Spatial Aspects of Imprinting and Homing in Coho Salmon, *Oncorhynchus kisutch*

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ABSTRACT: Analysis of seven years of coded wire tag data revealed that juvenile coho salmon, *Oncorhynchus kisutch*, released from two hatcheries in the Lake Washington watershed return almost exclusively to their hatcheries of origin. To determine if they learn the characteristics of more than one water source prior to seaward migration, coho salmon were reared in one of three hatcheries and were released from it or, after transportation, from a release site farther downriver. The locations to which adult salmon returned indicated that they had learned both the characteristics of their release site and the hatchery where they had been held prior to release. Salmon transported around much of their migratory route returned primarily to their release site, indicating that they needed to learn sequences of odors during their seaward migration in order to home in a complex river system.

The majority of salmonid fishes that survive to adulthood return to their natal site to spawn (Foerster 1936; Shapovalov and Taft 1954; Armstrong 1974; Swain 1982; Quinn and Fresh 1984; Berg and Berg 1987; Quinn and Tallman 1987; Quinn et al. 1987). The prevalence of homing in species with highly variable patterns of freshwater residence and anadromy (Rounsefell 1958) suggests that the process by which the fish learn the characteristics of their natal environment is flexible.

Coho salmon, *Oncorhynchus kisutch*, exposed to an artificial odorant prior to downstream migration as smolts are attracted to that odor at maturity (Scholz et al. 1976; Hasler and Scholz 1983). These and other results led Hasler and Scholz (1983) to hypothesize that salmon imprint only once, immediately prior to downstream migration. However, there is also evidence that wild coho salmon move considerable distances within watersheds before migrating to sea (Peterson 1982). Adult coho return to the site where they emerged from gravel nests as fry, not the site where they resided as smolts (Lister et al. 1981). Sockeye salmon, *O. nerka*, also typically home to tributaries of lakes experienced only as embryos or fry, not to the lake and its outlet experienced as smolts (see references in Quinn et al. 1987).

Transportation of juvenile salmon and trout within river systems has had mixed effects on homing. In some cases, fish captured during seaward migration, trucked to the lower Columbia River, and released, generally returned to the upriver rearing site (Ebel et al. 1973; Slatick et al. 1975). On the other hand, displacement from a hatchery to a release site downriver has often resulted in returns to the release site (Jensen and Duncan 1971; Vreeland et al. 1975; Cramer 1981; Vreeland and Wahle 1983).

It is thus unclear whether salmon learn the chemical characteristics of a single site at a specific developmental stage ("imprinting" by smolts: Hasler and Scholz (1983)) or if they learn a sequence of olfactory landmarks (Harden Jones 1968; Brannon 1982). By displacing smolts seaward, we can create gaps in their migratory experience as a way to examine the spatial aspects of olfactory learning. Specifically, we conducted two experiments in which salmon were released at their rearing sites or at a site downriver. The locations to which these salmon returned were compared among experimental groups and also compared to data from previous years on homing and straying within the watershed.

MATERIALS AND METHODS

Data Analysis on Homing in the Lake Washington Watershed

There are two major hatchery sources of coho salmon in the Lake Washington watershed (Fig. 1): the University of Washington's (UW) hatchery and the Washington State Department of Fisheries' hatchery on Issaquah Creek (Iss). We inspected the Washington Department of Fisheries and University of Washington data bases on coded wire tagged coho salmon and identified salmon recovered at these two hatcheries for return years 1979–85 to determine the extent of straying within this system.

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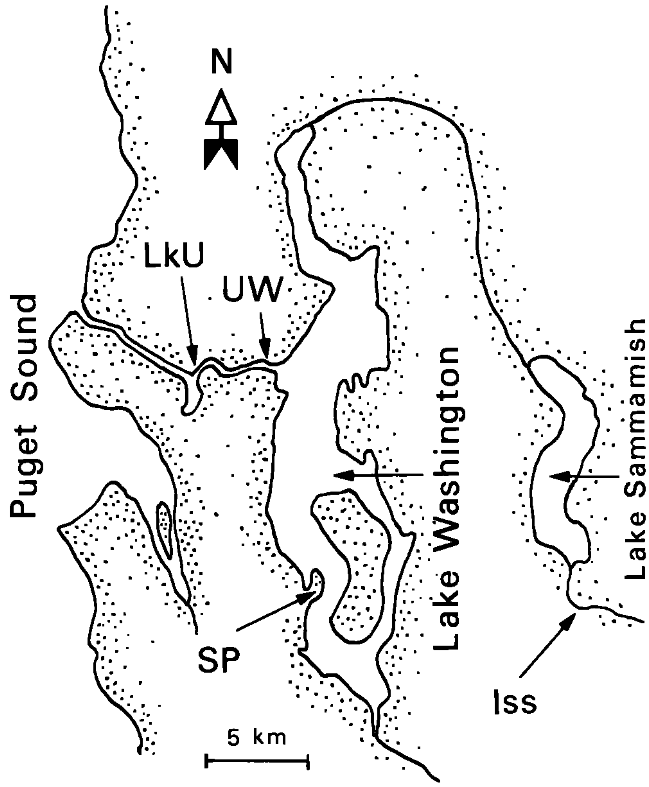

FIGURE 1.—Map of the Lake Washington watershed showing the locations of the release site on Lake Union (LkU) and the hatcheries at the University of Washington (UW), Seward Park (SP), and Issaquah Creek (Iss).

Treatment of Juveniles

In 1985 we initiated a study of patterns of imprinting and homing in the Lake Washington watershed. The basic experimental design was to expose coho salmon to the odors of Seward Park (SP) or Issaquah Creek (Iss) hatcheries and release them from those hatcheries or from a site 2.2 km downstream from the UW hatchery (Fig. 1). (The SP hatchery had been used for production of rainbow trout but not coho salmon prior to this experiment. Water for the SP hatchery is pumped from Lake Washington). Another group was reared in UW water and released at the downriver site.

Between 18 and 25 November 1985, adult coho salmon that had returned to the UW hatchery were spawned and the fertilized eggs incubated at the UW hatchery in dechlorinated city water. This is not the water source normally used in the hatchery; fish are normally incubated and reared in water pumped from the ship canal draining Lake Washington into Puget Sound (Fig. 1). The eggs hatched in January and yolk absorption was completed in March. In late March the fry were separated into three groups. Group 1, the control, was held at the UW hatchery and exposed to ship canal (UW) water during the smolt phase, from 20 May until 10–11 June, when the fish were tagged with internal coded wire tags. Fish in this study were judged to be smolts by their downstream migratory behavior and silvering. Only fish with silvery coloration and lacking parr marks were given coded wire tags. Group 1 fish were released into Lake Union, 2.2 km downstream from the UW hatchery, on 17 June. Groups 2 and 3 were transported to the SP hatchery on 21 March and reared there. They were tagged on 13 June (Group 2) and 14 June (Group 3). Group 2 fish were released into Lake Union on 1 July and Group 3 fish were released from SP on 27 June. Table 1 summarizes information on the treatments of the these groups.

On 19 March 1986 coho salmon at the Iss hatchery were marked by excision of the left or right ventral fin (10,000 fish per treatment). These salmon had emerged as fry in 1985 and smolted after one year in freshwater (average

TABLE 1.—Summary of coho salmon experimental treatments, indicating the date (in 1986) when fish were exposed to different water sources or moved. UW refers to UW hatchery water, CW refers to dechlorinated city water at the UW hatchery, SP refers to lake water at the Seward Park hatchery, Iss refers to the Issaquah Creek hatchery, and LkU refers to the Lake Union release site.

Developmental stage or operation		Experimental group 1	2	3	4	5
Eggs, alevins, and fry:	Site	CW	CW	CW	Iss	Iss
Parr:	Site	CW	SP	SP	Iss	Iss
	Date	—	3/21	3/21	—	—
Smolts:	Site	UW	SP	SP	Iss	Iss
	Date	5/20	—	—	—	—
Tagging:	Site	UW	SP	SP	Iss	Iss
	Date	6/10–11	6/13	6/14	3/19	3/19
Release:	Site	LkU	LkU	SP	LkU	Iss
	Date	6/17	7/1	6/27	3/19	4/9
	Size	10.0 g	12.6 g	11.3 g	26 g	26 g
	Number	8,491	10,020	10,148	10,000	10,000

weight = 26 g), unlike the UW coho, which smolted in their first spring. Those with their right fin clipped (Group 4) were trucked in two groups of 5,000 fish each to the Lake Union site and were released on 19 March. Those with the left ventral fin clipped (Group 5) were returned to the hatchery pond and released from the hatchery with the normal production fish on 9 April.

Recovery of Returning Adults

It was anticipated that most experimental coho escaping the fisheries would return to the hatcheries at UW, SP, or Iss, primarily in 1987. Coho salmon of the UW population almost all return in the second fall after their release (Brannon et al. 1982) and few precocious males ("jacks") occur. A trap to recover salmon returning to the SP hatchery was built in summer 1987; therefore no jack (1986) returns would have been collected that year, but the UW and Iss hatcheries were operating in 1986 to collect jacks. All hatcheries were also open in 1988 for salmon returning in the third fall after release. In addition to these primary recovery sites, the National Marine Fisheries Service (NMFS) operates a small hatchery on the opposite side of the ship canal. While no salmon released from NMFS were expected to return in 1987, the hatchery trap was operating and salmon entering it were checked. Some salmon released in Lake Union (where there is no hatchery or spawning ground) might have been expected to enter the NMFS facility if they had not imprinted on the UW hatchery.

RESULTS

Analysis of the historical data revealed that from 1979 to 1985, 5,465 coho salmon with coded wire tags from UW and Iss were recovered at these two hatcheries. Of 4,696 tagged UW coho salmon recovered, only two (0.04%) strayed to Iss. Similarly, of 769 tagged Iss coho, only one (0.13%) entered the UW hatchery. Thus, virtually no straying takes place between these two hatcheries when coho are reared and released at the hatcheries.

Only one jack from the UW-SP transfer groups (from Group 2) was recovered in 1986 at the UW hatchery, indicating that the absence of a return trap at SP did not bias the data significantly (Table 2). Group 1, exposed to UW water and released into Lake Union, returned exclusively to the UW hatchery (34/34). Group 2, which had not directly experienced UW water but had been reared at SP and released into Lake Union returned primarily to the UW hatchery (Table 2) but seven salmon were recovered at SP. Group 3 fish, reared in the same manner as Group 2 fish but released from SP, returned exclusively to SP.

In 1986 and 1987, 73 fish with clipped ventral fins were recovered at the UW and Iss hatcheries. Group 5, reared and released from Iss

TABLE 2.—Patterns of homing displayed by adult coho salmon from different experimental rearing regimes. Numbers listed represent actual fish returning while numbers in parentheses are the percentage of each experimental group returning to that recovery hatchery. Groups 3 and 5 were reared and released at Seward Park and Issaquah Creek hatcheries, respectively. Groups 1, 2, and 4 were released into Lake Union but had been reared at the University of Washington, Seward Park, and Issaquah Creek hatcheries, respectively.

Recovery hatchery	Experimental group				
	1	2	3	4	5
U. of Washington	34(100)	44(86)	0	15(88)	2(4)
Seward Park	0	7(14)	44(100)	0	0
Issaquah Creek	0	0	0	2(12)	54(96)

hatchery, generally returned to Issaquah Creek (54/56 recoveries). The return of transported fish (Group 4) was lower but they tended to enter the UW hatchery (15/17 recoveries). Fifteen coho salmon entered the NMFS facility in 1987 but none were from any of the experimental treatments.

DISCUSSION

The coded wire tagging data demonstrated that salmon home almost without fail to the UW and Iss hatcheries if they have been reared and released at these sites. The return of all members of Group 1 to the UW hatchery supported the findings of many previous studies (reviewed by Hasler and Scholz (1983)) that exposure to a water source at the smolt stage or at the time of release provides a sufficient basis for homing. Similarly, Group 3, released from SP, returned exclusively to SP. Fish from Group 2 had experienced a gap in their migration, relative to Group 3. They were reared at SP during the parr and smolt stages but did not experience the route from SP to the Lake Union release site, a distance of some 18 km. Most of these fish entered the UW hatchery but 7 of 51 returned to SP.

The Iss controls (Group 5) returned to that hatchery and the salmon trucked to Lake Union tended to enter the UW hatchery, though the return rate of the experimentals was quite low. The salmon held in Iss hatchery before being trucked to Lake Union presumably learned the characteristics of their hatchery but were unable to detect them when they returned to Lake Union as adults. Taken together, the results of the experiments support Harden Jones' (1968) hypothesis that salmon learn and subsequently retrace a sequence of odors. In situations where the home odor travels relatively undiluted or unchanged downriver, salmon artificially displaced downriver might be able to home successfully. However, if the home water is diluted or altered by passage through lakes (as may have occurred in our experiments), salmon may only return as far as their release site.

It is possible that the differences between the patterns of homing displayed by Groups 2 and 3 and Groups 4 and 5 could be due to differences in the degree of smolting. For example, if there is a very tight window for imprinting which is linked to some subtle (or unknown) changes during smoltification, then perhaps 7 of the 51 returning fish from Group 2 had reached and ended the imprinting phase prior to transport to Lake Union. This would imply that all the returning fish were able to detect SP water but that only the above 7 responded to it. This explanation seems unlikely, however, since these fish were released during a relatively late phase of the smolting process. If imprinting is linked to events such as natural thyroid hormone peaks and the onset of silvering and downstream migration (Hasler and Scholz 1983), then all the fish in Group 2, whether released at SP or transported to Lake Union, would have been expected to return to SP.

The gap in experience that we provided was relatively short in distance but great in effect on homing, compared with experiments on the Columbia River (e.g., Slatick et al. 1975) in which much longer displacements did not affect homing. However, extreme treatments, such as displacement 574 km downriver from Dworshak Hatchery to Bonneville Dam (Slatick et al. 1982), did impair homing. Presumably, if salmon can detect the upriver odor when they arrive at the release site, little effect of displacement will be recorded, regardless of the linear distance.

The fish displaced downriver to Lake Union as smolts tended to enter the UW hatchery even though they had not experienced its water. We hypothesize that these fish initially returned to the release site in Lake Union and found it unsuitable for spawning. The salmon could then have been attracted to the odors of the 1,708 adult coho salmon which were in the UW hatchery over the course of the season. By comparison, the equally proximate NMFS facility contained only 15 adult coho. Adult coho salmon can recognize waters conditioned by conspecifics (Dizon et al. 1973) and behavioral attraction to such species-specific odors has been documented

(Quinn et al. 1983). The return of Group 2 to Seward Park can be explained only by the fact that the salmon had been reared there. Iss hatchery produced about 12 times as many coho salmon as the UW hatchery in 1987, but no fish from Group 2 entered Iss, indicating that little wandering took place.

The patterns of freshwater residence and seaward migration vary greatly among and within salmonid species, yet homing to the natal site prevails throughout the family. There seems to be a flexible system by which site-specific odors are learned prior to and during seaward migration. Hasler and Scholz (1983) demonstrated a link between the thyroid hormones associated with smolt transformation (Dickhoff et al. 1978; Dickhoff and Sullivan 1987) and olfactory imprinting. However, the ability of salmon to learn odors on more than one occasion is not fully compatible with a single peak of thyroid hormones in spring. The solution to this problem may lie in the discovery by Dickhoff et al. (1982) that exposure of coho salmon to novel water sources at the time of year when they would migrate to sea induces transient peaks in thyroid hormone levels. Thus, if thyroid hormones are linked to olfactory learning, there may be feedback from migration to hormones, resulting in additional learning during migration. Exposure to novel waters (e.g., at the confluence of rivers) might induce elevated hormone levels and trigger learning of the water source as an olfactory way-point to be used during upstream migration years later.

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