FIELD TEST OF THE PHEROMONE HYPOTHESIS FOR HOMING BY PACIFIC SALMON

ERNEST L. BRANNON¹ and THOMAS P. QUINN²

¹College of Forestry, Wildlife, and Range Sciences
University of Idaho
Moscow, Idaho 83843
²School of Fisheries WH-J0
University of Washington
Seattle, Washington 98195

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Abstract—Experimental groups of juvenile coho salmon (Oncorhynchus kisutch) were released to elucidate the relative importance of site-specific ("imprinted") odors and intraspecific odors ("pheromones") in homing. Adult salmon returned to their release site rather than a hatchery containing both adult and juvenile salmon of their population. Furthermore, salmon sharing the same parents returned to different sites, suggesting that local movements are not strongly influenced by siblings or other conspecifics.

Key Words—Coho salmon, Oncorhynchus kisutch, homing, imprinting, olfaction.

INTRODUCTION

It is generally accepted that salmonid fishes use olfaction to locate their natal river in the final stages of homing (Wisby and Hasler, 1954). However, it is not clear which odors convey the identity of the river. It has been hypothesized that the fish are guided by chemicals from riverine features such as rocks, soil, and plants, which create a unique combination of odors (Hasler and Scholz, 1983). On the other hand, Nordeng (1971, 1977) propounded the hypothesis that population-specific odors ("pheromones") emanating from both juvenile conspecifics residing in freshwater and those migrating to sea (smolts) guide the homing adults. Studies with artificial odorants (e.g., Scholz et al., 1976) indicated that pheromones were not necessary for homing. However, recent laboratory studies have indicated that salmonids can discriminate between populations based on chemical cues (Groot et al., 1986; Olsen, 1986; Quinn and Tolson, 1986; Stabell, 1987). Moreover, coho salmon (Oncorhynchus kisutch)
can also distinguish siblings from nonsiblings (Quinn and Busack, 1985; Quinn and Hara, 1986). There is currently no evidence that discrimination of kin- or population-specific odors is involved in homing.

Larkin (1975) expanded upon Nordeng’s (1971) hypothesis that odors from juveniles guide returning adults and hypothesized that salmon from a given population might associate with each other while at sea on their homeward migration. Larkin’s hypothesis stemmed from the mathematical demonstration that errors in group orientation decrease as school size increases, if the individuals jointly orient to a mean direction (Larkin and Walton, 1969). Thus if salmon schooled with members of their population, migration might be more efficient.

To investigate the relative importance of site-specific odors and odors emanating from conspecifics in homing, coho salmon were reared under experimental conditions, marked, and released. The subsequent patterns of homing by adult salmon from the experimental groups were monitored. The study posed two specific questions: (1) Will adult coho salmon pass a site containing both adults of their population and juveniles directly related to them (full siblings) to reach an upriver site where they had been released? (2) Will the homing behavior of one group of salmon influence that of a genetically related group returning at the same time to a different site within a river system?

METHODS AND MATERIALS

Incubation and Treatment of Juveniles. Between November 18 and 25, 1985, adult coho salmon from the University of Washington population were spawned and the fertilized eggs divided into two groups. No parents were common to both groups or to any other juvenile coho produced that season. All embryos were incubated at the University of Washington (UW) hatchery using dechlorinated Seattle city water, a source not generally used in the hatchery. Previous experiments (Whitman et al., 1982; Quinn et al., 1983) demonstrated that adult salmon can distinguish between city water and hatchery water. Water temperatures averaged 7–9°C and the eggs hatched in early January 1986. Development of hatchlings (“alevins”) continued until yolk sac absorption was complete in March.

When the fry were free-swimming, they were moved to the Seward Park hatchery on Lake Washington (Figure 1) (March 8 for group 1 and March 21 for group 2). Both groups remained at this site in circular ponds, rearing in water pumped from the lake directly into the hatchery. Small individuals were culled from group 1, and 9489 fish were marked by excision of the adipose fin and internal coded wire tags on June 16. Group 2 was culled and divided into two subgroups (2A: \( N = 10,020 \) and 2B: \( N = 10,148 \)) for fin-clipping and tagging on June 13–14. The salmon began the process of transformation from
freshwater "parr" to marine-adapted "smolts" in late June, judged by silvery appearance and downstream swimming behavior. On July 8, 1986, the tagged members of group 1 were released from the Seward Park hatchery into Lake Washington. Approximately 4000 untagged coho from group 1 were retained at the hatchery. On June 27, the tagged fish from group 2B were released from Seward Park hatchery. On July 1, group 2A fish were trucked from Seward Park to a site on Lake Union about 2.2 km below the UW hatchery (Figure 1) and released. The release site was a boat launching ramp with no suitable spawning area in the vicinity. Table 1 summarizes the treatments which the three groups received.

Collection of Returning Adults. Salmon released as smolts in 1986 were expected to return as adults primarily in fall 1987. This population has relatively few precociously maturing males, known as jacks (Brannon et al., 1982). Jacks could have entered the UW hatchery return pond in fall 1986 and would have been detected in the regular surveys taken three times each week. The trap at
the return facility at Seward Park was not constructed until late summer 1987, however, and returning jacks would not have been collected there in 1986.

Dechlorinated city water, used to incubate the eggs and embryos, was not released from the UW hatchery at any time during the spawning season. The adult coho (and chinook, *O. tshawytscha*) salmon holding in the UW hatchery’s pond in the fall presumably produce a high concentration of salmon odors in the effluent. These odors were supplemented by the 4000 immature siblings from group 1, which were transferred from Seward Park to the UW hatchery prior to adult returns.

All salmon returning to the UW and Seward Park hatcheries were inspected for marks. Additionally, three other opportunities for recovering tagged fish were pursued. The U.S. National Marine Fisheries Service (NMFS) has a small hatchery across the ship canal from the UW hatchery. While no NMFS fish were expected to return in 1987, the hatchery’s trap was checked for stray experimental salmon. The Washington Department of Fisheries operates a large

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**Table 1. Coho Salmon Experimental Treatments, Indicating When (in 1986) Fish Were Exposed to Different Water Sources or Moved and Site to Which They Returned**

<table>
<thead>
<tr>
<th>Developmental stage or operation</th>
<th>Experimental group</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Group 1</td>
</tr>
<tr>
<td>Eggs, alevins, fry Site</td>
<td>CW</td>
</tr>
<tr>
<td>Parr</td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>SP</td>
</tr>
<tr>
<td>Date</td>
<td>3/8</td>
</tr>
<tr>
<td>Tagging (smolts)</td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>SP</td>
</tr>
<tr>
<td>Date</td>
<td>6/16</td>
</tr>
<tr>
<td>Release</td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>SP</td>
</tr>
<tr>
<td>Date</td>
<td>7/8</td>
</tr>
<tr>
<td>Size</td>
<td>13.9 g</td>
</tr>
<tr>
<td>Returns</td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>SP/UW</td>
</tr>
<tr>
<td>Nos.</td>
<td>39/0</td>
</tr>
</tbody>
</table>

*CW refers to dechlorinated city water at the University of Washington hatchery, SP refers to the Seward Park hatchery, LkU refers to the Lake Union release site and UW refers to the University of Washington return pond.*
hatchery for chinook and coho salmon on Issaquah Creek, a tributary to Lake Samammish above Lake Washington (Figure 1). Coho salmon returning to this facility were checked for coded wire tags. Additionally, a gillnet fishery in the north end of Lake Washington and in Lake Samammish targets Issaquah Creek hatchery salmon. Subsamples from this fishery were taken by the Washington Department of Fisheries and checked for tags.

RESULTS

Thirty-nine salmon from group 1, incubated in dechlorinated city water and reared in Seward Park water, bypassed the UW hatchery containing full-sib relatives and other adults of their population and returned to Seward Park. No members of this group entered the UW hatchery. Similar behavior was shown by group 2B coho with a similar rearing history: all 43 recoveries were at the Seward Park hatchery (Table 1). However, 32 salmon (including one jack in 1986) from group 2A, reared at Seward Park but trucked to Lake Union for release (Figure 1) returned to the UW hatchery and only six adults returned to Seward Park.

Fifteen coho salmon entered NMFS trap but none were from any of the experimental groups. No coho salmon from any of the three groups were recovered from the fishery in Lake Washington or at the Issaquah hatchery.

DISCUSSION

Salmon returning to Seward Park had to swim within about 100 m of the UW hatchery. The UW hatchery contained full-sibling relatives of group 1 as well as 1708 adult coho (and 506 chinook) salmon over the course of the spawning season. In spite of these odors in the hatchery’s effluent, salmon from groups 1 and 2B swam past the UW hatchery and approximately 16 km in Lake Washington to Seward Park. The tendency of salmon to return to a site experienced as juveniles rather than to one containing conspecifics’ odors is consistent with the attraction of adult coho salmon to hatchery water without coho odors over city water containing juvenile coho in a two-choice apparatus (Brannon et al., 1984). Our result is also consistent with the demonstration by Black and Dempson (1986) that Arctic char were not decoyed into a nonnatal river by the presence of adults.

Laboratory experiments have indicated that coho salmon are capable of population-specific and family-specific chemosensory discrimination (Quinn and Busack, 1985; Quinn and Hara, 1986; Quinn and Tolson, 1986; Courtenay, 1989). Intraspecific discrimination may be related to juvenile social behavior
or mate selection by adults, but it apparently is not crucial to homing as all adults swam past the UW hatchery to Seward Park.

The return of all members of group 2B to Seward Park corroborated the results with group 1: pheromones or other population-specific odors in the UW hatchery did not attract them. Moreover, the fish in group 2B were the full siblings of those in 2A. The return of 2A to the UW hatchery (32 of 38 adults) indicated that homing salmon were not influenced by the behavior of siblings. This particular experiment was motivated by Larkin's (1975) hypothesis that homing salmon might school preferentially with kin at sea and by the idea that the local movements of adult salmon in freshwater are influenced by density of conspecifics (Quinn and Fresh, 1984). While our results provided no evidence for kin-based schooling, the tendency of group 2A to enter the UW hatchery was noteworthy. These fish were never reared in UW hatchery water and were moved to Seward Park prior to the presumptive time of olfactory imprinting (Hasler and Scholz, 1983) on the same schedule as groups 1 and 2B.

The return migration of group 2A might be explained by the following scenario which assumes that smolts imprint on a sequence of odors during emigration (Quinn et al., 1989, in press). The smolts learned the characteristics of Seward Park water and the odors of the release site but were denied the opportunity to experience the waters in between. Upon return to the watershed, they located the release site in Lake Union. However, from that point they could not detect Seward Park effluent odor, and they lacked experience of the homeward path. In this situation the fish were decoyed to the UW hatchery, the site that either most resembled the odors of home or contained familiar salmon odors (Brannon and Quinn, 1989). Some of the group 2A salmon (16%) were apparently more persistent in their search and returned to Seward Park. Thus this study indicates that salmon odors were not used to guide salmon home, although in the absence of primary cues they may facilitate the selection of spawning sites by straying salmon.

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REFERENCES


