Pacific Salmon Migrations and Homing: Mechanisms and Adaptive Significance

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Pacific salmon are noted for their lengthy foraging migrations and for their precise homing ability. Extensive sampling has documented the general migratory patterns of the major populations, but many basic aspects of their marine ecology are still poorly understood. Their life history pattern has been interpreted as an adaptation to exploit the higher productivity of the marine environment over that in fresh water. The adaptive significance of homing is implied by the specializations of populations for their natal habitat and the competitive superiority of locally adapted populations over transplants from other rivers. However, the establishment of new populations by strays and the levels of gene flow between natural populations have only recently received much attention. Research on salmon migrations has also focused on the mechanisms that guide homing at sea and in fresh water. While salmon have highly developed sensory systems, the ways in which inputs are integrated to guide migration through diverse and complex habitats are still being investigated.

The study of fish migration has been dominated by work on Pacific salmon (Oncorhynchus spp.) and the confamilial Atlantic genus Salmo. The species in these and other less-known salmonid genera spawn in fresh water, usually in streams. Juveniles emerge from gravel nests in spring and may reside in streams, or migrate to lakes or to the ocean. Some species spend only the summer in coastal waters near the mouth of their natal river, but many species migrate thousands of kilometers to oceanic feeding grounds. After a variable period at sea or in fresh water, virtually all the surviving fish return to their natal stream to spawn. Depending on the species and population, individuals may or may not all die after spawning.

Ocean migrations

Enormous quantities of data on marine migration patterns have been collected and summarized by Japanese, Canadian and American scientists under the mandate of the International North Pacific Fisheries Commission (e.g. Ref. 1; Fig. 1). While a great deal is now known about oceanic migration patterns, many important questions remain unanswered.

For example, do present population levels approach the ocean's carrying capacity? While the foraging grounds of salmon are vast, there is some evidence of density-dependent growth and survival. Consideration of the ocean as a foraging area leads to a related question: what factors determine the general ranges of populations and species at sea? The distributions of populations and species overlap but they do not coincide. For example, North American steelhead (O. mykiss) may migrate extensively into the western Pacific to forage, while chinook (O. tshawytscha) and coho (O. kisutchi) salmon, with similar prey requirements, generally remain in coastal waters. In spite of our knowledge of salmon distribution patterns, diets, and physical oceanography, no comprehensive foraging model has been assembled. Moreover, neither the magnitude nor the variation in mortality at sea has been fully explained.

The foraging patterns of salmon at sea may be viewed not only as local responses to prey density and oceanographic conditions but also as an evolutionary adaptation to oceanic productivity patterns. Northcoastreviewed fish migration and concluded that it is best viewed as an adaptation to increase foraging success, growth, survival and eventually reproductive output. On a global scale, anadromy (see Box 1) is most prevalent at higher latitudes, where marine productivity generally exceeds that in fresh water. In more tropical regions, freshwater productivity generally exceeds marine productivity, and diadromous fishes tend to be catadromous rather than anadromous. In the case of salmonids, the growth rate at sea greatly exceeds that in fresh water. This growth may be converted by females into higher fecundity or larger eggs. Large size in males increases fitness through greater access to females. While anadromy appears to be obligatory in some species of salmon (e.g. O. keta and O. gorbuscha), both anadromous and entirely freshwater forms exist in other species. Assortative mating may reduce gene flow when the forms are sympatric. In some salmonids, males often spawn before going to sea and then return to spawn again at a much larger size (e.g. Atlantic salmon, S. salar). In masu salmon (O. masou), many males spawn in fresh water but never go to sea, whereas most females are anadromous.

The variable patterns of migration and reproduction are usually interpreted in the context of a freshwater origin for salmonids. In this scenario, the prototypical migration would have been from spawning areas (stream riffles) to feeding areas (pools) by isolated populations. Exploitation of coastal and oceanic feeding grounds evolved later, perhaps in association with glacial events, and presented opportunities for colonization and gene flow between watersheds. However, the assumption of freshwater origin has been questioned if salmonids had a marine origin, colonization by genetically generalized marine ancestors would have founded populations spawning in fresh water. In this scenario, highly variable freshwater habitats would have driven selection for homing and site-specific specialization.

Population differentiation

Regardless of whether salmon evolved from marine or freshwater ancestors, it is clear that salmon of one population (operationally defined as fish originating in the same river) differ from salmon of other populations, and that some differences have a heritable component. Genetically controlled differences between populations have been demonstrated for such diverse characteristics as age at maturity, spawning date, egg size and developmental rate, disease resistance, agonistic behavior, rheotactic responses (see Box 1).
adult size and morphology\textsuperscript{4}, and even homing behavior\textsuperscript{8}.

One excellent example of these specialized adaptations to freshwater habitats is the rheotactic response of sockeye salmon (O. nerka) fry after they emerge from their gravel nests. Most populations are obligate lake dwellers and migrate from their incubation site to a lake for the first year or two of rearing prior to seaward migration. The incubation sites are usually in the inlets or outlets of the nursery lakes and therefore, upon emergence, fry must swim either upstream or downstream to reach their lake. To examine the genetic contribution to these behavior patterns, Brannon\textsuperscript{17} collected eggs and milt (semen fluid and sperm) from adults that had returned to the Chilko and Stellako rivers in British Columbia. Fry emerging in the Chilko River must swim upstream to reach Chilko Lake whereas those emerging in the Stellako River must move downstream to rear in Fraser Lake. Fertilized eggs from each population and hybrid eggs were incubated at a laboratory, and upon emergence the fry were tested for responses to water current. Most of the Chilko River fry (87.9\%) swam upstream, and most of the Stellako River fry (65.6\%) went downstream. The behavior of the hybrids was intermediate between the parental populations (47.5\% upstream), indicating at least partial genetic control over this migratory behavior pattern.

The adaptive significance of the myriad local specializations is evidenced by the failure of salmon transplanted to a non-natal river to survive as well as locally adapted salmon\textsuperscript{11\&19}. However, while homing is linked to habitat-related specializations, it is known that some salmon stray and spawn in non-natal sites. Precise estimates of straying are difficult to obtain\textsuperscript{20}, but variation among and within species may occur. In some cases the straying can be associated with a degradation in water quality, such as occurred when volcanic ash contaminated streams following the eruption of Mt St Helens\textsuperscript{21}.

Straying is not only a proximate avoidance response of individuals to adverse conditions; it is also the key to the species' colonization of new habitats. Colonization of much of the salmon's present range in North America and Europe and the evolution of highly specialized populations have taken place since the last glacial period\textsuperscript{22}. The processes of straying and colonization continue to occur as new habitats become accessible to salmon. For example, in Glacier Bay, Alaska, recession of the glacier is creating habitat for salmon\textsuperscript{23}.

Orientation mechanisms

Most of the research on salmon migration has been concerned with the sensory systems and physiological processes underlying the many distinct migrations that characterize the salmon life cycle (Fig. 2). In particular, researchers have attempted to elucidate the orientation mechanisms of adult salmon returning from oceanic feeding grounds to their natal rivers. Although it is widely accepted that the final, freshwater phase of the spawning migration is primarily governed by olfactory discrimination of home-stream waters, the mechanisms operating at sea are still not known. The open-ocean migrations often cover 1000–2000 km in 4–10 weeks, implying that the salmon have some sensitive guidance system(s). Sun compass, polarized light, ocean currents, temperature, olfaction and electrical and magnetic stimuli have all been proposed as sources of guidance information\textsuperscript{24}. However, definitive experiments on oceanic orientation have not been conducted.

As an alternative to studying adult salmon at sea, experiments have been conducted on juvenile sockeye salmon migrating in large lakes. These studies have revealed that sockeye orient to the sun's position, to polarized light patterns and to the earth's magnetic field\textsuperscript{25\&26}. Recent investigations have shown that in the ethmoid region of the skull of sockeye salmon, there are single-domain crystals of magnetite that are suitable for use in magnetoreception\textsuperscript{27\&28}. Following these exciting findings, we await definitive neurobiological research on magnetic field detection and studies demonstrating its use in the field.

Upon reaching coastal waters from the open ocean, Pacific salmon are faced with a new set of orientation challenges. The coastline of the Box I. Glossary

\begin{itemize}
  \item Diadromous: migrating between sea water and fresh water.
  \item Anadromous: migrating from salt to fresh water to spawn.
  \item Catadromous: migrating from fresh water to sea water to spawn.
  \item Rheotaxis: a directed response of a motile organism to a water or air current.
\end{itemize}
northern North America is an intricate maze of islands and inlets containing rapid, reversing tidal currents and complex hydrographic regimes. In such an environment, the ability to maintain an appropriate compass heading might not be sufficient to ensure timely homing, and some transition to olfactory guidance seems likely. Ultrasonic tracking studies indicate that salmon do not merely follow the shoreline. Rather, they seem to swim on a homeward course until they encounter land. They then swim back in the opposite direction for a few hours, turn around, and resume homeward orientation. This behavior pattern is appropriate for migration through complex, unfamiliar waterways.

It is not clear whether the salmon can discern and compensate for the strong tidal currents that characterize these regions. It is also difficult to understand how they are able to derive directional information from the extremely weak horizontal concentration gradients of familiar odors that would be present in these waters. The patterns of vertical movements of Atlantic salmon and sockeye suggest that they may be using vertical odor gradients and current shears at the halocline to determine the source of home-stream odors, but this hypothesis has not been definitively tested.

By far the most thoroughly studied component of the homing migration is the final, freshwater phase. Overwhelming evidence indicates that olfaction is the primary mechanism for home-water discrimination and is essential for successful completion of the homing migration. Before (and perhaps during) their seaward migration, juvenile salmon ‘imprint’ on odors specific to their natal stream and, upon return to the river’s vicinity, detection of these odors stimulates the salmon to swim upstream. This was elegantly demonstrated by exposing juvenile coho salmon to artificial odors and subsequently decoying the adults to unfamiliar streams by metering in the odors during the spawning season.

While the imprinting phenomenon has been repeatedly demonstrated, a number of questions regarding it remain unanswered. First, there is conflicting evidence concerning the time or developmental stage when salmon imprint. Experiments with artificial odors indicated that imprinting occurs at the time of peak thyroid hormone levels during smolt transformation (the physiological processes that prepare salmon for ocean residence). Hasler and Scholz injected pre-smolt coho salmon with thyroid hormones, subsequently exposed them to artificial odors, and demonstrated that only treated fish were able to retain long-term memory of the odors. Recent experiments with Atlantic salmon are consistent with these results. However, several species of salmon commonly move from their incubation site and rear elsewhere in fresh water prior to seaward migration, suggesting that olfactory imprinting and smolt transformation may not be inextricably linked. For example, sockeye salmon typically spawn in tributaries of large lakes, but the juveniles rear in the lakes and emigrate from their outlets. It has been proposed that salmon learn odors at more than one place and time during freshwater residence, and that they use the sequence of learned odors to guide their homeward migration. The resolution of this controversy may lie in the discovery that transient increases in plasma thyroid hormones occur not only during smolt transformation but also when juvenile salmon are exposed to novel water sources such as they might experience at river forks during downriver migration.

A second major gap in our understanding of imprinting is the lack of information on the nature of the odors that identify the natal stream. Hasler and colleagues hypothesized that the salmon recognize a combination of odors from soil, plants, rocks and other riverine features; yet a single artificial odor was sufficient for homing. On the other hand, Nordeng postulated that population-specific odors from juvenile conspecifics residing in fresh water guide homing adults. Salmon can distinguish not only populations but also full-sibling families on the basis of odors. However, these odors are not essential for homing and their functional significance is not known. In fact, many aspects of olfactory imprinting and homing under natural conditions are still unclear.

Conclusion

Much of our understanding of fish migration is based on salmonids. The diversity of habitats used by these fishes, their specializations for these habitats, and the balance between learned and innate orientation mechanisms guiding their migrations, make them ideal subjects for studies of mechanistic and evolutionary aspects of migration.
The rapid accumulation of nucleotide sequence data on viral genes has allowed, for the first time, the development of detailed phylogenies of viruses based on an objective criterion. This has been demonstrated clearly in the recent analysis of the evolutionary relationships of HIV – the AIDS virus. When first characterized, HIV seemed aberrant and almost unique in many features. Now it is known to be one of a large group of immuno-deficiency viruses, which are widely distributed among primates and other mammals.

Immunodeficiency viruses form a subgroup of the retroviruses, a clearly monophyletic group of RNA viruses. They have a remarkable life cycle, shared with a class of cellular elements termed retrotransposons. Retroviruses are simple in structure, with a protein core that surrounds the genetic material and is encapsulated in a segment of cell membrane in which the membrane glycoproteins are located.

The genome of these viruses consists of an RNA molecule between five and ten kilobases in length, two copies of which are present in every virus particle. In simple retroviruses this encodes three genes: gag, pol and env. These are the structural genes for the core protein (gag), the virally encoded enzymes (pol) and the envelope glycoproteins (env). However, unlike some other RNA viruses, the viral mRNAs are not expressed immediately upon infection. Instead, a DNA copy is made of the RNA genome by reverse transcriptase, which is also packaged in the virus core and is one of the three enzymes encoded by pol. As a consequence of the mechanics of reverse transcription, the DNA copy of the genome differs from the RNA template by the presence of a precise terminal duplication – the long terminal repeat or LTR. Within the LTR are the elements that control virus gene expression, including the promoter and the transcription termination signal.

The retrovirus life cycle

While the structure of retroviruses is sufficient to distinguish them from all other viruses, it is their life cycle that makes them stand out. The DNA copy that is made following entry into a cell is then integrated into the host genome at one of a very large number of possible sites, using a single, very precisely defined sequence in the virus LTR known as the att site; in this way, the