

FEATURE

# Causes and Consequences of Straying into Small Populations of Pacific Salmon

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Most Pacific salmon *Oncorhynchus* spp. migrate to their natal sites to spawn. Some, however, stray into nonnatal habitats and interact (e.g., reproduce) with individuals from other populations. Pacific salmon straying has been heavily studied for several decades, particularly from the perspective of the populations that donate the stray migrants. Conservation consequences are experienced primarily by the populations that receive strays, though, and there is recent evidence of significant levels of genetic introgression in small recipient populations, which could contribute to the loss of local adaptations. Straying may also provide the benefit of a demographic rescue effect that could save declining recipient populations from extirpation. We highlight the influence of population abundances on the magnitude of straying into recipient populations and demonstrate this using evidence we collected from a small population of Sockeye Salmon *O. nerka* in British Columbia, Canada. We also review potential factors that might promote higher donor stray rates and therefore recipient straying. Evidence of factors that affect straying is limited and we identify several knowledge gaps, as well as anthropogenic activities that could promote straying. We encourage further discussion and research on the potential effects of recipient straying and the factors that affect straying rates.

### STRAYING INTO SMALL RECIPIENT POPULATIONS

The Pacific salmon *Oncorhynchus* spp. spawning migration is characterized by the return of adults to their natal waters. Though most salmon home successfully, there is a tendency for some to diverge from their natal migratory route (Quinn 1993). Such divergences are temporary (i.e., “temporary straying”; Keefer et al. 2008a; Peterson et al. 2015) if the salmon return downstream and continue on to their natal spawning grounds. Sometimes, however, the salmon do not return and instead attempt to spawn in nonnatal habitat. This latter behavior is considered “permanent straying” (Keefer and Caudill 2014, p. 346) and will be referred to as simply “straying” hereafter. Typically, straying is discussed as a loss of individuals from a source or donor population and methodological limitations make it difficult to track the ultimate fate of the strays. Notably, some migrate to nonnatal sites that are inhabited by recipient populations of the same species, which will experience an inverse effect relative to donor populations: rather than losing individuals, recipient populations receive them. Recent work has begun to demonstrate the importance of recipient populations (Keefer and Caudill 2014), and we wish to expand on this work to draw further attention to the occurrence of recipient straying. Our objective is to discuss the influence of population sizes on recipient straying, the consequences of straying for recipient populations, the environmental factors that influence straying rates, and human activities that might encourage straying into recipient populations.

Only a minority of Pacific salmon stray, perhaps in part due to several negative effects associated with this behavior. For example, straying can decrease the likelihood of locating suitable spawning habitat and eliminate local adaptive advantages such as optimized body shapes or egg sizes (Crossin et al. 2004; Hendry et al. 2004). Nevertheless, straying consistently occurs and can reduce resource competition and kin competition (Hendry et al. 2004). Straying can also buffer donor populations against disturbances in habitat quality, such as flooding events that can cause increased mortality of eggs and alevins (Lapointe et al. 2000). Most populations of Pacific salmon lose some individuals to donor straying (although not necessarily every year), and the amount is typically fewer than 10% (Keefer and Caudill 2014) and can be as low as 1% (Quinn 2005). There is little evidence to suggest that such levels of straying can have a large effect on the donor population. The risk of attrition to the point of extirpation, for example, is unlikely, because it would require an exceedingly high amount of straying.

Unlike donor populations, recipient populations may be highly influenced by straying due to the comparatively large number of strays relative to the number of recipients. The proportion of strays in a recipient population is simply the number of strays

divided by the total size of the recipient population, inclusive of both strays and nonstrays. Thus, an increase in the number of strays will necessarily increase the relative abundance of stray salmon within the recipient population. If the cumulative abundance of the donor populations is large, the rate of straying is high, or the abundance of the recipient population is small, the relative proportion of strays entering a recipient population will be high (Figure 1). Even when the stray rate is low, as is often the case, a relatively large number of individuals may stray if the absolute abundance of the donor populations is large (Brenner et al. 2012; see *Case Study* on p. 223 for a demonstration of this scenario using original data on wild Sockeye Salmon *O. nerka*). Alternatively, the effect of strays may be minimal in large recipient populations unless the number of stray immigrants is exceptionally high.

Over the past few years, researchers have found evidence of relatively high levels of straying into small recipient salmon populations (Brenner et al. 2012; Johnson et al. 2012; Zhivotovsky et al. 2012; Jasper et al. 2013; Hess and Matala 2014), which could have several consequences. One major potential consequence is that introgression from donor populations could cause the loss of local adaptive advantages and reduce recipient population fitness (Grant 2012). The local adaptive advantages could be lost even when strays come from nearby donor populations because adaptive advantages occur in Pacific salmon at fine spatial scales (Reisenbichler 1988; Fraser et al. 2011). The potential for fitness costs is greatest when straying occurs over large distances, though, because differences in fitness increase with distance between populations (Fraser et al. 2011). Moreover, Hess and Matala (2014) demonstrated with Chinook Salmon *O. tshawytscha* that even low levels of immigration, when sustained over multiple generations, can substantially alter a population’s genetic composition.

Researchers have found evidence of increasing genetic introgression (or the potential for introgression) in small recipient populations throughout the natural range of Pacific salmon (Brenner et al. 2012; Johnson et al. 2012; Zhivotovsky et al. 2012; Jasper et al. 2013; Hess and Matala 2014). Some of the most threatened recipient populations are likely to be uniquely adapted ones because the fitness costs might be greatest and unique behaviors could be lost. Zhivotovsky et al. (2012) provided evidence that a wild beach-spawning population of Chum Salmon *O. keta* in Kurilskiy Bay, Russia, is being diluted by a hatchery stock released in the same system. And if these hatchery salmon are unable to spawn in beach habitats, this life-history adaptation may be lost through continued mixing between wild and hatchery stocks. Straying of hatchery salmon into wild populations, as in this case, could incur particularly high fitness costs for wild salmon (Grant

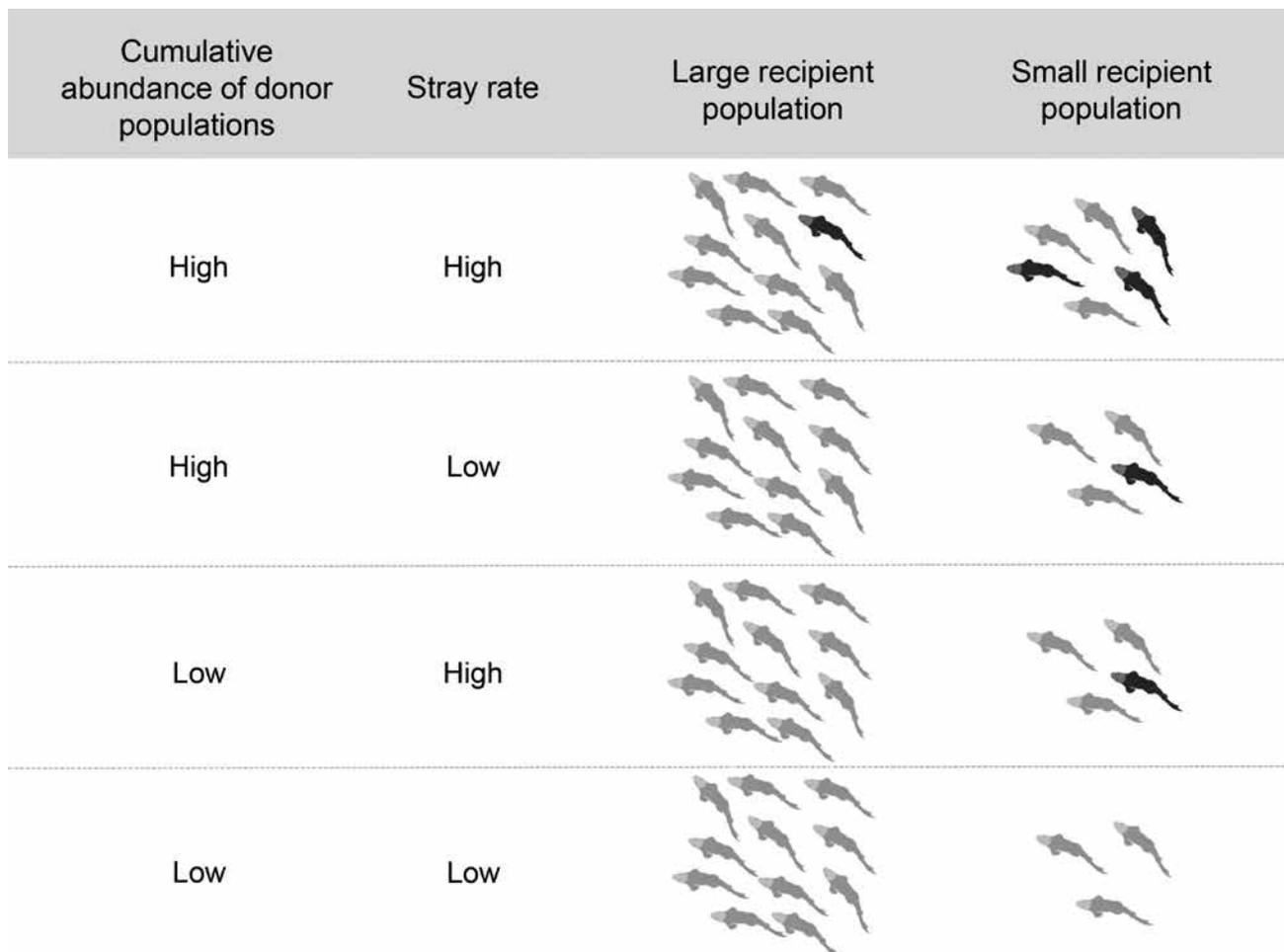


Figure 1. Interactions between population abundances and stray rates on recipient straying. A large source of potential strays (i.e., high abundance of donor populations) and/or a high stray rate can lead to a high proportion of strays (represented as dark fish) in small recipient populations (represented as light fish). Under similar conditions, the proportion of strays in a large recipient population will be lower.

2012; Rand 2012), especially if the hatchery stocks are domesticated (Berejikian and Ford 2004; Araki et al. 2008). Spawning of hatchery salmon in the wild has been a long-standing concern in fisheries management (Grant 1997; Bisson et al. 2002) but continues to occur in many systems. In California’s Sacramento River system, for example, Johnson et al. (2012) used isotopic analyses to estimate that over 90% of adults returning to the wild habitat of a small population of Chinook Salmon were of hatchery origin. There is also evidence of hatchery Chum Salmon straying into wild populations in Southeast Alaska (Piston and Heintz 2012).

Negative impacts of recipient straying may also include reduced spawning success through increased competition for breeding sites (Essington et al. 2000) or increased exposure to foreign pathogens, though this latter impact has not yet been directly explored. The spread of pathogens among salmonids has been well documented (Naylor et al. 2005), such as infectious hematopoietic necrosis virus, which in one instance was transferred from hatchery Steelhead to wild populations in the Columbia River (Kurath et al. 2003). In addition to the risk of direct pathogen transfer between stray and native fish, genetic introgression of stray salmon could reduce a recipient population’s resistance to endemic microparasites (Miller et al. 2014). Recipient straying could also further increase extirpation risk through the reduction

of “portfolio effects” (temporal stabilization resulting from the presence of numerous, diverse sub-populations within a metapopulation; Schindler et al. 2010).

Though these issues associated with genetic introgression warrant concern, there is also the potential for demographic rescue (Carlson et al. 2014) of small populations through recipient straying. In recipient populations that have been previously isolated, for example, straying can create a demographic rescue effect by providing a crucial influx of individuals as the population transitions toward self-sustainability, as found in Chinook and Coho *O. kisutch* salmon upstream from a newly constructed fish ladder in Washington’s Cedar River (Anderson et al. 2015). Asymmetric gene flow into small recipient populations may also maintain genetic diversity, which might otherwise be lost through genetic drift (Consuegra et al. 2005). The identity of the population, however, could change as native fish are replaced by strays.

Demographic rescue through recipient straying could also save populations that are unable to adapt to increasing temperatures. River temperatures throughout much of the Pacific salmon’s range are rising (Keefer et al. 2008b; Martins et al. 2012b), which increases the risk of en route mortality during the spawning migration (Naughton et al. 2005) and also increases predation rates and pathogen susceptibility in juveniles (Martins et al. 2012a). As

## CASE STUDY: RECIPIENT STRAYING IN THE SETON RIVER

We collected evidence of potentially high levels of straying into the migratory habitat of a small ( $n = 26,179$  in the year of study; Casselman et al. 2012) recipient population of wild Sockeye Salmon, which serves as an example of the magnitude at which straying can occur. In 2012, we collected DNA samples from 152 Sockeye Salmon in the Seton River, a tributary of the Fraser River in British Columbia (Figure 2). Fish were captured by dip net from the top pool of the Seton Dam fishway, 4 km up the Seton River from its confluence with the Fraser River. The Gates Creek spawning areas are located a further 40 km upstream from the capture site. The mean run size for Gates Creek Sockeye from 1953 to 2010 was 53,000 (DFO 2014), making it one of the smaller Sockeye Salmon populations in the Fraser River system. We collected adipose samples from each fish, which were used to identify population through microsatellite and major histocompatibility complex variation (methods detailed in Beacham et al. 2005).

Of the 152 Sockeye Salmon we captured, 55 were strays. Although the salmon were not captured while spawning and therefore cannot be confirmed as permanent strays, there are no tributaries or side channels between the capture location at the dam and the Gates Creek spawning grounds, which are separated by two large lakes (Figure 2, inset). It is therefore likely that many of the salmon we captured would either attempt to spawn in Gates Creek or not attempt to spawn at all if they continued upstream, although we cannot confirm their ultimate fate. They had successfully ascended the fishway and though entrainment is possible, video data collected at the top of the dam confirmed that such behavior is exceedingly rare in this system (D. McCubbing, Instream Fisheries Research Inc., personal communication, 2014), which suggests that few or even none of these fish returned downstream. Each of the 55 stray salmon belonged to alternative Fraser River populations whose run timing overlaps with that of the Gates Creek population. Furthermore, 84% (46/55) of them were from Chilko and Stellako rivers, which contain two of the largest populations in the Fraser River basin (both populations are wild). In this case, the donor populations are one to two orders of magnitude larger than the recipient: estimated abundance of the Gates Creek population that year was 26,179, compared to mean run sizes of 1,405,000 and 461,000 for the Chilko and Stellako river populations, respectively (abundances for these two populations estimated based on data collected from 1953 to 2010; DFO 2014).

Fraser et al. (2011) conducted a meta-analysis of local adaptation in salmonids and found that fitness advantages in local populations increased in frequency and strength with increasing geographic distance between populations. Chilko

River and Stellako River are located 160 km and 425 km from Gates Creek, respectively (Figure 2), both far enough that we might expect differential fitness (Fraser et al. 2011). Physiological differences among these populations further suggests that introgression could have a negative effect on offspring fitness. For example, Sockeye Salmon from Nechako (which includes the Stellako River population) have a narrower range of aerobic scope than the Gates Creek population (Eliason et al. 2011), and compared to other Fraser River populations that migrate shorter distances, Chilko River Sockeye Salmon have smaller eggs, lower fecundity, shallower bodies, and shorter body lengths (Crossin et al. 2004). Such population-level differences could incur significant fitness costs in the Gates Creek system if interbreeding between the stray and native populations occurs.

Our findings underline the role of population sizes in estimating the effect of stray rates. Even if stray rates are low, the total number of strays that enter a recipient stream could be relatively high if the donor populations are large. For example, 17% of the Sockeye Salmon captured in the Seton River in 2012 were from Chilko River. If we extrapolate this percentage to the level of the Gates Creek population (i.e., if the run size for Gates Creek is 26,179 and 17% of these salmon were actually from Chilko River), 4,478 Chilko River Sockeye Salmon could have strayed into this area, which is only 0.3% of the Chilko River population. The same method of calculation yields an estimate of 0.7% of the Stellako River population straying into this system to achieve the proportions we observed. Furthermore, these numbers could be supplemented by hybrids, which were not identified as strays through the genetic analyses. Given that the strays had already traveled 300 km up the Fraser River and had made the decision to not only enter the Seton River but also ascend a fishway in a nonnatal stream is suggestive that these individuals could have been motivated to continue the subsequent 40 km to Gates Creek spawning areas. We lack evidence that any of these stray Sockeye Salmon arrived at Gates Creek and successfully spawned (no routine DNA sampling takes place on these spawning grounds), but nevertheless this case study demonstrates that even low stray rates could affect the recipient population if the donor populations are an order of magnitude larger. It is populations such as Gates Creek—low in abundance and commigrating with relatively larger populations—that may be the most susceptible to impacts associated with straying. There is a risk in overharvesting small recipient populations when capturing strays from large donor populations (Brenner et al. 2012), though, and this possibility should be taken into consideration when managing recipient straying.

Table 1. Factors that might promote straying from a donor population. \*Indicates anthropogenic influence.

Factor		
Trait of factor that could promote straying	State of knowledge	References
<b>Temperature</b>		
Increasing temperatures during spawning migration (could be associated with human-induced climate change*)	Moderate evidence	Goniae et al. (2006); Keefer et al. (2008b); Valiente et al. (2010); Horreo et al. (2011); Westley et al. (2015)
<b>Conspecific interactions</b>		
Decreased population size	Moderate evidence	Sholes and Hallock (1979); Quinn and Fresh (1984); Hard and Heard (1999); Berdahl et al. (2014); Westley et al. (2015)
Presence of conspecifics in nonnatal river	Limited evidence	Jonsson et al. (2003); Dittman et al. (2010)
Delay downstream from dams during spawning migration, increasing density of conspecifics and associated chemical cues*	No data available	
Increased size of comigrating populations	Limited evidence	Brenner et al. (2012); Ford et al. (2015)
<b>Water flow</b>		
Increased discharge of nonnatal river	Conflicting evidence	Labelle (1992); Unwin and Quinn (1993); Jonsson et al. (2003)
Decreased probability of return to natal migratory route following passage of dam in nonnatal river*	No data available	
<b>Spawning location</b>		
Decreased distance from ocean	Limited evidence	Brenner et al. (2012); Westley et al. (2015)
Decreased distance from other suitable spawning sites	Limited evidence	Olsen et al. (2010); Keefer and Caudill (2014)
<b>Genetics</b>		
Propensity of some stocks/populations to stray more than others	Moderate evidence	Bams (1976); Hard and Heard (1999); Brenner et al. (2012); Westley et al. (2013, 2015); Ford et al. (2015)
Sex-linked differences	Conflicting evidence	Unwin and Quinn (1993); Hard and Heard (1999); Thedinga et al. (2000); Hamann and Kennedy (2012)
Transplanted stocks (relative to native populations)*	Conflicting evidence	McIsaac and Quinn (1988); Candy and Beacham (2000); Westley et al. (2015)
<b>Rearing conditions</b>		
Ocean-type life history (in comparison to stream-type)	Limited evidence	Westley et al. (2013)
Increased dispersal from incubation site	Limited evidence	Hamann and Kennedy (2012)
Hatchery rearing (in comparison to natural spawning)*	Limited evidence	Ford et al. (2015)

temperatures increase, many populations of Pacific salmon may be unable to adapt quickly enough to the changing conditions (Reed et al. 2011). For example, Martins et al. (2012b) predicted that the survival of Fraser River Sockeye Salmon will decrease if the Fraser River continues to warm as expected, and Muñoz et al. (2015) predicted the possibility of catastrophic losses of Chinook Salmon under current warming projections, although the latter study also found the potential for heritable variation in cardiac performance that could allow populations to adapt to higher temperatures. If these predicted warming trends are realized, straying may play an important role in salmon survival not only by augmenting small recipient populations (i.e., demographic rescue), but via an evolutionary rescue effect whereby warm-adapted strays mix and successfully reproduce with recipient salmon (Carlson et al. 2014). In this manner, recipient straying could act as a buffer against temporal environmental variation, as theorized by Hendry et al. (2004).

#### ENVIRONMENTAL AND BIOLOGICAL INFLUENCES ON RECIPIENT STRAYING

Understanding the environmental and biological factors that influence donor stray rates may help fisheries managers to predict the occurrence of donor straying and therefore the risk of

recipient straying. We have assembled preliminary evidence from previous salmon research to identify environmental and biotic factors that may promote straying (Table 1).

#### Temperature

Large-scale homing studies on Chinook Salmon in the Columbia River system have found that straying into nonnatal tributaries increases with increasing water temperature and fish are more likely to enter nonnatal tributaries when main-stem temperatures are high, both temporarily (Goniae et al. 2006; Keefer et al. 2008b) and permanently (Westley et al. 2015). During the period in 2012 during which we found many Sockeye Salmon wandering into the Seton River (see Case Study), the Fraser River's temperature was  $1.9^{\circ}\text{C} \pm 0.9^{\circ}\text{C}$  (mean  $\pm$  standard deviation) higher than in the Seton River. During this same time of year in 2013 and 2014, the Seton River was warmer, but the difference between the two rivers was less pronounced (2013:  $0.5^{\circ}\text{C} \pm 0.8^{\circ}\text{C}$ , 2014:  $0.0^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$ ). In those 2 years, we captured fewer stray Sockeye Salmon than in 2012 (2013: 4% of 436 captured salmon; 2014: 8.5% of 1,043 captured salmon). These findings suggest that increased straying may be a form of behavioral thermoregulation whereby migrating individuals seek thermal refugia in nonnatal streams. Furthermore, we do not believe that salmon

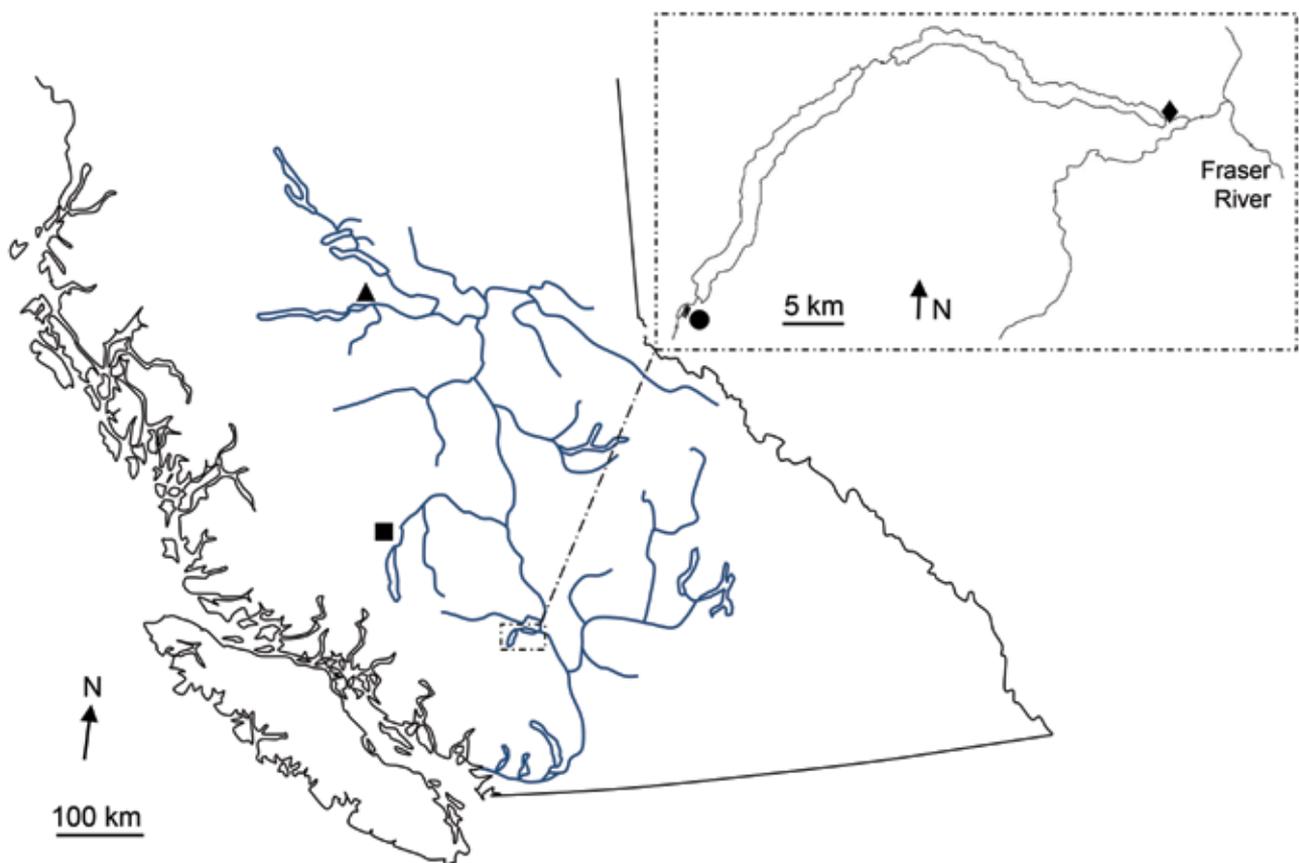


Figure 2. Map of British Columbia's Fraser River system. Sockeye Salmon from Stellako River (triangle), Chilko River (square), and Gates Creek (circle) were captured from the top of the Seton Dam fishway (diamond) in August 2012. The capture location is situated 40 km downstream from Gates Creek (inset).

may be waiting for cooler temperatures before returning downstream, as our Seton River case study demonstrated that salmon continued upstream past a fishway.

A positive relationship between temperature and donor stray rates has also been documented in Atlantic Salmon *Salmo salar*. Horreo et al. (2011) used microsatellite markers to identify stray Atlantic Salmon in northern Spain over 2 decades (1988–2007), demonstrating that straying increased with warming river temperatures. Similarly, Valiente et al. (2010) found increased gene flow—a consequence of increased straying—in Atlantic Salmon populations in southern France that was associated with regional climate warming. It is worth noting that Atlantic Salmon populations are often an order of magnitude smaller than “small” Pacific salmon populations and the risks associated with recipient straying are, therefore, heightened for Atlantic Salmon.

### Rearing Conditions

Environmental conditions in rearing grounds may influence straying via the imprinting process, which occurs during the freshwater residency of juveniles (Hasler and Scholz 1983) at multiple developmental periods (Dittman et al. 2015). During imprinting, a juvenile fish forms a memory of the unique chemical mixture of its natal site and the imprinted odor subsequently acts as a directional cue during the spawning migration (reviewed by Dittman and Quinn 1996; Bett and Hinch 2016). Evidence for a link between rearing conditions and straying is currently limited, but some clues can be drawn from previous research on juvenile life history variation. For instance, Westley et al. (2013) docu-

mented increased straying in ocean-type Chinook Salmon, which migrate to the ocean during their first year of life, when compared to stream-type Chinook or Coho salmon, which remain in freshwater for at least one year. Furthermore, straying increased when ocean-type Chinook Salmon were held in freshwater longer, possibly due to disruption of their normal imprinting process—ocean-type Chinook Salmon undergo earlier seasonal peaks in plasma thyroxine (T4) concentration compared to stream-type Chinook and Coho salmon (Westley et al. 2013), which appears to reflect an earlier outmigration. Additionally, juvenile movement in freshwater could also influence straying: juvenile Chinook Salmon that disperse further from their incubation sites during freshwater residency later exhibit reduced homing accuracy as adults (Hamann and Kennedy 2012). Juvenile movement can be affected by a variety of factors, such as food availability, habitat quality, and density-dependent competition (Grant and Noakes 1987; Gowan et al. 1994; Achord et al. 2003; Dittman et al. 2010; Cram et al. 2013), which could explain why straying may occur more frequently in fish that incubated or reared in lower quality habitat (Leider 1989; Ford et al. 2015).

### Location of Spawning and Rearing Habitats

Spatial positioning of rearing habitat within the river network may also affect donor stray rates. Brenner et al. (2012) found that gene flow among intertidal populations of Pink Salmon *O. gorbuscha* was significantly greater than gene flow among upstream populations, suggesting higher stray rates in intertidal areas. Similarly, Westley et al. (2015) documented higher stray rates

in Chinook Salmon populations with shorter freshwater migration distances. Proximity to nearby spawning grounds has been highlighted as a relatively strong indicator of straying (Olsen et al. 2010; Keefer and Caudill 2014), and the close proximity of intertidal spawning grounds could lead to increased straying among these populations. Proximity to release site can influence straying patterns in hatchery salmon as well, with more strays entering tributaries closer to release sites (Piston and Heintz 2012). Also, Chinook Salmon tend to search nonnatal streams more actively when they are close to their natal area (Keefer et al. 2008a), a behavior that could contribute to an increased likelihood of straying into nearby nonnatal rivers.

### Genetics

Straying may also be influenced by genetics. Hard and Heard (1999), for example, reared and released two transplanted Chinook Salmon populations together and found differences in stray rates between them. Brenner et al. (2012) studied straying rates in Pink Salmon and found variation in fish from different hatcheries, which the authors suggest could indicate genetic differences among stocks that affect the propensity to stray, although differing environmental conditions at the different hatcheries may also be a factor. Bams (1976) created a hybrid stock of Pink Salmon by crossing males from a local population with females from a distant donor population and found that introduction of a local male genetic component improved homing accuracy to the natal river system. Similarly, Candy and Beacham (2000) provided evidence that hybrid Chinook Salmon stocks are more likely to stray than natal stocks, and McIsaac and Quinn (1988) found evidence of a heritable component to homing. Ford et al. (2015) compared the returns of progeny of stray hatchery Chinook Salmon that spawned naturally with returns of progeny from a local population. The authors found that progeny of the hatchery fish strayed significantly more, further suggesting a possible local genetic component that improves homing accuracy. Together, these results indicate that homing accuracy may be improved by locally adapted, heritable traits. Progeny of immigrant salmon from donor populations would lack these traits and stray more. Unfortunately, Carlson and Seamons (2008) reviewed the heritability of various traits in salmonids and concluded that we know very little about the heritability of straying and homing behaviors and that we are currently unable to predict whether these traits could respond to selective pressures. In addition, the findings of some research on links between genetics and straying have been equivocal (McIsaac 1990).

In addition to a locally adapted genetic component that could improve homing accuracy, there may also be a sex-linked genetic component to straying. Hamann and Kennedy (2012) and Hard and Heard (1999) documented increased occurrences of straying in male Chinook Salmon. Other studies, however, have found similar rates of straying in males and females (Unwin and Quinn 1993; Thedinga et al. 2000), and age and sex are often confounded because younger fish are more frequently male.

### Conspecific Interactions

Intraspecific interactions may influence donor straying rates. Donor straying appears to decrease with increased population abundance (Sholes and Hallock 1979; Quinn and Fresh 1984; Hard and Heard 1999; Westley et al. 2015), which may reflect a collective navigation mechanism during spawning migrations whereby individuals in larger groups are better able to sense and respond to navigational cues. Overlap in run timing of different populations could also affect straying. Brenner et al. (2012) noted

that hatchery Pink Salmon stocks with higher stray rates typically had later run times that coincided with the run timing of wild Pink Salmon. They noted similar interactions between run timing and straying in Chum and Sockeye Salmon as well. Ford et al. (2015) documented higher stray rates in salmon originating from less populated spawning areas and suggested that strays may be attracted to spawning grounds with large concentrations of conspecifics. Behavioral tests on Sockeye Salmon indicate that strays are attracted to conspecific olfactory cues, or pheromones (Bett and Hinch 2015), which could explain the apparent tendency for strays to enter rivers already occupied by conspecifics (Jonsson et al. 2003; Dittman et al. 2010). Therefore, size of donor and recipient populations could inversely affect straying: large donor populations could exhibit less straying due to a strengthened collective navigation, and large recipient populations could receive more strays by providing a stronger concentration of conspecific cues. Interestingly, each of these effects could potentially reduce the occurrence of recipient straying into small populations.

### Water Flow

Hydrology may also affect straying. Olsen et al. (2010) found that water flow and the number of drainage basins influenced population structure—a reflection of differences in the occurrence of straying. The authors suggest that variation in the spatial scale and discharge of tributaries alters the level of straying by influencing the complexity or strength of olfactory directional cues. Unwin and Quinn (1993) also found an interaction between flow and straying, with Chinook Salmon straying more frequently into rivers with higher discharge. Similarly, Labelle (1992) documented large numbers of stray Coho Salmon in a British Columbia river, which he suggested might be attributed to the river's large size and discharge relative to nearby streams. Labelle (1992) also noted that much of the straying occurred when a drought reduced flows in upstream tributaries, possibly discouraging fish from migrating further upstream. A study on Atlantic Salmon, however, found that straying was not influenced by discharge (Jonsson et al. 2003), suggesting that a relationship between flow and stray rate may only exist under certain conditions. In addition to discharge, complex flow patterns may enhance straying. For example, White (1934) attributed high straying in Atlantic Salmon to confusion that may have been caused by two stream channels converging in a common estuary. Environments such as this could make olfactory directional cues difficult to discern.

### Influence of Human Activity on Stray Rates

Some of the factors discussed previously are affected by human activity, and the influence of these activities on straying should be taken into consideration by fisheries managers when attempting to predict or alter donor stray rates and their influence on recipient populations.

### Climate Change

In regions where river temperatures are rising—potentially associated with human-induced climate change—donor (and therefore recipient) straying could become more frequent, as has been found in European Atlantic Salmon (Valiente et al. 2010; Horreo et al. 2011). Many Atlantic Salmon populations are small, often numbering in the hundreds, and Valiente et al. (2010) predicted that as climate change continues to encourage straying, neighboring populations will become less genetically distinct over time, although the potential benefit of demographic rescue might outweigh the risks of genetic homogeneity when abundances are so low. Over the past several decades, Pacific salmon

have faced increasing summer river temperatures, particularly in their southern range. For example, mean summer temperatures in the Fraser River increased  $\sim 1.5^{\circ}\text{C}$  in the latter half of the 20th century (Patterson and Hague 2007) and temperatures in the Columbia River have increased  $\sim 4^{\circ}\text{C}$  (Crozier et al. 2008). In addition to promoting straying, high river temperatures can cause migration mortality (Hague et al. 2011; Martins et al. 2012b). During warm years, the combined effects of increased migration mortality and increased donor straying could threaten small recipient populations, although, as previously discussed, straying could also provide a rescue effect for recipient populations unable to adapt to warming conditions.

### Hatcheries

Hatcheries constitute unnatural rearing conditions that might disrupt the imprinting process (Dittman and Quinn 1996) and subsequently promote donor straying. The potential for hatchery immigrants to lower the fitness of a wild recipient population is particularly high when hatchery stocks are domesticated (Berejikian and Ford 2004; Araki et al. 2008). Comparisons of donor straying in hatchery and wild fish are difficult due to the traditional reliance on marked juveniles and visual assessment of their returns, resulting in a bias towards the collection of hatchery data (Quinn 1993). However, new methods using microsatellite techniques to measure donor straying in wild and hatchery Chinook salmon provided evidence that hatchery fish stray more than wild fish (Ford et al. 2015). Other research, though, has not found an influence of hatcheries on straying (McIsaac 1990; Labelle 1992), and evidence of hatchery-induced straying is still lacking. Particularly concerning is the possibility that large numbers of stray hatchery salmon could mask the decline of a wild recipient population and confound efforts to monitor escapement. Such an occurrence was demonstrated by Johnson et al. (2012), who noted that the influx of hatchery Chinook Salmon in Mokelumne River, California, has created the false appearance of population growth in the declining wild population—a troubling consequence that, if left undetected, could preclude intervention by fisheries managers.

Concern over the potential for hatchery rearing to promote donor straying has prompted suggestions for alternative rearing strategies to improve homing accuracy. For example, many hatcheries do not rear eggs, alevins, or emergent fry in the targeted “natal” water, and Dittman et al. (2015) proposed adding targeted water to hatchery setups to allow embryonic imprinting. Early and late releases of smolts, meanwhile, can increase the probability of straying (Pascual et al. 1995; Westley et al. 2013), perhaps due to disruption of their normal imprinting process. There is also evidence that older salmon tend to stray more (Quinn and Fresh 1984; Unwin and Quinn 1993; Pascual et al. 1995), and Pascual et al. (1995) suggested that releasing hatchery fish at a larger size (relative to wild fish) could result in earlier age at maturity and lower stray rates. Clarke et al. (2014), however, found increased donor stray rates in steelhead *O. mykiss* smolts released at a larger size. In addition, attempts to rear fish to a larger size could delay their release and thereby promote straying. Ultimately, hatchery-rearing practices that deviate more from the natural ecology of juvenile salmon could impair the imprinting process and practices that attempt to emulate natural conditions may offer the best approach to reducing donor stray rates.

### Transplanting Stocks

Transplanting stocks may also promote donor straying. The apparent genetic influence on homing ability indicates that trans-

planted fish could lack locally adapted genes and stray more frequently and also that transplanted fish may have a tendency to return to their ancestral site. Studies on transplanted Chinook Salmon, for example, have demonstrated that they stray to their ancestral site more frequently than nontransplanted fish, despite never experiencing water from the ancestral location (McIsaac and Quinn 1988; Candy and Beacham 2000). Furthermore, gene flow from transplanted stocks into wild populations can threaten the genetic structure of the wild populations (Horreo et al. 2011). Westley et al. (2015), however, did not find any evidence that donor straying increases when juvenile Chinook Salmon are displaced to a new location before release, even though they experienced their natal waters during early rearing stages, although displacement was highly confounded among populations, making it difficult to tease apart population effects from displacement.

If displacement does encourage straying, it is possible that the homing ability of transplanted stocks could improve relatively quickly following transplantation. Hard and Heard (1999) transplanted Chinook Salmon gametes to an uninhabited river in Alaska and found that the stray rate of the first generation transplants was twice as high as that of their progeny. These results suggest that selection for homing to the transplanted site could significantly reduce donor stray rates over just a few generations. If a stock is transplanted to a location already occupied by a local population, however, the genetic composition of the local population could be substantially altered, particularly if the population’s abundance is small.

### Hydroelectric Dams

Hydroelectric development is prevalent in many salmon-bearing rivers (Nehlsen et al. 1991; Slaney et al. 1996), where it disrupts natural flow patterns and can make navigation using olfactory directional cues more difficult. For example, Fretwell (1989) documented persistent atypical migratory behavior among Gates Creek Sockeye Salmon—the same small population in which we found high levels of recipient straying—in response to altered flow patterns. In this system, a dam diverts much of the water from their nursery lake down a power canal. Tagged salmon repeatedly returned from the main channel to the impassable power canal and many eventually left the area, potentially in favor of other streams. Dams may also influence straying by creating large, dense aggregations of holding salmon. As noted above, Pacific salmon may tend to track conspecific cues (Quinn et al. 1983; Dittman et al. 2010; Bett and Hinch 2015) and this tendency is likely to increase with the size of a local aggregation of conspecifics (Quinn et al. 1989; Brenner et al. 2012; Ford et al. 2015). We therefore hypothesize that the large aggregations of salmon that form immediately downstream of dams may attract migrants. Migration delay regularly occurs downstream from dams (Caudill et al. 2007), and we observed delay below the dam in the Seton River (Burnett et al. 2014) where we captured many strays in 2012.

### CONCLUSION

A common perception of homing in Pacific salmon is that straying only occurs in a small proportion of fish and is therefore unlikely to have a significant effect on the population that loses the strays. The demographic and genetic structure of recipient populations, however, could be affected by straying, particularly under the following conditions: (1) when the donor populations are large, (2) when donor straying is frequent, and (3) when the recipient population is small. The second of these conditions can be influenced by several environmental factors, including tem-

perature, rearing conditions, location of spawning habitat, conspecific interactions, and water flow. Resulting changes in recipient populations could lower population-level fitness and increase the risk of local extirpation or the loss of locally adapted traits, although immigration could also provide a demographic and genetic rescue that sustains some small populations. We hope that the information provided here will stimulate further discussion on the possible risks of recipient straying and the factors that influence straying rates, and we encourage natural resource managers to consider the risks associated with straying and the activities that promote its occurrence.

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