Evidence for a Hereditary Component in Homing Behavior of Chinook Salmon (Oncorhynchus tshawytscha)

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Returns from three groups of coded wire tagged fall-run chinook salmon (Oncorhynchus tshawytscha) in the Columbia River were analyzed to determine the learned and innate components of homing behavior. Homing of an experimental group produced from intercepted adults, reared and released at a hatchery 370 km downstream from the ancestral location, was compared with the homing of the ancestral stock from their natural site and with the stock native to the downriver release site. Controls from the ancestral location and release site homed to their expected destinations with high accuracy. The experimental group demonstrated an intermediate homing response: 58% returned to the release site, 5% returned to hatcheries 12–50 km upstream, 28% were accountably in an intercepting fishery 15–200 km upstream, and 9% returned to the ancestral spawning area, despite total lack of contact with this area.

On a étudié la remonte d’autonne de trois groupes de saumon quinnat (Oncorhynchus tshawytscha) marqués avec des étiquettes de fil métallique codées dans la rivière Columbia afin de connaître les facteurs acquis et innés du comportement de retour aux eaux ancestrales. On a observé les poissons d’un groupe expérimental produits avec des adultes interceptés, élevés et relâchés à une station de pisciculture située à 370 km en aval des eaux ancestrales, pour comparer leur comportement avec celui des poissons du stock ancestral venant de leur milieu naturel et du stock originaire du point de lâcher en aval. Les témôns des eaux ancestrales et du point de lâcher ont atteint la destination prévue avec un grand degré de précision. Les poissons du groupe expérimental sont intermédiaires: 58% sont retournés au point de lâcher, 5% se sont rendus à des stations de pisciculture situées à 12–50 km en amont, 28% ont été retrouvés dans une pisciculture d’interception 15–200 km en amont et 9% sont retournés dans les eaux de frai ancestrales, bien qu’ils n’y soient jamais allés auparavant.

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The migratory behavior of salmonid fishes has stimulated a great deal of interest, e.g., in the distances travelled and the accuracy of homing (see review by Brannon 1982). Since the acceptance of the "parent stream theory" (Scherr 1939), various mechanisms have been proposed to explain how salmonids achieve these migrations. Salmon migrations can be divided into three general phases: emigration from freshwater to oceanic feeding grounds, feeding migrations of immature fishes, and the return from feeding grounds to the home stream to spawn. It is generally believed that the first two phases involve innate responses (McINerney 1964; French et al. 1976; Leggett 1977; Hager and Hopley 1981; Wahle et al. 1981). The factors guiding salmon returning from the sea are poorly understood, but the riverine homing phase is generally believed to involve olfactory memory (Hasler and Scholz 1983). However, there is evidence that the progeny of transplanted salmon may not home as accurately as locally adapted stock, implying a heritable component in the final phase of migration (reviewed by Rickers 1972; see Bams 1976; Brannon and Hershberger 1984 for examples).

Studies evaluating the respective roles of learned and innate components in salmonid home stream selection have produced varied results. In a study by Donaldson and Allen (1957) on coho salmon (Oncorhynchus kisutch), juveniles reared at one site were transferred to two hatcheries, 50 km apart, in a different watershed for release. Adults returned to the hatcheries of release, not to the ancestral site, suggesting the homing had been based on learned information. However, Bams' (1976) study suggested that there was a genetic component to homing accuracy in pink salmon (O. gorbuscha). Salmon with locally adapted paternal genes homed better than pure nonnatal stock, even though survival of the two groups was similar. This paper reports the results of a transplant experiment conducted on chinook salmon (O. tshawytscha) in the Columbia River system, in an effort to shed further light on the question of possible genetic components in homing.

Methods and Materials

Study Populations and Sites

The study involved fall-run chinook salmon found in the Columbia River in eastern Washington State, United States (Fig. 1). Two races return to the area above Bonneville Dam
The White file as it passes Bonneville Barn. These salmon originated in the Bonneville Dam and in Bonneville Hatchery, located at Bonneville Hatchery for at least produced migration over Rest URBURNBIA.

Table 1. Numbers of tagged fish released, release date, and average size at release for control and experimental groups of 1980 brood Columbia River chinook salmon.

<table>
<thead>
<tr>
<th>Group</th>
<th>Number of tagged fish released</th>
<th>Release date</th>
<th>Average size at release (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>URB control</td>
<td>236,600</td>
<td>5-6/81</td>
<td>5.3</td>
</tr>
<tr>
<td>Tule control</td>
<td>188,500</td>
<td>5/81</td>
<td>8.2</td>
</tr>
<tr>
<td>URB experimental</td>
<td>201,800</td>
<td>6-7/81</td>
<td>10.1</td>
</tr>
</tbody>
</table>

(Howell et al. 1985). One race, locally known as upriver brights (URB), is characterized by bright (oceanic) skin color and lack of development of secondary sex characteristics during its migration over Bonneville Dam. This race primarily spawns on the free-flowing Hanford Reach between McNary and Priest Rapids dams and has smaller populations in hatcheries near Priest Rapids and Ice Harbor dams and a wild natural population in the Deschutes River. The other race, locally known as tules, is characterized by dark skin color and advanced sexual maturity as it passes Bonneville Dam. These salmon originated in the White Salmon River 23 km upstream from the present location of Bonneville Dam, and during the study were additionally produced in four hatcheries on tributaries to the pool above Bonneville Dam and in Bonneville Hatchery, located immediately below Bonneville Dam. Tules have been produced at Bonneville Hatchery for at least 20 generations.

Peak abundance of both races occurs at Bonneville Dam the same time of year (early September), but the URB migration begins sooner and ends later (Pattillo and McIsaac 1982). The tule race spawns primarily during the month of September and spawning is complete by early October; the peak of spawning by the bright race is mid-November but continues at a low level through December (Howell et al. 1985).

Experimental Methods

An experiment, initiated in 1980, permitted evaluation of homing by three groups of hatchery reared chinook salmon: (1) a control group of URB reared at their ancestral location, (2) a control group of tules reared at their natal location about 370 km downstream from the URB site, and (3) an experimental group of URB reared at the same downstream site as the tules. The URB control group consisted of progeny of fish that returned to the Priest Rapids Hatchery area (Table 1). The eggs were incubated and the progeny reared and released at Priest Rapids Hatchery. The tule control group consisted of progeny of fish that returned to Bonneville Hatchery. The experimental group consisted of progeny of the URB race trapped between September 1 and 30 while migrating over Bonneville Dam. Based on unpublished racial verification studies of skin color by the Washington Department of Fisheries in 1979, the possibility of a tule having bright skin color and being misidentified is <5%. The URB experimental group is presumed to be predominantly Hanford Reach origin fish, with some mixture from the other smaller populations. The trapped adult fish were trucked to Bonneville Hatchery, held until sexually mature, and
then spawned. The progeny of these fish were incubated, reared, and released at Bonneville Hatchery and never experienced the environment of their ancestral area or the 370-km downstream migration route between the ancestral area and Bonneville Hatchery. The URB control and experimental groups were released at their typical outmigration time (Allen and Meekin 1973), as was the tule control group (Smith and Wahle 1981).

All salmon received coded wire tags (CWT) unique to each group and were identified externally by excision of the adipose fin. A comprehensive search for returning mature chinook salmon without adipose fins occurred throughout the Columbia River basin during 1982–85 to recover CWT from these and other experimental groups from various hatchery and naturally produced populations. Searching rate varied by fishery, escape- ment area, and year of return. Fish returning to any hatchery facility in the Columbia River basin were examined for fin clips. Salmon returning to many Columbia River hatcheries, including Bonneville Hatchery and three of the four hatcheries in the Bonneville Pool, enter traps only 100–800 m from the stream mouths that prevent their return to the Columbia River. Basin- wide random sampling of 30–40% of gillnet fishery catches, 5–15% of sport fishery catches, and 3–30% of the salmon reaching natural spawning grounds occurred. Sampling proportions on the Hanford Reach natural spawning grounds ranged from a high of 0.067 in 1982 to a low of 0.032 in 1985. Total CWT present from areas with <100% sampling was estimated by dividing total recoveries by the sampling fraction.

Results

All salmon from all three test groups passed 23 salmon hatcheries located downstream from Bonneville Hatchery during upstream migration; 13 of these hatcheries produced fall-run chinook salmon. All recovered salmon from the URB control group passed Bonneville Dam and were recovered either at their natal site (72%), upstream from their natal site (1%), or were intercepted by the gillnet fishery below the natal site (27%, Table 2). The tule control group returned primarily (94%) to their release site at Bonneville Hatchery, with a single recovery (<1%) in one of the four hatcheries producing tule fish above Bonneville Dam. The remaining 6% of the tule control group were caught in the gillnet fishery above Bonneville Dam. In contrast with the two control groups, 58% of the experimental groups were recovered in Bonneville Hatchery, 5% strayed to hatcheries in the Bonneville Pool, 28% were caught in gillnet fisheries between Bonneville and McNary dams, and 9% were estimated to have returned to their ancestral location. Fish from the experimental group migrated over Bonneville Dam in all four return years. A total of five CWT’s from the experimental group were recovered in the ancestral spawning location.

The proportion of the experimental group that returned to its release site was significantly smaller than that of the tule control group (p < 0.001, chi-square test). Further, the proportion returning to the ancestral location was also significantly smaller than that of the URB control group (p < 0.001, chi-square test). The proportion of the experimental fish passing Bonneville Dam estimated to have been caught in the gillnet fishery between Bonneville and McNary dams was significantly greater than that of the URB control group (p < 0.001, chi-square test).

The age structure at return for the URB experimental and control groups was typical of URB in general and the age structure of the tule control group was typical of tules. The maturity schedule for the URB race involves a dominant 4-yr-old age

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**Table 2. Actual and estimated recoveries of tagged experimental and control study groups to areas within the Columbia River, by age of return (ages 2, 3, 4, and 5).**

<table>
<thead>
<tr>
<th>Recovery location</th>
<th>Recovery type</th>
<th>URB control</th>
<th>Tule control</th>
<th>URB experimental</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatcheries and tributaries below Bonneville Hatchery</td>
<td>A* (%)</td>
<td>0 0 0 0 0 (0)</td>
<td>0 0 0 0 0 (0)</td>
<td>0 0 0 0 0 (0)</td>
</tr>
<tr>
<td>Bonneville Hatchery</td>
<td>A (%)</td>
<td>0 0 0 0 0 (0)</td>
<td>21 117 23 0 161 (94)</td>
<td>0 0 0 0 0 (0)</td>
</tr>
<tr>
<td>Bonneville Pool hatcheries</td>
<td>A (%)</td>
<td>0 0 0 0 0 (0)</td>
<td>0 1 0 0 1 (&lt;1)</td>
<td>22 12 8 5 47 (5)</td>
</tr>
<tr>
<td>Gillnet fishery between Bonneville–McNary dams</td>
<td>A (%)</td>
<td>1 8 32 13 54 (27)</td>
<td>0 2 2 0 4 (6)</td>
<td>14 56 141 42 253 (28)</td>
</tr>
<tr>
<td>Hanford Reach natural spawning</td>
<td>A (%)</td>
<td>2 0 6 1 9 (30)</td>
<td>0 0 0 0 0 (0)</td>
<td>15 0 32 29 76 (9)</td>
</tr>
<tr>
<td>Hatcheries adjacent to Hanford Reach</td>
<td>A (%)</td>
<td>10 53 99 59 221 (42)</td>
<td>0 0 0 0 0 (0)</td>
<td>0 0 0 1 1 (&lt;1)</td>
</tr>
<tr>
<td>Hatcheries upstream from the Hanford Reach</td>
<td>A (%)</td>
<td>0 0 2 1 3 (1)</td>
<td>0 0 0 0 0 (0)</td>
<td>0 0 0 0 0 (0)</td>
</tr>
</tbody>
</table>

* A = actual recoveries.
* E = estimated recoveries when subsampling of fishery or escapement areas occurred.
* Percent group total.
* Trapped at Ice Harbor Dam, transported to Lyons Ferry Hatchery.
* Wells Hatchery.
Discussion

The accuracy of homing in the two control groups was high compared with values reported in the literature. Quinn and Fresh (1984) reported a homing precision rate of 98.6% for spring chinook salmon from Cowlitz Hatchery, located on a Columbia River tributary below Bonneville Dam. The URB control group passed 20 major tributaries and 38 hatchery facilities to home to the release site and ancestral location at the rate of 99.2% (378 of 381 estimated recoveries in hatcheries and spawning grounds). A single recovery of the URB control group occurred in one of the 13 hatchery facilities above the ancestral location. Ninety-four percent of the tule control group returned to Bonneville Hatchery. This group did not stray to any of the 23 hatchery facilities downstream from Bonneville Hatchery, nor to any of the 19 hatchery facilities above Bonneville Pool. The only stray recovered in a spawning area was in the first hatchery facility (1 km) above Bonneville Dam, although 10 salmon were estimated taken from the gillnet fishery above Bonneville Dam.

If the homing of the URB experimental group had been entirely determined by experience prior to release, they would have returned primarily to Bonneville Hatchery, with perhaps a few caught above Bonneville Dam as was the case with the tule controls. On the other hand, homing based on genetic responses would have brought most fish to the Hanford Reach spawning grounds and Priest Rapids Hatchery, with about 27% intercepted enroute by gill nets between Bonneville and McNary dams. The response of the experimental group was clearly intermediate between these two scenarios. The return of 58% of the experimental to Bonneville Hatchery but none to the other hatcheries on the lower river suggests that sufficient learning occurred to lead most salmon to their juvenile rearing site. However, the fact that 42% of this group ascended Bonneville Dam contrasts with 6% of the tule controls that did so.

The proportions of the URB control and the experimental groups passing Bonneville Dam that were caught in the gillnet fishery between Bonneville and McNary dams differed from one another. Only 27% of the URB controls were intercepted and 73% reached their natal hatchery, nearby spawning grounds, or stayed upstream. However, 67% of the URB experimental that passed Bonneville Dam were caught in the gill nets. This information implies that the experimental fish migrated slower or in a less direct manner, something supported by the more protracted pattern of recoveries in the gillnet fishery than the URB control group. The appearance of a confused homing response could be due to the hybridization of the URB populations that comprised the experimental group, as occurred with pink salmon (Bams 1976), as well as conflict between learned and innate responses. Significantly, more experimental fish passing Bonneville Dam migrated over McNary Dam than ascended tributaries, despite the formidable task of negotiating mainstem Columbia River hydroelectric dams (Gibson et al. 1979). It is reasonable to assume that a proportion of these fish could have reached ancestral spawning locations had they not been intercepted by the gillnet fishery.

The four actual recoveries of tagged URB experimental fish on the ancestral spawning grounds were few, because locating marked fish is difficult on the Hanford Reach. However, population estimates for this area, and hence, expansion factors for CWT estimates, are reliable because absolute counts were made of fish at dams above and below this area (United States Army Corps of Engineers 1983, 1984, 1985, 1986; Public Utility District of Grant County 1983, 1984, 1985, 1986). The recovery of experimental fish in three of the four possible return years lends evidence to the conclusion that return to this location was not an aberration.

The learned response of the experimental group is consistent with conventional explanations of salmon homing involving imprinting (Hasler and Scholz 1983). Evidence for genetic influence is contained in the return of some experimental fish to the ancestral spawning grounds and in the intermediate homing response of experiments compared with the control groups. The four lines of evidence indicating intermediate homing by the experimental group are as follows: (1) the experimental group returned to the release site at a lesser rate than the tule control group, (2) some did return to the ancestral location but at a frequency less than the URB control group, (3) 5% strayed to hatcheries in the Bonneville pool, and (4) they experienced a higher capture rate than the URB control group in gillnet fishing area.

Different types of inherited responses could have influenced the observed behavior of fish in the experimental group. They may have been "programmed" to swim for a distance or a period of time after reentering freshwater exceeding those required to the point of release used in the experiment. They may have had inherited olfactory response to riverine (nonpheromonal) odors of the ancestral area, normally hypothesized to be a learned response for salmon (Hasler and Scholz 1983). There may have been an innate response to population specific pheromones (Nordeng 1977). Inherited preferences for non-site-specific physical criteria such as water temperature and velocity and substrate composition may also have been involved, especially in the extreme terminal migratory phase.

Genetic instructions to swim a long distance after reentering freshwater would be compatible with the sexually immature state (relative to the tule race) of the URB race and the distance to the natal site. Genetic programs for persistence of migratory activity are known in birds (Berthold 1985). However, physiological maturity alone cannot explain upriver migration, as the spring-run chinook that return to the Cowlitz River on the lower Columbia River system typically arrive between March and June, but mature in the Cowlitz River and do not spawn until fall (Quinn and Fresh 1984). The fact that some experimental URB fish returned to Bonneville Hatchery, 370 km short of the ancestral target, does not negate the possibility of genetic instructions for swimming persistence because once trapped at Bonneville Hatchery, salmon were prevented from further upriver progress having been confined to ripening ponds.

There is presently no evidence for population-specific pheromone recognition in chinook salmon, but coho and sockeye (O. nerka) salmon can distinguish odors of their population from those of other populations (Quinn and Tolson 1986; Groot et al. 1986). Assuming pheromone recognition, presence of native URB chinook on the upriver spawning grounds and in the Priest Rapids Hatchery while the experiments were returning allows that population-specific pheromones may have influenced the behavior of those experiments that ascended Bonneville Dam. However, pheromone recognition alone does not explain the results of this study because no URB controls were decoyed into Bonneville Hatchery by the pheromones of the many experimental URB's present there.
In conclusion, the results obtained do not permit us to determine which factors caused 42% of the experimental chinook to pass their rearing and release site and continue upriver. However, because 9% of the experimental groups accomplished migration to the ancestral site while lacking any experience with the route between that site and their rearing area, a genetically coded response to native habitats and/or population characteristics is indicated. It seems likely that some combination of inherited olfactory response, upstream swimming persistence, and preference for spawning site characteristics was involved.

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References


