Physiological mechanisms of homing migration in salmon

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SUMMARY: There are still many mysteries about the amazing abilities of salmon to migrate long distances from open water to their home streams for spawning. Three different approaches ranging from molecular biology to behavioral biology have been applied to investigate mechanisms of salmon homing migration using chum salmon (Oncorhynchus keta) from the Bering Sea to Hokkaido as well as lacustrine sockeye salmon (O. nerka) and masu salmon (O. masou) in Lake Toya and Shikotsu, Hokkaido, Japan. These fish offer good model systems for studying salmon homing migration. The endocrinological studies revealed that the brain-pituitary-gonadal axis plays leading roles in homing migration. The sensory physiological studies suggested that amino acids dissolved in the natal stream water are possible home stream odorants. The biotelemetrical studies provided new concepts for orientation ability in open water, energetics of migration, and environmental preferences of migrating fish. We are confident that these approaches using our useful model system will provide valuable new information about the physiological mechanisms of homing migration in salmon.

KEY WORDS: hormones, olfaction, biotelemetry, homing migration, salmon

INTRODUCTION

A number of studies have investigated the amazing abilities of salmon to migrate long distances from the ocean to their natal streams for spawning, but there are still many unknowns because of the lack of a suitable model system to follow the whole life cycle, especially during the oceanic migration.1) In addition to chum salmon (Oncorhynchus keta) migrating from the Bering Sea to Hokkaido, we have used lacustrine sockeye salmon (O. nerka) and masu salmon (O. masou) in Lake Toya and Lake Shikotsu, Hokkaido, Japan, where the lakes serve as a model “ocean”, as good model fish for studying the physiological mechanisms of the homing migration in salmon. Experiments using three different approaches have been conducted using these model fish. First, the hormonal controlling mechanisms were compared between male and female sockeye salmon during the spawning season. This study revealed that sexual differences in the time required to home and homing accuracy in lacustrine sockeye salmon in Lake Shikotsu were reflected by serum steroid profiles, and a shortened homing duration following gonadotropin-releasing hormone analog (GnRHa) administration was also influenced by gonadal steroids, especially testosterone (T) and 17β,20β-dihydroxy-4-pregnen-3-one (DHP). Second, the olfactory discriminating ability of sockeye and masu salmon was studied by electrophysiological techniques, and we proposed that olfactory organs of lacustrine masu salmon respond to the artificial stream water based on the compositions of amino acids, which may be natal stream odors. Third, the homing behaviors of mature sockeye and masu salmon were tracked from the center of the lake to their natal area using biotelemetorical techniques, and showed the straight migration of widely distributed sockeye salmon and the coastal migration of narrowly distributed masu salmon. These results have confirmed the suitability of our lacustrine model for studying the physiological mechanisms of the homing migration in salmon.

HORMONAL CONTROLLING MECHANISMS

The salmon homing migration is closely related to gonadal maturation, which is regulated mainly by the brain-pituitary-gonadal axis. Expressions of salmon GnRH (sGnRH) in the brain and GtH subunit (GtH α, β, and β) genes in the pituitary were compared between chum salmon in the coastal sea and those on the spawning ground. The levels of pro-sGnRH mRNA in the ventrocaudal telencephalon (VT) and the preoptic area (POA) of fish on the spawning ground were higher than that in the coastal sea.2) The level of GtH α mRNA in fish of both sexes on the spawning ground was higher than in the coastal sea. No significant changes were observed in the GtH β
mRNA in either sex, but the level of GtH IIβ was higher in fish on the spawning ground than in the coastal sea. Changes in serum steroid hormones were also measured from the coastal sea to the spawning ground. Serum estradiol-17β (E2) in females and 11-ketotestosterone (11KT) levels in males showed a peak in the coastal sea. Serum T levels in both sexes showed peaks during upstream migration at the pre-spawning period. Serum DHP levels in both sexes were very low until the pre-spawning period, and increased dramatically at the spawning ground (Matsumoto et al., unpubl. data, 2001).

In Lake Shikotsu, adult sockeye salmon were captured from September to November adjacent to their natal hatchery prior to spawning. They were sampled for serum steroid hormones, tagged and released in the center of the lake. Fish were again sampled at recapture to characterize changes in steroid hormone levels in individual migrants as well as homing duration and percentage of homing rate in each month. Homing duration was significantly shortened from September to October in males and from October to November in females. All males returned faster than females early in September and October, although half of the males did not return to the natal site in November. In contrast, 78-90% of females returned over the entire three month sampling period. It is interesting to note that the average homing percentage of both sexes over three months was 83%, indicating no differences in the total number of homing individuals between males and females.

Because GnRH treatment has been reported to be highly effective in inducing GtH release, ovulation and spermiation in teleost fishes, we investigated the effect of GnRHa implantation on both homing profiles and serum steroid hormone levels of fish in September. GnRHa implantation was highly efficient in shortening the homing duration, and caused dramatic increases in serum DHP levels in both sexes. An interesting discrepancy was observed between rapidly and slowly returning individual males: rapidly returning males showed higher serum T levels and lower serum DHP levels than slowly returning individual males. To examine the direct action of T and DHP on homing duration, T and DHP were implanted in fish in September in comparison with GnRHa-implantation. GnRHa-implanted fish returned significantly earlier than the control fish regardless of sex. T implantation tended to reduce homing duration in both males and females, but there was no statistical significance. DHP implantation also significantly shortened homing duration in females, but it did not have any significant effect in males. These steroid hormone implantations did not affect serum T and DHP levels. It is quite interesting to note that the direct actions of T and DHP on homing migration are sex dependent. The peak of plasma T levels in land-locked sockeye salmon of both sexes was observed at the time when they gathered at the mouth of their natal stream in Lake Chuzenji, Japan. The functional roles of T and DHP on the salmonid homing migration should be further investigated with special attention to their action on the central nervous system.

**OLFATORY DISCRIMINATING ABILITY**

We examined the olfactory discriminatory ability of lacustrine sockeye and masu salmon, which were reared in the culture pond of Toya Lake Station, by recording the integrated olfactory nerve response according to the technique of Sveinsson and Hara. The olfactory organs of both species elicited different response properties to freshwater from various sources regardless of sex or gonadal maturity. The source and effluent water from the culture pond evoked the minimum and maximum response magnitudes, respectively. In cross-adaptation experiments, the culture pond water abolished the secondary response to the river water, but the river water did not abolish the secondary response to the culture pond water. The minimum concentration (threshold) to induce the olfactory nerve response to the culture pond water after adaptation to the lake water was between 0.1 and 1.0%. This threshold level suggests that the olfactory discriminatory ability of salmonids during homing migration must function within a limited distance from the natal river.

Unlike olfactory organs of terrestrial animals, fish olfactory organs respond only to a limited number of chemical species dissolved in water. Chemicals that elicit the response from the olfactory organs of salmon are amino acids, steroids, bile acids, and prostaglandins. We analyzed the compositions of amino acids, inorganic cations and bile acids in waters from three streams which flow into Lake Toya. Application of mixtures of inorganic cations or bile acids, combined based on their compositions in stream waters to the olfactory epithelium induced only very small responses. On
the other hand, application of mixtures of amino acids induced large responses. The response to artificial stream water based on the compositions of amino acids and salts closely resembled the response to the corresponding natural water. Cross-adaptation experiments with three combinations of the mixtures were carried out. The response pattern for each combination closely resembled that to the corresponding combination of the stream waters. According to these results, we concluded that amino acids dissolved in the natal stream water are possible natal stream odors. It is likely that amino acids in stream waters come from a variety of organisms, including plants.

**PHYSIOLOGICAL BIOTELEMETRY**

During the migration from coastal waters to the natal stream, salmon are likely using their olfactory discriminatory ability, but it is still unclear which sensory cues are involved in open water orientation. Recent rapid advances in biotelemetry technologies make it possible to study underwater fish movement in great details. The homing migrations of mature sockeye and masu salmon, whose sensory cues were impaired, were tracked over a period of several hours from the center of Lake Toya to their natal area using an ultrasonic tracking system. Both a mature male sockeye salmon with a brass ring attached as a control and a mature male sockeye salmon whose magnetic cues was interfered with magnetic ring returned straight to the natal area after 1 h of random movement. A mature male sockeye salmon whose visual and magnetic cues were both blocked moved in a direction opposite to the natal area, and was rediscovered in the natal area on the following evening. A blinded male sockeye salmon also moved to the shore of Naka-Toya far from the natal area in the evening. A mature control male masu salmon moved constantly along the coast, and stopped his movement at the mouth of river. A mature male masu salmon whose olfactory cue was blocked moved randomly along the coast, and then tended to move away from the coast. A blinded mature female masu salmon was released and moved randomly away from the coast. We tracked these masu salmon for several hours, and could not monitor the fate of these fish. The accuracy of homing of masu salmon is not clear since parr or smolts could migrate between the streams and lake at any time. It seems possible that there is no critical imprinting period in masu salmon to memorize their natal stream or it is not relevant to their freshwater life history. It is quite interesting to compare the straight movements of sockeye salmon with the coastal movement behaviors of masu salmon. These two species show large differences in ocean distribution with sockeye salmon being distributed widely in the North Pacific Ocean, while masu salmon are narrowly distributed in the western North Pacific Ocean. These data suggest some evolutionary aspects of successful homing migration of salmonids where the narrowly distributed masu salmon only need coastal recognition ability, but widely distributed sockeye salmon must obtain open water cues for orientation.

Although ultrasonic tracking is particularly important to monitor the homing behavior of the ablated individual through constant tracking, both electromyographic (EMG) radiotransmitters that can estimate the energetics of migration and micro-dataloggers that can record swimming depth and ambient water temperature of migrating fish have also been used in Lake Toya. In adult masu salmon, the preferred swimming speeds of individuals within the lake (during their pre-migratory searching phase) were compared with the same individuals in streams using EMG radiotransmitters (Leonard et al., unpubl. data, 2001). Masu salmon in the lake swam at a preferred speed of approximately 2 FL/s with remarkably little variation. In the stream, the variability in selected swimming speed was much larger, and often showed a bimodal pattern with one peak in the aerobic swimming speed range and the other in the anaerobic speed range. Micro-dataloggers were used to assess the environmental preferences of mature masu salmon during their spawning migration. The behavior of one male during searching period was characterized by movements in relatively shallow water while it traveled around the periphery of the lake. During the period prior to upstream migration, the fish seemed to be selecting habitat by depth or lake area rather than by temperature. Between two upstream attempts, the fish was characterized as being a recovery period where it stayed in deep, cool water.

Although our lake system has provided several interesting findings in salmon homing migration as a result of various types of tracking telemetry, these techniques have both advantages and disadvantages. In order to overcome these disadvantages, ten experts in the fields of ship engineering, signal processing, acoustic engineering,
and computer science have carried out a collaborative research project to develop an automatic salmon-tracking robot boat in Lake Toya since 1999. We are trying to develop four interrelated equipment systems; 1) a robot boat, 2.5 m in length, 1.3 m in width, with a loading capacity of 120 kg, operating at 2 knots using two electric thrusters, 2) an ultrasonic tracking system detecting distance and direction of miniature pingers, 3) a signal processing and control system consisting of DGPS, acoustic signal, and gyroscope, 4) a telecommunication system between a land base and the boat. The final goal of this project is to build a robot boat that can track an acoustic signal acquired from a salmon at a distance of 100 m. In the future, we plan to track salmon using the robot boat in the ocean.

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