

# A review of homing and straying of wild and hatchery-produced salmon

Thomas P. Quinn

*Fisheries Research Institute, School of Fisheries, WH-10, University of Washington,  
Seattle, WA 98195, USA*

## Abstract

This paper reviews studies on the patterns of straying of adult salmonids from their river or hatchery of origin, with emphasis on Pacific salmon. The prevalence of straying varies greatly among populations. In general, introduced (i.e. non-native) populations and salmon displaced from their rearing site for release stray more than native salmon and those reared and released on-site. Evidence that standard hatchery practices increase the tendency of salmon to stray is equivocal but releases of salmon at a different season from the normal migration period can increase straying. Estimates of straying vary greatly between hatcheries and rivers, so general statements on straying proportions have minimal biological significance. Straying between hatcheries and spawning grounds gives cause for concern because there is evidence that the offspring of hatchery-produced salmon may be less viable than those from local wild fish. The impact of straying on local gene pools depends not only on the prevalence of straying but on the degree of assortative mating and survival differential between populations. At present, fundamental gaps in our understanding of the genetic and environmental factors that influence straying hinder accurate prediction of the levels and consequences of straying.

## Introduction

Homing to the natal site for reproduction is characteristic of salmonid fishes (Scheer, 1939; Hasler and Scholz, 1983; Quinn, 1990), but it has long been known that some individuals stray and spawn elsewhere. Straying is important for salmonids because it leads to the colonization of new habitats (Milner, 1987; Milner and Bailey, 1989) and avoidance of unfavorable local conditions (Lucas, 1985; Leider, 1989). However, research has revealed a wide variety of genetic differences among populations within species (see reviews by Ricker, 1972; Saunders, 1981; Taylor, 1991). Such differentiation presumably results from the scarcity of strays and/or their high mortality rate, relative to locally adapted salmon. The preservation of indigenous populations is one objective of salmon management (McDonald, 1981; Wright, 1981), in part because these fish are often more productive than transplanted populations (Ricker, 1972; McIntyre, 1984; Reisenbichler, 1988).

Hatcheries differ from rivers in many respects, and it is not surprising that

genetic differences between hatchery and wild salmonids arise (e.g. Swain and Riddell, 1990; Skaala et al., 1990; Johnsson and Abrahams, 1991; reviewed by Hindar et al., 1991). To the extent that these genetic differences reduce the fitness of hatchery fish in the wild (Reisenbichler and McIntyre, 1977; Chilcote et al., 1986; Leider et al., 1990), the straying of hatchery-produced salmonids to interbreed with wild fish is cause for concern (Thorpe, 1986; Barbat-Leterrier et al., 1989). Moreover, if the disparity in abundance between wild and hatchery-produced salmon is great, the presence of strays may frustrate efforts to estimate population sizes correctly. In this paper I review studies of homing and straying, with emphasis on Pacific salmon (*Oncorhynchus* spp.) to facilitate assessment of the possible genetic interactions between hatchery-produced and wild salmon.

### **What is straying?**

Straying is the migration of mature individuals to spawn in a stream other than the one where they originated. The spatial scale implied by 'where they originated' is vague. Quinn et al. (1987) documented the return of sockeye salmon (*O. nerka*) to the lake of origin but not necessarily to the tributary of origin. The extent to which wild salmon return to the reach within a stream where they were spawned is also not known. However, experiments have indicated that salmon released as smolts in a particular section of a river are more likely to return to that section than other sections (Wagner, 1969; Cramer, 1981).

From the standpoint of orientation, a salmon strays if it ascends a non-natal river and does not subsequently make its way to its natal river. If the fish enters a hatchery, it is seldom given the chance to retreat, so there is some question as to whether 'strays' entering hatcheries would have eventually left. However, data on autumn chinook salmon (*O. tshawytscha*) returning to the lower Columbia River did not reveal consistently higher levels of straying to hatcheries than to adjacent spawning grounds (Quinn et al., 1991).

When hatcheries rear salmon for a period of time and then release them in other streams (e.g. Nickelson et al., 1986), it is not clear whether 'home' is the hatchery of origin or the stream of release. Similarly, when salmon are trucked around long stretches of the Columbia or Sacramento rivers (Ebel et al., 1973; Slatick et al., 1975; Sholes and Hallock, 1979), is 'home' the hatchery or the release site? In my view, the term 'homing' should be used relative to the site of incubation and initial rearing.

### **What proportion of naturally produced salmon stray?**

Among the earliest large-scale studies of homing was Foerster's work at Cultus Lake, British Columbia (summarized by Foerster, 1968). All the

sockeye salmon (*O. nerka*) smolts leaving the lake in 1931 and 1936 were marked with fin-clips. Marked adults comprised 99.4% and 98.5% of the returning adults of the appropriate age group, indicating that very few sockeye from other Fraser River populations entered the lake. The vast majority of sockeye in the watershed must pass Cultus Lake to return to their natal rivers, so the absence of strays into the lake was noteworthy. However, there was no record of the number of marked Cultus Lake sockeye straying from the lake. Patterns of parasite prevalence and protein polymorphisms (Quinn et al., 1987), however, indicated that other sockeye salmon populations seldom strayed between lakes. Life history differences among populations within lake systems imply that homing to spawning areas within lakes is probably precise as well (e.g. Blair et al., 1993).

To what extent is the homing precision of sockeye salmon representative of other species? A marking study of chum salmon (*O. keta*) on Hokkaido, Japan, revealed that 97.8% of the 275 in-river recoveries were in the river of origin and the rest were found in nearby rivers (Sakano, 1960, in Sano, 1966). MacQuarrie and Bailey (1980) reported that 5.4% and 5.2% of the chum salmon fry produced in artificial incubation facilities on Thornton Creek strayed to Salmon Creek, British Columbia, in 1979 and 1980, respectively.

There is a widely held notion that pink salmon, *O. gorbuscha*, are more prone to stray than other Pacific salmon species. This was supported by the recolonization of Sashin Creek, Alaska, after deliberate extermination of the even-year cycle (Merrell, 1962) and the recolonization of the upper Fraser River, British Columbia, by pink salmon after the rock slide at Hell's Gate (Vernon, 1962). Parker (1967) also reported "substantial straying within a fairly large 'home' area". Tagging of hatchery-produced pink salmon in the Soviet Far East revealed considerable straying in some cases (Glubokovsky and Zhibbotovski, 1989; Table 1). Finally, the rapid colonization of the Great Lakes by pink salmon after accidental introduction (Kwain and Lawrie, 1981) and of the White and Barents Seas after introduction to the Kola Peninsula (Bakshtansky, 1980) imply extensive straying. However, studies reviewed by Lister et al. (1981) revealed no particular tendency to stray, and Gharrett (1985) reported that "no straying was observed from the genetically marked Auke Creek population into the unmarked Waydelich Creek implying accurate homing to stream of origin". I have been unable to locate a comprehensive study of straying by wild pink salmon populations, hence the conclusion that they stray more commonly than the other salmon species seems premature.

There is both practical and theoretical interest in comparing straying prevalences of species (Quinn, 1984). The long-term study by Shapovalov and Taft (1954) at Scott and Waddell creeks in California revealed that coho salmon, *O. kisutch*, strayed between the creeks much more frequently than did steelhead, *O. mykiss* (15 and 27% vs. 2 and 3%). There is considerable

Table 1

Patterns of recovery (%) of pink salmon marked as fry and recovered as adults in hatcheries in the Soviet Union (Glubokovsky and Zhibbotovski, 1989)

Tagging region and year	Region where marked fish were recovered			
	West Sakhalin	Gulf of Aniva	East Sakhalin	Iturup Province
<i>West Sakhalin</i>				
1961	62.60	21.20	7.90	7.70
1962	24.24	7.07	28.29	34.34
1963	99.89	0.05	0.06	0.00
1977	43.01	0.00	41.27	15.72
<i>Gulf of Aniva</i>				
1979	0.48	92.54	6.82	0.16
<i>East Sakhalin</i>				
1977	1.06	6.02	52.15	40.77
1977 <sup>a</sup>	2.38	28.71	65.12	3.78
1979	2.26	1.71	34.43	61.60
<i>Iturup Province</i>				
1974	0.00	0.18	11.22	88.60
1977	0.05	0.01	0.05	99.89
1979	0.01	0.00	0.07	99.92

<sup>a</sup>Data are from two different hatcheries.

variation in straying prevalence among rivers, as several Vancouver Island, British Columbia, coho salmon populations had much lower incidences of straying than Shapovalov and Taft (1954) reported (Labelle, 1992). Unfortunately, the work of Shapovalov and Taft (1954) seems to be the only study on more than one species in the same rivers.

In addition to studies of the distribution of adults that had been marked as juveniles, a number of experiments have assessed the fidelity of marked adults displaced from their spawning stream (presumed to be their home river). In general, the great majority of recoveries are in the river where the salmon were first captured (e.g. Hartman and Raleigh, 1964; Heggberget et al., 1988). Variation in the proportion of displaced salmon returning may be related to site-specific characteristics (McCart, 1970; Blair and Quinn, 1991) or water flow at the time of the experiment (Helle, 1966). In general, there are so few comprehensive studies of straying by naturally produced salmon and there is so much variation in straying within species that interspecific comparisons are unwarranted.

## Are salmon from hatcheries more inclined to stray than naturally produced salmon?

Juvenile salmon from hatcheries are often marked to evaluate their marine survival and distribution, hence most data on homing and straying patterns are from hatchery populations. There is usually no comparable tagging effort on naturally produced salmon in the same river, so it is not possible to determine if the hatchery influenced the proportion of salmon straying. However, two recent studies provide information on this question. Labelle (1992) tagged three groups of juvenile coho salmon from the Quinsam River, on the east side of Vancouver Island: naturally produced fish, fish reared in the hatchery but released into the watershed as pre-smolts (termed ‘colonization’) and fish reared and released from the hatchery. There was no significant difference in the proportion of strays among the groups (Table 2). On the other hand, McIsaac’s (1990) study of a wild stock of autumn chinook salmon in the Lewis River, Washington, indicated that even a brief period of hatchery rearing increased the proportion of strays, relative to naturally produced salmon from the same population (Table 3). Jonsson et al. (1991)

Table 2

Mean annual percentage of coho salmon straying from the Quinsam River, British Columbia, in relation to rearing history: spawned, reared and released from the hatchery (‘hatchery’); spawned and initially reared in the hatchery but transplanted into the river (‘colonization’); naturally produced (‘wild’) (data from Labelle (1992))

Age group	Rearing history		
	Hatchery	Colonization	Wild
Adults (age 3 years)	0.0	0.1	3.9
Jacks (age 2 years, males)	0.2	0.4	0.0

Table 3

Homing of Lewis River, Washington, autumn chinook salmon caught, tagged and released on site as fry (‘wild’), caught, reared for about 10 weeks in a hatchery, tagged and released (‘wild/hatchery’), or reared entirely in a hatchery (‘hatchery’); adult salmon were classified as having returned to the Lewis River, to adjacent rivers (one major tributary above and below the Lewis River), to other Columbia River locations or to locations outside the Columbia River system (McIsaac, 1990)

Rearing history	Distribution of returning adults (%)			
	Lewis River	Adjacent rivers	Columbia R. system	Outside the Columbia R.
Wild	96.8	<0.1	3.2	0.0
Wild/hatchery	90.7	4.8	4.5	0.0
Hatchery	89.7	5.7	4.6	<0.1

reported that hatchery-reared Atlantic salmon strayed more from the River Imsa, Norway, than did wild fish. However, the hatchery was only 100 m above the mouth of the river and the researchers attributed the poor homing performance of hatchery fish to inadequate exposure to river waters. Thus the evidence is limited and equivocal on whether hatchery rearing per se increases the tendency of salmon to stray.

### **Are there spatial and temporal patterns of straying?**

Given that some salmon stray, it would be useful to know whether they tend to stray to rivers below their origin (as might be expected if exhaustion influenced straying) and whether straying salmon tend to enter rivers or hatcheries with certain characteristics. Such information was seldom available in the past, owing to the difficulties of surveying non-natal rivers in an extensive and unbiased manner. However, current widespread use of the coded wire tag in hatcheries and selected rivers has presented the opportunity to study straying over large spatial scales.

Analysis of data on spring chinook salmon released from the Cowlitz River Salmon Hatchery, Washington, indicated that most (98.6%) of the returning salmon ascended the Cowlitz River (Quinn and Fresh, 1984). However, most of the strays went upstream beyond the Cowlitz River, and 76.6% (446) of the estimated 582 strays were recovered in the Lewis River, 30 km upstream. This is more than four times the number that strayed to the Kalama River (108, 18.6%), even though the Kalama River is only 9 km upstream from the Cowlitz River.

Analysis of five populations of autumn chinook salmon on the Columbia River below Bonneville Dam revealed considerable variation among hatcheries in the tendency of salmon to stray, ranging from 9.9 to 27.5% (Quinn et al., 1991). More dramatic, however, was the variation in attractiveness of rivers to strays. Two hatcheries (Abernathy and Washougal) received virtually no strays whereas about 30% of the marked salmon in the Kalama and Lewis rivers were strays. New Zealand chinook salmon straying patterns also seem to reflect some combination of proximity to the natal river and flow (Unwin and Quinn, 1993), although temperature and presence of conspecifics might also be expected to influence the tendency of strays to enter a river.

Events that affect water quality in the home river can also influence straying (e.g. the eruption of Mt. St. Helens; Leider, 1989). In addition to these dramatic situations, there is also some 'background' year-to-year variation in straying (Quinn and Fresh, 1984; Quinn et al., 1991). On a finer spatial scale, the tendency of hatchery-produced salmon to enter their hatchery, as opposed to spawning in the river, can vary greatly from year to year. Nicholas and Downey (1983) reported that the proportion of hatchery-produced chinook

salmon entering Elk River Hatchery, Oregon, averaged 22.8% over a 9 year period but ranged from 5.9% to 52.2%. Some of the factors that presumably affect general attractiveness of rivers and hatcheries (such as flow, temperature or conspecifics) may also influence interannual patterns of straying and the tendency to enter hatcheries.

### Are there demographic patterns of straying?

There is evidence from several studies that older salmon are more prone to stray than younger salmon from the same population. Quinn and Fresh (1984) reported that 0.34%, 1.55%, 1.99% and 3.55% of the spring chinook salmon from Cowlitz River Salmon Hatchery aged 2, 3, 4 and 5 years strayed, respectively. Quinn et al. (1991) reported straying proportions of 3.3%, 16.0%, 14.6% and 18.7% for autumn chinook aged 2, 3, 4 and 5 years, respectively from five lower Columbia River hatcheries. Labelle's (1992) study of Vancouver Island coho salmon populations revealed that fewer jacks (2-year-old males) strayed than 3-year-old adults (0.4% vs. 1.0%). Finally, data on chinook salmon entering Lyons Ferry Hatchery on the Snake River also indicate that strays are made up of greater proportions of older than younger age groups (Table 4). It is possible that older salmon are more likely to stray because they have 'forgotten' the odor of their natal stream. However, subtle changes in the odor of the river or hatchery may make it progressively less similar to the imprinted odor as years go by.

### What hatchery practices encourage straying?

Juvenile salmon learn the odors of their home stream (or hatchery) before seaward migration (Hasler and Scholz, 1983). Most studies indicate that the critical period of imprinting is at the time of smolt transformation. Salmon transplanted before the smolt stage tend to return to their release site, not the site of their initial rearing (e.g. Donaldson and Allen, 1958). However, it

Table 4

Variation in straying with the age of the salmon, based on estimated returns of chinook salmon to Lyons Ferry Hatchery, on the lower Snake River, for return years 1984–1989 (see also Table 7; D.O. McIsaac, Washington Department of Fisheries, unpublished data, 1990)

Age	Origin of chinook salmon (%)		
	SNAKE RIVER (native)	UMATILLA RIVER	OTHER STRAYS
2	93.2	5.1	1.7
3	84.2	13.6	2.2
4	84.5	9.0	6.5
5	62.4	9.9	27.7

appears that salmon also learn and remember odors experienced before the smolt stage. If the release and rearing sites are close to each other, especially if they are on the same river, the salmon are likely to return to the rearing site, rather than the release site (Lister et al., 1981; Table 5). Moreover, the release site's position within the watershed also affects homing. Johnson et al. (1990) reported: "Almost all returning [coho salmon] released as yearlings at a site 23 km upstream from the rearing hatchery returned to the rearing site, whereas only 7–26% of adults originally released in a tributary 11 km downstream from the rearing hatchery returned to the rearing site."

Displacement distance alone does not determine whether salmon will return as adults to their release site, however. Even short displacements can produce returns to the release site if the water characteristics of the release and rearing sites differ (Quinn et al., 1989). On the other hand, salmon displaced long distances (e.g. around dams on the Columbia River) may return to the rearing site (Ebel et al., 1973; Slatick et al., 1975).

Although displacements from one freshwater site to another before release may affect the proportion of salmon straying, releases in saltwater also tend to increase straying. Solazzi et al. (1991) reared coho salmon at Cascade Hatchery, near Bonneville Dam on the Columbia River. Coho smolts were released at six locations: below Bonneville Dam (river km (rkm) 234), at Tongue Point (rkm 29), the bar of the river (rkm 2), 19 km offshore in the river's plume, 19 km offshore outside the river's plume and 38 km offshore in non-plume water. These six locations, progressively far from the rearing site, produced the following proportions of salmon that returned to rivers outside the Columbia River system: less than 0.1%, 3.4%, 4.1%, 6.1%, 21.0% and 37.5%. The large proportion of salmon reared entirely in a hatchery on the Columbia River system that failed to return to the watershed after release in non-plume water was particularly striking. This is consistent with the results of work on Atlantic salmon in Norway (Gunnerød et al., 1988; Heggberget et al., 1991).

In some cases, hatchery-produced salmon are reared in saltwater net pens

Table 5

The relationship between straying of coho and chinook salmon and steelhead trout from the release site and the distance between rearing and release sites within the same river system; data from the compilation of studies reviewed by Lister et al. (1981)

	Distance from rearing to release sites (km)		
	0	4–29	47–485
Number of studies	10	5	7
Mean % straying	3	74	8
Range	0–13	37–100	1–39
% Straying to rearing site	–	77	55



for some period before release. Sockeye salmon released from net pens homed to the nearby hatchery where they had been incubated and few strayed to nearby streams (Wertheimer et al., 1983). Similarly, Heard and Crone (1976) found that coho fry seined from Sashin Creek and reared in net pens near the mouth homed to the creek as adults. In both the above studies, however, the freshwater and saltwater rearing sites were very close to each other. Rensel et al. (1988) reported that coho salmon transported from their natal hatcheries and released from pens in the south part of Puget Sound, Washington, tended to be caught in that region or strayed to rivers there. Similarly, escapees from Atlantic salmon pen rearing facilities enter nearby rivers (Gausen and Moen, 1991). However, their distribution within the river system may differ from that of wild salmon (Webb et al., 1991).

Taken together, the displacement studies indicate that maturing salmon tend to reverse the sequence of their outward migration as juveniles. Under natural conditions, this will lead them to the river or hatchery where they began life. Displaced salmon return first to the odors of their release site and will continue to the rearing site if its odors can be detected. If not, they will seek the nearest river or hatchery (Quinn et al., 1989; Quinn, 1990).

Disruptions in the sequence of odors associated with freshwater life and seaward migration caused by artificial displacement can result in straying. It is also possible that changes in hatchery water source during the rearing period or use of different sources (e.g. river vs. well water) when juvenile rearing and adult return take place might affect homing even though no physical displacement occurred. However, I am not aware of any study that has examined this possibility.

Olfactory imprinting is apparently linked to the complex processes of smolt transformation and migration (Hasler and Scholz, 1983). These processes occur at specific times for populations, hence we might expect salmon homing to be influenced by the season of release from a hatchery. Consistent with this prediction, Hansen and Jonsson (1991) reported that winter releases of Atlantic salmon from a marine site produced more strays and a wider geographical range of straying than did releases in other seasons. In New Zealand, chinook salmon releases in the winter have also produced higher proportions of strays (Unwin and Quinn, 1993).

To the extent that salmon homing is based on odors learned during juvenile stages, one would expect that a non-native population would home as well to a new site after having been reared there as would native fish (though their survival rates might differ). However, there is some evidence to the contrary, indicating a genetic component in homing (Bams, 1976; McIsaac and Quinn, 1988). Labelle (1992) also reported that salmon were more likely to home if reared and released from their ancestral stream than another site (Table 6). It is not clear from these studies what makes a river more attractive to native than non-native fish. Perhaps innate preferences for particular temperature,

Table 6

Straying (mean of yearly percentages) by east coast Vancouver Island, B.C., coho salmon reared and released in their river of origin or the Rosewall Creek experimental hatchery (Labelle, 1992)

River of origin	Rearing and release site	% Straying	
		Adults	Jacks
Trent River	Trent River	10.2	7.6
	Rosewall Creek	27.7	13.9
Black Creek	Black Creek	1.3	0.6
	Rosewall Creek	24.1	0.0
Little Qualicum River	Little Qualicum River	0.5	0.7
	Rosewall Creek	8.3	2.3

flow or substrate characteristics exist among populations. When these habitat preferences conflict with homing clues, straying may result.

In addition to the various influences of culture and release practices on homing, one final possibility should be mentioned. Morrison and Zajac (1987) reported that 18 of 44 chum fry (averaging 0.67 g) marked with half-length coded wire tags showed histological damage to one of the mainstem olfactory nerves. It is thus possible that poor tag injection may interfere with olfactory learning and hence homing, though the generally high levels of homing to hatcheries suggest that this is not a widespread problem.

### What are the consequences of straying?

The genetic integrity of a population could be compromised by strays entering the river or hatchery, regardless of the strength of the native population's homing tendency. The Lyons Ferry Hatchery, on the Snake River, Washington, has recently reported a large proportion of stray autumn chinook salmon into the hatchery (Washington State Department of Fisheries, unpublished memorandum). Many of these strays are from the Umatilla River, a tributary of the Columbia River below the Snake River (Table 7). At such levels of straying, only extremely severe outbreeding depression (i.e. natural selection against the progeny of the strays) could prevent introgression in the Lyons Ferry population.

There is no doubt that salmon stray; only the consequences can be disputed. Ricker (1972) and Reisenbichler (1988) have indicated that transplanted populations may be less productive than locally adapted ones. Thus, if a hatchery is established with non-local stock, strays might interbreed with local salmon and reduce their fitness. Even if the hatchery is initiated with local stock, genetic changes over generations may render the hatchery fish less fit than the wild fish for survival outside the hatchery (Hindar et al., 1991).

Table 7

Estimated percentage returns of native (Snake River) and stray autumn chinook salmon into Lyons Ferry Hatchery (D.O. McIsaac, Washington Department of Fisheries, unpublished data, 1990)

Year	Total return	Origin (%)		
		Snake River	Umatilla River	Other strays
1984	746	99.1	0.9	0.0
1985	608	90.3	9.2	0.5
1986	1430	96.3	1.6	2.1
1987	3530	92.2	5.9	1.9
1988	1674	82.5	14.2	3.3
1989	2205	52.9	34.5	12.6
1990	1760	66.4	21.1	12.6

To the extent that this is true, interbreeding of wild and hatchery salmon could also have a detrimental effect on the native gene pool.

The most thorough study of genetic interaction between hatchery and wild Pacific salmonids has been conducted on Kalama River steelhead (Chilcote et al., 1986; Leider et al., 1990). The results of this study indicated that steelhead of hatchery origin were less productive, when spawning naturally, than were wild steelhead. Unfortunately, the hatchery-produced steelhead were not native to the Kalama River, hence the hatchery–wild comparison was confounded by potential differences between stocks. There is a pressing need for studies of the genetic interactions and fitness patterns of wild and hatchery salmon of local origin. The evidence that the reproductive behavior of wild and hatchery-produced salmonids differs is particularly interesting (Jonsson et al., 1991; Fleming and Gross, 1992).

Although there is concern that strays from hatcheries will affect wild gene pools, there is also the possibility that wild salmon will stray into the hatchery. Nicholas and Van Dyke (1982) estimated that 2022 (64.7%) of the 3124 wild coho salmon returning to the Yaquina River watershed in 1981 entered the Oregon Aqua-Foods hatchery. Such decoying of wild salmon into hatcheries both reduces the number of wild fish in the stream and contributes to genetic mixing.

## Conclusion

The straying is an integral component of salmon behavior and population biology. Intra-specific variation in straying and the dearth of information on wild populations preclude judgment on whether some species are more inclined to stray than others. Hatchery-produced salmon may stray more than those produced naturally, but the evidence is equivocal at this point. However, the homing patterns of transplanted salmon often differ from those of

salmon released from the hatchery. The return location of transplanted fish seems to be determined by the spatial relationship between rearing and release sites and by their endocrinological state (e.g. parr–smolt) at the time of displacement.

There is evidence that older salmon stray more than younger ones, though the reason is unclear. Straying salmon do not necessarily enter the nearest river, but the environmental factors influencing straying are also unknown. Indeed, perhaps the most fundamental question remains unanswered: why do salmon stray? Are strays lost (unable to detect or recognize the odor of their home river) or have they located the home river and then actively compared home with non-home sites?

Whatever the reason, straying by even a small proportion of salmon from a large hatchery population can lead to interbreeding with wild salmon. Unless salmon select their mates based on genotype, interbreeding is likely to occur. Such assortative mating is entirely possible (Groot et al., 1986) but has not been demonstrated. Assuming that interbreeding takes place, the hatchery and wild salmon may hybridize and produce progeny with a genetic composition different from that of the wild gene pool. If the hybrids are poorly adapted to local conditions and fail to survive to adulthood, the wild gene pool will be preserved but at the cost of the potential reproduction of the wild fish that spawned with the hatchery fish. To understand fully the genetic interactions between wild and hatchery-produced salmon (Hindar et al., 1991), we must improve our understanding of straying, reproductive patterns, hybrid fitness and the genetic changes that occur in hatcheries.

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