho = 0.24$, $p < 0.05$) and between stream-type Chinook salmon and coho salmon ($n = 87$, $\rho = 0.31$, $p < 0.01$). We detected continued inverse associations between Chinook salmon and steelhead straying when comparisons were paired by year of return ($n = 37$ including Umatilla, $\rho = -0.45$, $p < 0.01$; $n = 26$ excluding Umatilla, $\rho = -0.39$, $p < 0.05$). Similarly, comparisons paired by year of return also revealed significant positive correlations in straying between stream-type and ocean-type Chinook salmon ($n = 56$, $\rho = 0.52$, $p < 0.01$).

Taken together, based on paired comparisons of straying in the year of smolt release and year of adult return, these analyses suggested that yet unknown conditions during both the outward and return migrations may influence straying.

Discussion

Paired releases of fish into the same rivers in the same years revealed fundamental differences in straying among Chinook salmon, coho salmon, and steelhead, and between life history types of Chinook salmon. Ocean-type Chinook salmon strayed at significantly higher rates than stream-type Chinook salmon and coho salmon, consistent with the hypothesis that straying by adults may reflect juvenile migration, extent of freshwater residency, and patterns of imprinting earlier in life. Paired comparisons between Chinook salmon and steelhead revealed species-specific patterns, but these results were less clear than comparisons between other species and may be affected by seasonal differences in spawning timing (fall versus spring) or by the variation in return timing and duration of holding in the river prior to spawning by these two species. We detected positive correlations between straying by Chinook salmon and coho salmon and between ocean-type and stream-type Chinook salmon re-

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Fig. 3. Percentage of tagged (*a*) coho salmon, (*b*) stream-type Chinook salmon, and (*c*) ocean-type Chinook salmon recovered as strays from release locations in the Columbia River basin and (*d*) association between stray rates of coho and stream-type Chinook salmon (black numbers corresponding to location number in Fig. 2) and between coho and ocean-type Chinook salmon (grey numbers corresponding to location number in Fig. 2) produced at given hatcheries. In ascending distance from the mouth of the Columbia River: 1, Elochoman River; 2, Cowlitz River; 3, Toutle River; 4, Fallert Creek; 5, Kalama Falls; 6, Lewis River; 7, Washougal River; 8, Umatilla River; 9, Lyons Ferry; 10, Dworshak NFH. Washougal and Elochoman are abbreviated for clarity on boxplots. Note markedly different scales on vertical axes.
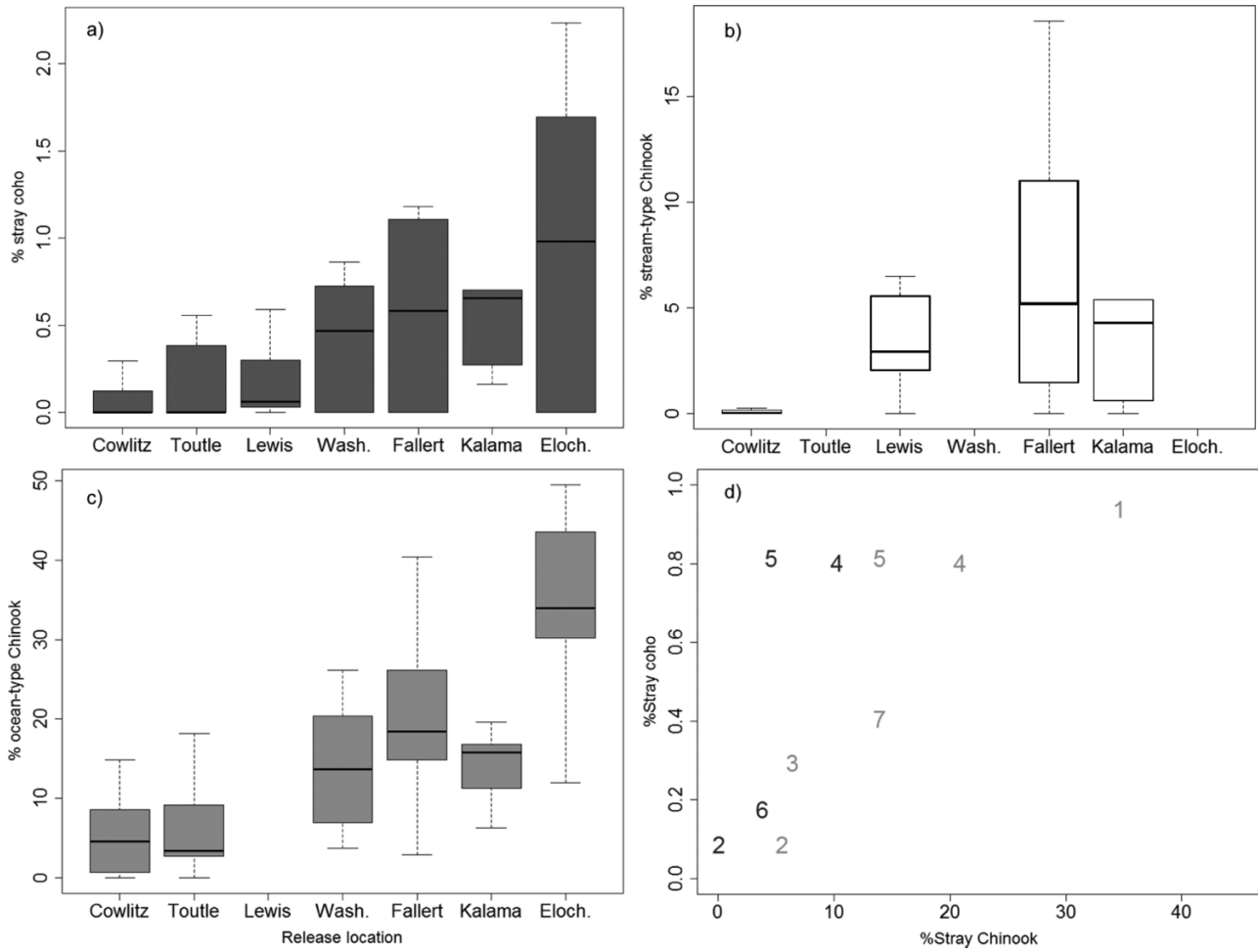
Fig. 4. (*a*) Percentage of tagged Chinook salmon (grey bars) and steelhead (open bars) recovered as strays from the Dworshak, Lyons Ferry, and Umatilla hatcheries in the Columbia River basin and (*b*) association between stray rates of Chinook salmon and steelhead released from those locations.
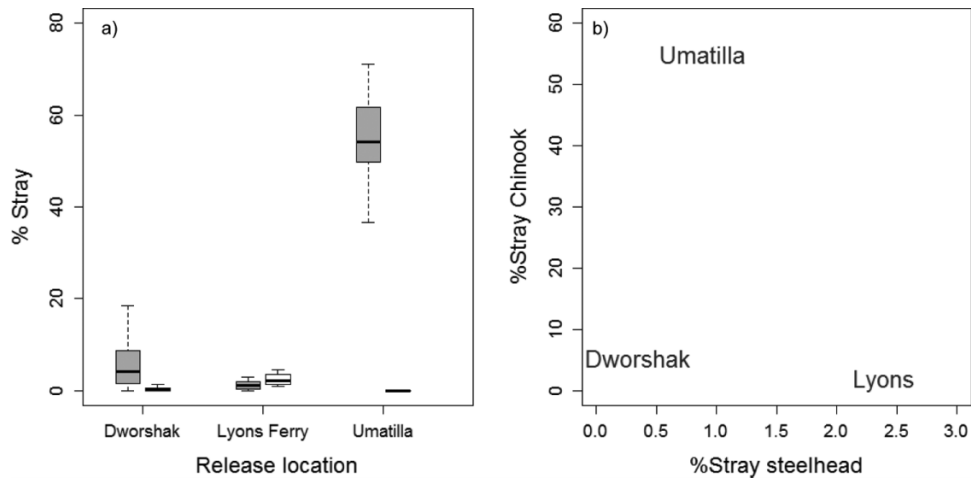
Fig. 5. (*a*) Percentage of tagged stream-type Chinook salmon (open bars) and ocean-type Chinook salmon (grey bars) recovered as strays from the Cowlitz River, Fallert Creek, and Kalama Falls hatcheries in the Columbia River basin and (*b*) association between stray rates of stream-type and ocean-type Chinook salmon released from those locations. Note markedly different scales on vertical axes.
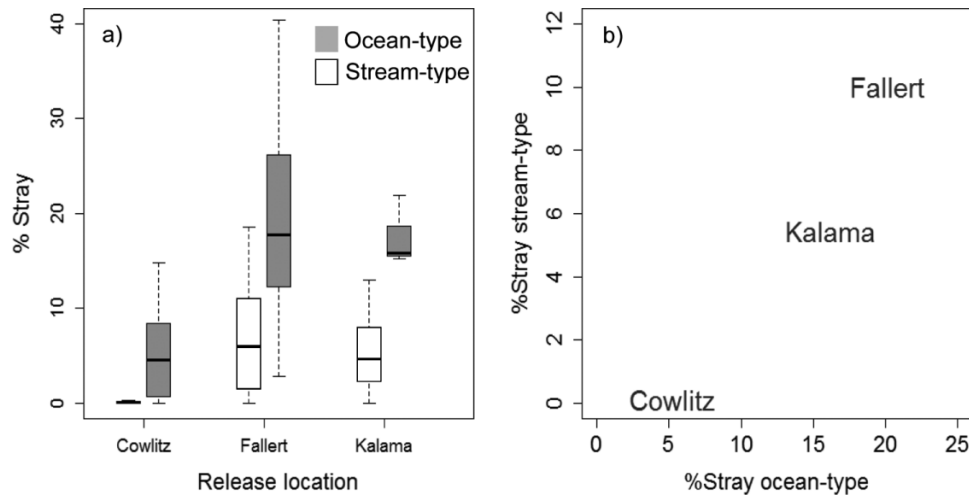
leased in the same year in the same locations, but negative correlations between Chinook salmon and steelhead. Moreover, rates of straying resulting from paired comparisons by year of return yielded similar interpretations to comparisons based on year of release, which suggests that conditions during both the outward smolt migration and return adult migration may affect straying rates. In addition to species and life history differences, we detected population-specific straying rates and observed that locations producing high or low rates of straying did so irrespective of species or life history.

Overall, our estimates of straying rates in stream-type Chinook salmon are generally consistent with reviews (Pess 2009; Keefer and Caudill 2012). Stream-type Chinook salmon in our study were estimated to stray at an average rate of 4.7%, excluding data from the Umatilla, from which 55% of the Chinook salmon strayed. The most recent review by Keefer and Caudill (2012) reported an average stray rate of 3.4% for Chinook salmon. The exceedingly high straying of stream-type Chinook salmon from the Umatilla hatchery is consistent with previous reports of ocean-type Chinook salmon released in this location (reviewed by Hayes and Carmichael 2002), though no data for ocean-type Chinook salmon were available that met our criteria for inclusion for analysis. High straying from the Umatilla hatchery has been attributed to low water flow as a result of agricultural withdrawals and correspondingly high water temperatures. Curiously, summer-run steelhead straying rates from the Umatilla were low (0.88%), which may reflect sufficient water flows and tolerable temperatures during the spring steelhead spawning season. Life history differences between the species, notably the residence in nonnatal rivers with suitable flow and temperature by maturing steelhead before moving to natal streams for reproduction (Keefer et al. 2008*a*, 2009), may also contribute to the large differences observed for stray rates of Umatilla steelhead and Chinook salmon.

In contrast with stream-type Chinook salmon, we observed substantial differences in our estimates of straying in ocean-type Chinook salmon, coho salmon, and steelhead compared with recent reviews. We estimated that ocean-type Chinook salmon, coho salmon, and steelhead strayed at average respective rates of 15.8%, 0.5%, and 1.2% compared with 34.9%, 9.8%, and 13.8% reported in Keefer and Caudill (2012). As noted by Keefer and Caudill (2012), their review included many of the sources of variation that we controlled for here (e.g., population amalgamations versus discrete units, off-site rearing and release, experimental groups, different tagging methods, etc.). Despite accounting for potential

variation, ocean-type Chinook salmon have been previously reported to stray at relatively high rates (e.g., see Quinn et al. 1991; Pascual et al. 1995; Hayes and Carmichael 2002), which combined with the results here indicate a robust biological pattern. Though we have shown that comparisons from different locations must be made with caution, the generally lower rates of straying in coho salmon compared with steelhead contrasts sharply with the pattern reported by Shapovalov and Taft (1954): >15% in coho salmon and <3% in (winter-run) steelhead. The low rate of coho salmon straying estimated in our study was consistent with rates of <2% observed in 14 coho salmon stocks on Vancouver Island reported by Labelle (1992).

We detected consistent patterns of straying in species and life history types across locations with the rank order of ocean-type Chinook salmon > stream-type Chinook salmon > coho salmon. However, we detected markedly different absolute rates of straying across sites, and average rates of straying between species tended to correlate across the landscape. This pattern may reflect different hatchery practices in the Columbia River basin that are not easily quantified. Alternatively, the patterns of straying may reflect adaptive responses of populations to local conditions. Theory predicts that straying should be inversely related to environmental stability (Quinn 1984). The extent to which the environments of the populations vary is not known, but the pattern implies environmental stability in the following ascending order: Elochoman, Washougal, Kalama, Fallert, Toutle, Lewis, Cowlitz.

Markedly higher straying by ocean-type Chinook salmon compared with stream-type Chinook salmon or coho salmon is consistent with predictions that processes during juvenile imprinting and downstream migration may influence homing ability in salmonids (reviewed by Dittman and Quinn 1996). Our review of studies reporting species-specific patterns of physiological change associated with imprinting and parr–smolt transformation yielded the general pattern of earlier seasonal T4 peaks in ocean-type Chinook salmon compared with stream-type Chinook salmon, coho salmon, and steelhead (Fig. 1). Many studies, but not all, also reported multiple seasonal peaks in T4 in both ocean-type and stream-type Chinook salmon and coho salmon, but that peaks came earlier in the season and lasted longer in ocean-type Chinook salmon than in other species. This coincides with the ocean-type Chinook salmon life history of migrating to sea in the first year of life and a more gradual migration compared with the more compressed and rapid migrations of the other species or life history types (though see Connor et al. 2005). Consistent with

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these patterns, we observed that stream-type Chinook salmon, steelhead, and coho salmon that spend a full year in fresh water prior to seaward migration strayed significantly less than ocean-type Chinook salmon that migrate to sea in the first year of life. That being said, the release of ocean-type Chinook salmon as yearlings rather than subyearlings was associated with increased straying. Presumably, this reflects a disruption of the normal seasonal patterns of growth, endocrine events, imprinting, and migration for the yearling releases. Though the mechanisms underpinning this finding are unclear, the patterns suggest that attempts to rear ocean-type Chinook salmon an extra year in fresh water to increase the size of smolts may come at a cost of extra straying (see Unwin and Quinn 1993).

Patterns of straying based on paired comparisons by return year suggest an additional role of factors during the adult return migration; however, the mechanisms leading to these patterns are not unknown. Straying by Atlantic salmon (*Salmo salar*) from the River Imsa, Norway, varied inversely with total run size within a return year, perhaps because of higher concentrations of population-specific odors (Jonsson et al. 2003). A similar pattern was observed by Quinn and Fresh (1984) in Chinook salmon straying from the Cowlitz River. In the Columbia River basin, some tributaries appear to differ in apparent "attractiveness" to strays, suggesting the yet unknown influence of environmental factors such as stream flow or temperature (Quinn et al. 1991; Pascual and Quinn 1994). The roles of conditions during the return migration notwithstanding, we interpret our results to be more consistent with the influence of juvenile rather than adult life history on straying in adults. If, for example, the state of reproductive maturation or adult run timing were strong determinants for straying, one would expect ocean-type Chinook salmon and coho to stray at more comparable rates than stream-type Chinook salmon or summer-run steelhead (Myers et al. 2006). Moreover, increases in stress hormones associated with maturation may facilitate olfactory memory recall and aid in homing (Carruth et al. 2002), suggesting that ocean-type Chinook salmon and coho salmon should perhaps stray less than other species. But again, we detected markedly different patterns of straying by ocean-type Chinook salmon and coho despite similar adult return timing and reproductive status. Our results also challenge the hypothesis that straying should inversely scale with variation in age at maturity (Quinn 1984). In contrast with the above prediction, we observed that coho salmon had the lowest average rate of straying despite exhibiting the least variation in age at maturation. Future research would benefit from comparisons between species such as pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*), which exhibit similar juvenile life histories (individuals typically migrate soon after emergence) but differ markedly in variation in age at maturation. Pink salmon maturation is fixed at 2 years, whereas maturation in chum commonly occurs at 3, 4, or 5 years (Heard 1991; Salo 1991).

The interpretations derived from these analyses include several caveats worthy of discussion. Estimates of stray rates depend heavily on recovery efforts in non-natal sites. We assumed that virtually 100% of individuals returning to hatcheries are screened for tags, whereas the effort to recover tags on spawning grounds is undoubtedly less and ultimately not knowable for such a complex long-term dataset (Nandor et al. 2010). Moreover, the probability of detecting and retrieving carcasses undoubtedly differs among species, owing to differences in body size, spawn timing and associated seasonal water conditions, and life histories that include repeat spawning in the case of steelhead versus semelparity in Chinook salmon and coho salmon. Thus, it is not surprising that over 75% of the recoveries were from hatcheries and that the larger-bodied Chinook salmon spawning early in the fall were recovered at higher rates on spawning grounds (~23% of recoveries) compared with coho salmon or steelhead (both <1% of recoveries on spawning grounds). However, while parallel analyses of

just hatchery recoveries changed the estimated rates of straying (especially in Chinook salmon), the overall conclusions were not altered. Another consideration is that the spatial arrangement of potential detection sites may be influencing the patterns observed, where one might predict that individuals released from locations with higher densities of detection sites might be more likely to be recovered off-site and therefore presumed to stray more. However, the data were not consistent with such a bias. Given its proximity to the mouth of the Columbia River, the Elochoman River's populations of coho salmon and ocean-type Chinook salmon must stray upstream to be detected, whereas other populations can stray upstream or downstream. Despite the lower densities of detection sites near the Elochoman River, we observed consistently higher stray rates in these populations compared with others.

Second, the data reflect entirely hatchery-produced fish, and it remains unclear whether wild individuals stray at comparable rates. Hatchery fish may be expected to stray more than wild fish for various reasons, yet to date, empirical comparisons have been few and equivocal (McIsaac 1990; Labelle 1992). It is clear that hatchery practices such as timing and life stage of releases can profoundly affect straying (Pascual et al. 1995; Candy and Beacham 2000), yet it remains an open question whether hatchery fish stray more than wild individuals as a rule. Domestication to hatchery growth conditions can occur quickly (Christie et al. 2012), and patterns of growth are hypothesized to influence differential patterns of smolting and potential for imprinting (Dittman and Quinn 1996). Given these possible differences between wild and hatchery-produced fish, we do not suggest applying the specific rates of straying observed here in hatchery individuals to wild populations.

Despite these caveats and limitations, the results make an important point; the use of average straying rates from the literature or simply assuming that straying varies solely as a function of distance between watersheds (e.g., Cooper and Mangel 1999) may give highly erroneous interpretations of how populations are connected in natural systems.

Acknowledgements

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