Salmon homing: is the puzzle complete?

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The return of adult salmon from vast oceanic feeding areas to spawn in the stream of their birth is one of the most spectacular examples of animal migration. In 1951, Arthur Hasler and his student, Warren Wisby, proposed that salmon identify their home river by its unique odor, which they memorized as juveniles before migrating to sea. Aided by a series of graduate students at the University of Wisconsin, Hasler conducted experiments investigating various aspects of his ‘olfactory hypothesis’ until his recent retirement.

This book, coauthored by his last doctoral student, Allan Scholz, has two parts. The book begins by reviewing the life history and migrations of salmon and the evidence that detection of imprinted odors enables them to locate their home stream for spawning. The second part deals with the hormonal control of smolt transformation, imprinting, and olfactory responses, and is drawn from Scholz’s dissertation at Wisconsin and subsequent research at Eastern Washington University. The authors make no attempt to review or discuss the oceanic phase of salmon migrations.

The book itself is quite readable and serves as an organized review of a large and complex literature. Scholz’s work on hormonal influences has not been published elsewhere, and this part of the book presents very exciting experimental results. What emerges is an extraordinarily neat story that runs more or less as follows: Juvenile coho salmon (Oncorhynchus kisutch) spend one year in a stream after emerging from gravel nests. In their second spring, an endogenous circannual rhythm, synchronized by increasing daylength, triggers release of thyroid hormones. Thyroid hormones control the complex process of smolt transformation, including replacement of parr marks with silvery color, increased salinity tolerance, and the onset of downstream migratory activity. In addition, thyroid hormones activate olfactory imprinting: the rapid memorization of odors which will enable the salmon to return to the river after 1½ years at sea. Other species of salmon have somewhat different life histories, but the essential aspects of hormonal control of olfactory imprinting are believed to be the same.

While the book presents an elegant and apparently flawless case for imprinting at the time of smoltling, based on a wide variety of studies, it may be a serious oversimplification of what actually takes place. This judgement is founded primarily on the observed behavior of wild salmon. The authors are correct in stating that coho salmon migrate to sea as year-old smolts, but many other coho leave freshwater in their first spring as parr with no visible signs of smolt transformation. These fish often spend the summer in an estuary and depart as smolts in the fall. Some, however, will swim back into freshwater, to leave the following spring. Of the coho that spend a year or more in freshwater, many move substantial distances within river systems. If the adults are to return to their natal stream, they must imprint on that water. Where alevins emerge in one area but leave as...
smolts from another, we must infer that some olfactory learning was accomplished by alevins.

The strongest evidence for imprinting at the alvein or early juvenile interval is in sockeye salmon (O. nerka). In this species, adults spawn in streams that typically drain into lakes. As soon as the young emerge from gravel nests, they migrate from the natal stream to the lake. After usually one year in the lake, the sockeye leave the lake as smolts via the outlet, not their natal stream. Clearly such fish imprint on the natal inlet stream (though perhaps also on the outlet stream as smolts) but the authors make no mention of this situation. Moreover, some sockeye salmon migrate to sea as newly emerged fish, further indicating the importance of imprinting by alevin or parr. In chincok salmon (O. tshawytscha), downstream migration often occurs immediately after emergence, three months later, or the following spring. This variable migration pattern makes a fixed connection between smolting and imprinting unlikely. Another case which seems to necessitate separation of smolting from imprinting involves chum salmon (O. keta). While most chum emerge near the ocean and migrate to sea almost immediately, populations have been reported as far as 2700 km inland in the Yukon River system. It is not known how long it takes these fish to get to the ocean, but it would seem that the natal stream that they experienced as parr would be spatially and temporally separated from the water experienced as smolts. These complex cases of migration and smolt transformation are not discussed in the book and will not be familiar to many readers. However, they suggest that imprinting occurs at the parr interval as well as the smolt interval.

If the process of olfactory imprinting is complex, how can we explain the utterly convincing case the authors make for the relationship between thyroid hormones, smolt transformation, and imprinting? The answer may lie in their system of rearing, imprinting and releasing salmon. The authors' salmon were incubated and reared in hatcheries in central Wisconsin. They were then exposed to morpholine or phenethyl alcohol and released into Lake Michigan. Eighteen months later, the artificial chemicals were metered into streams tributary to the lake, attracting the adult salmon. Since the hatchery (rearing) water did not enter the lake, the only odors familiar to the salmon were the artificial chemicals that they had experienced as smolts. It is not surprising that they sought these odors when ready to spawn. Evidence from transplants shows that when salmon are reared in one river but released as smolts into a distant river, they return to the river where they were released. However, when the rearing and release sites are more proximate, salmon often return to the rearing site. It appears that they return first to the odors they experienced as smolts. If the odors experienced as parr are not detectable, the fish seldom wander. However, they often locate their rearing site if it is in the same river system as the release site. Evidence for imprinting at the parr interval does not contradict the authors' emphasis on the relationship between smolt transformation and imprinting. However, we must bear in mind that for many salmon life is not so simple.

Besides the controversy over when and how imprinting occurs, another major unresolved issue in salmon homing is the nature of the odor(s) involved. Hasler and co-workers have emphasized the importance of chemicals from the soil, rocks, plants and other features of the river. However, in virtually all their experiments described in this book the fish were imprinted on morpholine or phenethyl alcohol. While there are advantages to using artificial chemicals, this technique precludes further understanding of the important natural odors. It has long been suggested that the odors of conspecifics might play an important role in homing. Recently, Hans Nordeng and co-workers have revived and expanded the 'pheromone hypothesis', proposing that population-specific pheromones guide homing salmonids. Hasler & Scholz briefly discuss this hypothesis. They correctly point out that the homing of salmon to artificial odors demonstrates that pheromones are not a prerequisite for homing. However, they concede that pheromones may contribute to homing in natural situations. Later in the book (Section 4.2) the authors speculate that the odors of adult conspecifics may influence spawning stream selection by straying (non-homing) salmon. They demonstrate that as the spawning season progresses, salmon re-
responses to home odor decline. They state (but do not document) that responses to conspecifics' odors increase at this time. This is an important point, and the evidence should have been presented. Moreover, the numerous studies by other authors documenting attraction to the odors of adult conspecifics should have been cited. The roles of juvenile and adult pheromones in homing and spawning behavior need to be more fully investigated. This should be part of a general analysis of the chemicals involved in imprinting and homing in natural systems.

In addition to my major concerns regarding evidence for imprinting by parr and the need for more work on the odors imprinted by wild salmon, I have a few minor criticisms. First, while we have all been enthralled by the ability of salmon to home, we often forget that some salmon stray (spawn outside their natal river). Hasler & Scholz cite a general figure of 95% homing accuracy for salmon. In fact, evidence for homing/straying rates in wild populations is almost non-existent, and homing is probably more variable than the authors suggest. Strays are an annoying aberration for those who, like Hasler & Scholz, study sensory mechanisms underlying behavioral patterns. However, straying may be more than just a failure of the homing mechanism, and it has certainly played a crucial role in the evolution and distribution of salmon species. Thus, I am disappointed that the subject of straying is largely neglected, and that the term does not even appear in the index.

I am also concerned about the inferences which the authors draw from electrophysiological data. Olfactory electroencephalographic (EEG) recordings seemed to be a promising tool for studying salmon olfaction and homing responses in the middle and late 1960s. However, it soon became clear that the magnitude of the EEG response to a chemical gives little if any indication of how the animal will actually respond to it. The authors mention but seem to minimize the problems inherent in EEG techniques. Moreover, they conclude that the olfactory systems of sexually mature salmon are more sensitive than those of immature fish, on the basis of behavioral and EEG responses. While this may be true, the obvious importance of motivation to respond to homestream odors is not discussed.

In summary, this book concisely reviews the literature on salmon homing, though there is some slant towards papers from the Wisconsin group, and some papers presenting alternative views are absent. Scholz has conducted a wide variety of well-conceived experiments on hormonal control of imprinting and the expression of homing responses. This is a fertile area for future research. However, in the Historical Perspective (p. XVII), Scholz states that the book includes '... a collection of general impressions that we have formed about the life history, behavior, physiology, and ecology of salmon'. Unfortunately, too little natural history appears in the book and the information presented seems to have been selected to fit the smolt-imprinting hypothesis. We get what I regard as a misleadingly simple view of salmon migratory behavior. Nevertheless, the literature and new results make this book a 'must read' for anyone concerned with salmon or fish migratory behavior. Indeed, it should be widely read by scientists interested in migration, homing, olfaction, and the relationship between hormones and behavior.

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