

Lacustrine Sockeye Salmon Return Straight to their Natal Area from Open Water Using Both Visual and Olfactory Cues

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Abstract

Mechanisms of the amazing ability of salmon to migrate a long distance from open water to natal streams for spawning are still unknown. Lacustrine sockeye salmon (*Oncorhynchus nerka*) in Lake Toya offers an excellent model system for studying the orientation mechanism in open water, because mature fish return to the natal area with a high degree of accuracy. First we examined the percentage of fish returning to the natal area after they were released 7 km south of the natal area. Forty percent of control male mature fish and 25% of the fish blinded by injection of a mixture of carbon toner and corn oil into the eyeball were captured in the natal area within 5 days. Forty-four percent of fish with brass rings (control) and 31% of fish with NdFe magnetic rings which interfere with the magnetic cue were captured in the natal area within 3 days. These experiments suggested that, although the number of blinded fish captured in the natal area was less than that of the controls, the difference was not statistically significant. In the fish captured in the natal area within 3 or 5 days, fish which found the natal area using their olfactory cue after random swimming for a long time and returned to that area may be included. Hence we tracked fish telemetrically using an ultrasonic tracking system, and found that mature males released at a long distance (3.6 or 6.8 km) from the natal area swam straight to the vicinity of the natal area. Interference of the magnetic cue by the attachment of a magnetic ring did not affect their direct return. Blockage of the visual cue caused them to move randomly. These data suggest that lacustrine sockeye salmon return straight to the vicinity of the natal area using their visual cue and finally reach the exact homing point using their olfactory cue.

Introduction

Salmon have an amazing ability to migrate thousands of kilometers from ocean to natal streams for spawning after oceanic life for a number of years. It is well established that salmon return from the coast to the natal branch of rivers using their olfactory sense (Hasler and Scholz, 1983; Stabell, 1992; Nevitt *et al.*, 1994). As to open water orientation, the contribution of vision (Lorz and Northcote, 1965; Hiyama *et al.*, 1967; Groves *et al.*, 1968; Jahn, 1969; Bertmar and Toft, 1969; LaBar, 1971) or rheotaxis to water current (Isaksson, 1980) has been discussed. Furthermore, it has been reported that magnetites are detectable in salmonids, suggesting the importance of a magnetic cue for open water

orientation (Quinn and Groot, 1983; Mann *et al.*, 1988; Walker *et al.*, 1988, 1997; Moore *et al.*, 1990; Sakaki *et al.*, 1990; Ogura *et al.*, 1992; Yano *et al.*, 1996). Tracking of adult salmon during oceanic migration has been carried out using transponding transmitters (Westerberg, 1982; Døving *et al.*, 1985; Pearson and Storeton-West, 1987; Potter, 1988; Yano and Nakamura, 1992) or a high-resolution sector scanning sonar (Arnold *et al.*, 1990). Recently, tracks of four species of Pacific salmon using depth-sensing ultrasonic transmitters showed that maturing salmon moved in particular directions, suggesting that the salmon have a compass orientation ability (Ogura and Ishida, 1995). It is,

however, rather difficult to explore the detailed mechanisms of the orientation using salmon in ocean.

The lacustrine sockeye salmon, *Oncorhynchus nerka*, in Lake Toya offers a good system for studying the orientation mechanism in open water, because mature fish return to the natal area with a high degree of accuracy. We examined homing ability of mature male lacustrine sockeye salmon whose visual and/or magnetic cues were impaired. First we examined the percentage of fish returning to the natal area after they were released. Then we tracked the fish telemetrically and found that mature fish released at a long distance from the natal area returned straight to the vicinity of the natal area using mainly their visual cue.

Materials and methods

Source of fish

In Lake Toya (surface area 70 km², average diameter 9.4 km and average depth 116 m), lacustrine sockeye salmon are artificially fertilized and released from the shore of the Akebono Hatchery and Kame-iwa, ~1 km from the Akebono Hatchery. Hence both areas can be regarded as the natal area of these lacustrine sockeye salmon.

One hundred and thirty-five mature males (4 years old (3+), average fork length, 33.5 cm; average body wt, 474.0 g) were captured in the natal area by a towing net on October 10–12, transported to the Toya Lake Station and maintained in a 2 ton tank for several days before experiments. Two maturing males (4 years old, average fork length 31.9 cm, average body wt 401.5 g) captured in the middle of the lake by a fishnet on September 19, transported to the Station and maintained in a 2 ton tank for several days were also used.

Treatment of fish

Fish were anesthetized with ethyl *m*-aminobenzoate methanesulfonate (Nacalai Tesque, Kyoto, Japan), tagged with a numbered disk on their backs and subjected to one of the following treatments: (i) injection of a mixture of carbon toner (Canon Inc., Tokyo, Japan) and corn oil (Nisshin Oil Co., Tokyo, Japan) into eyeball using 0.4 × 19 mm needles to cause detached retinas; (ii) attachment of a NdFe magnet ring (6.5 mm in diameter, with a 2.0 mm diameter center hole, 1.0 mm thick, HS 32BV, Br 11300 G, Hc 10700 Oe, Hitachi Metal Co., Tokyo, Japan) on the lateral head to interfere with the magnetic cue; (iii) detached retinas plus attachment of magnetic ring; and (iv) attachment of a brass ring (the same size as the magnet ring) on the lateral head for control. Average treatment time was ~3 min.

Telemetric experiments

For telemetric experiments, an ultrasonic transmitter (65–77 KHz, 8 mm in diameter, 36 mm in length and weighing 2.1 g in water; V8-2L, Vemco Limited, Halifax, Canada) was inserted into the stomach of fish. Tracking was carried out

Table 1 Results of lacustrine sockeye salmon return to the natal area

Experiment	Number of fish released	Number of fish recaptured	Percentage of fish returned
Magnet ring-attached fish	43	19	44
Brass ring-attached fish	48	15	31
Blind fish	20	5	25
Normal fish	20	8	40

by a single vessel (0.8 tons, 4.55 m in length) using three angled hydrophones (V-10, Vemco) and a receiver (VR-60, Vemco) which detect a strong trackable signal from maximum straight distance of 300 m in water. The location of the vessel was monitored by a global positioning system (IPS-760, Sony, Tokyo, Japan) at 5 min intervals. The weather was clear on all days when fish were released.

Results

Numbers of fish which returned to natal area

First we determined the percentage of fish which returned to the natal area after they were released (Table 1). Mature male with either brass rings (control) or magnetic rings on the head were released 2.2 km south of the natal area. Nineteen (44%) out of 43 fish with the magnetic rings and 15 (31%) out of 48 fish with the brass rings were captured in the natal area within 3 days. Similar experiments were carried out with the blinded fish. The fish were released 7 km southeast of the natal area; 40% of control fish (8/20) and 25% of the blinded fish (5/20) were captured in the natal area within 5 days. In both experiments, the numbers of treated fish recovered were different from those of the controls, but the differences were not statistically significant.

In the above experiments, the total numbers of fish captured in the natal area within 3 or 5 days after release of fish were counted. Those fish which happened to find the natal area using their olfactory cue after random swimming for long time and returned to the area may be included in the number of fish captured. In addition, it is uncertain whether all the fish which returned to the natal area were captured. We then tracked fish telemetrically using an ultrasonic tracking system.

Telemetrical tracking of fish

We captured maturing male fish swimming in the middle of the lake near the Toya Lake Station by a fishnet on September 19, which is early in the homing season. Figure 1 shows the tracking of fish released at two different sites. The fish released south of Nakajima Island (point A) on September 21 moved randomly for ~1 h and failed to move

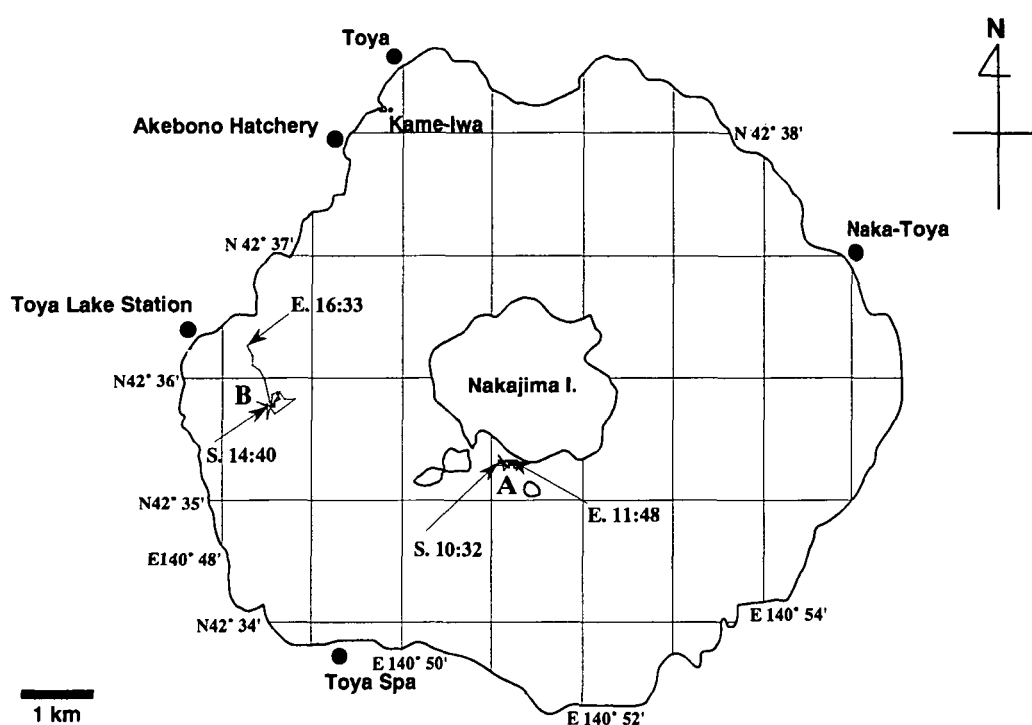


Figure 1 Tracking of two maturing male lacustrine sockeye salmon. Fish were released south of Nakajima (point A) at 10:32 on September 21 (cloudiness 1/10) and 3.6 km south of the natal area (point B) at 14:40 on September 22 (cloudiness 3/10). The first fish moved randomly for ~1 h and did not move rapidly again until 11:48. The second fish moved randomly for ~2 h and reached the shore close to the Toya Lake Station at 16:33. S, start of tracking; E, end of tracking.

out of the area. The other fish, released 3.6 km south of the natal area (point B) on September 22, moved randomly for ~2 h and reached the shore close to the Toya Lake Station.

Next we captured a male mature fish at the Akebono Hatchery (natal area) on October 10–12 and released it at point B (Figure 2) on October 15. After ~1 h of random movement, the fish moved directly toward the natal area at a speed of 1.97 km/h and returned to the area. A fish whose magnetic cue was interfered with was released 6.8 km southeast of the natal area (point C) on October 14. Similar to the control fish, it returned straight to the vicinity of the natal area at a speed of 1.98 km/h after 1 h of random movement. The target point at the shore extrapolated from the straight track of the fish is only ~300 m away from the homing point. At 1.1 km distance from the natal area, this fish selected a more direct course to the homing point (Figure 2).

A fish whose visual and magnetic cues were both blocked was released at point B on October 26 (Figure 3). The fish moved randomly for ~1.5 h, moved in a direction opposite to the natal area and was recorded south of Nakajima Island in the evening. This fish was rediscovered in the natal area on the following evening (October 27). A blinded fish was also released at point C on October 27 (Figure 3). The fish moved randomly and finally reached the shore of Naka-Toya far from the natal area in the evening.

Discussion

The tracking experiments showed that the blinded fish did not return directly to the natal area and was found at the natal area ~30 h after release. It seems that the blinded fish moved randomly, happened to reach the shore of the lake, moved along the shore and finally found the natal area using his olfactory cue.

In the first part of this paper, we showed that 25% of the blinded fish returned to the natal area within 5 days. Similar results were reported by previous investigators (Lorz and Northcote, 1965; Hiyama *et al.*, 1967; Groves *et al.*, 1968; Jahn, 1969; Bertmar and Toft, 1969; LaBar, 1971). The results of the tracking experiment suggest that the fish recaptured for a few days must include fish which returned indirectly using the olfactory cue. Hence recapturing experiments do not offer accurate information as to which types of cue are used in open water migration.

In a separate study, we examined homing duration for returning to the natal area from the middle of Lake Shikotsu, which is located 30 km northeast of Lake Toya, using lacustrine sockeye salmon (Sato *et al.*, 1997). In general, males returned to the natal area much faster than females. The homing duration for males was much shorter in October and November than in September, and that for females greatly shortened in November. Implantation of gonadotropin-releasing hormone into females captured in

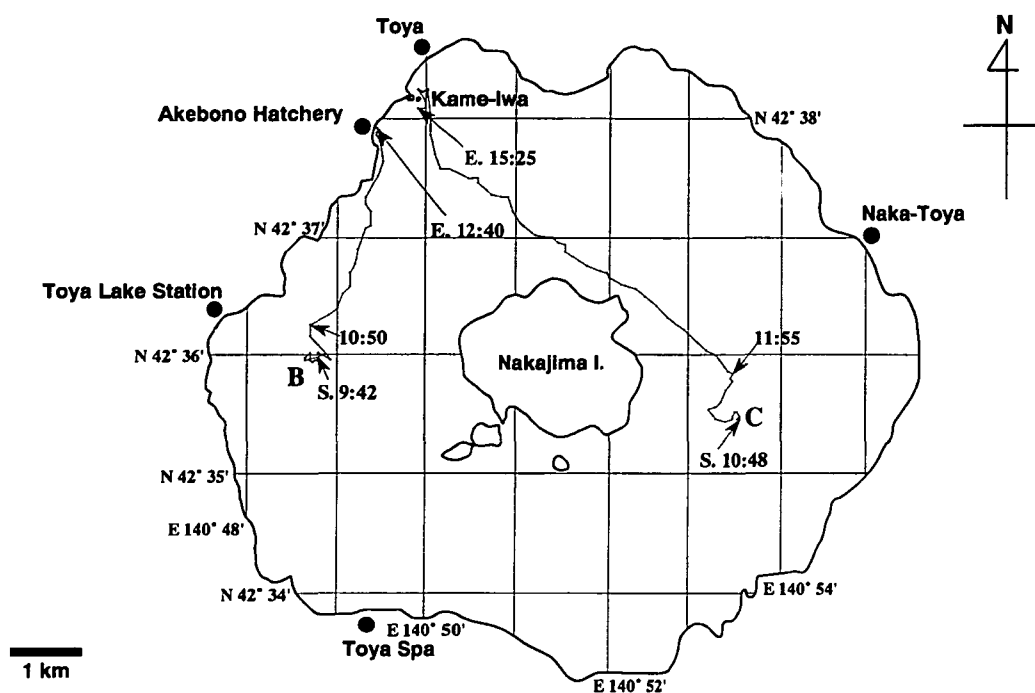


Figure 2 Tracks of mature male lacustrine sockeye salmon. The control fish with a brass ring was released at point B at 9:42 on October 15 (cloudiness, 0/10). The fish showed random movement for ~1 h, moved directly to the natal area at 10:50 and reached to the natal area at 12:40. The fish with magnetic interference was released 6.8 km southeast of the natal area (point C) at 10:48 on October 14 (cloudiness, 2/10). The fish also showed 1 h of random movement, moved directly to the natal area at 11:55 and reached the natal area at 15:25. S, start of tracking; E, end of tracking.

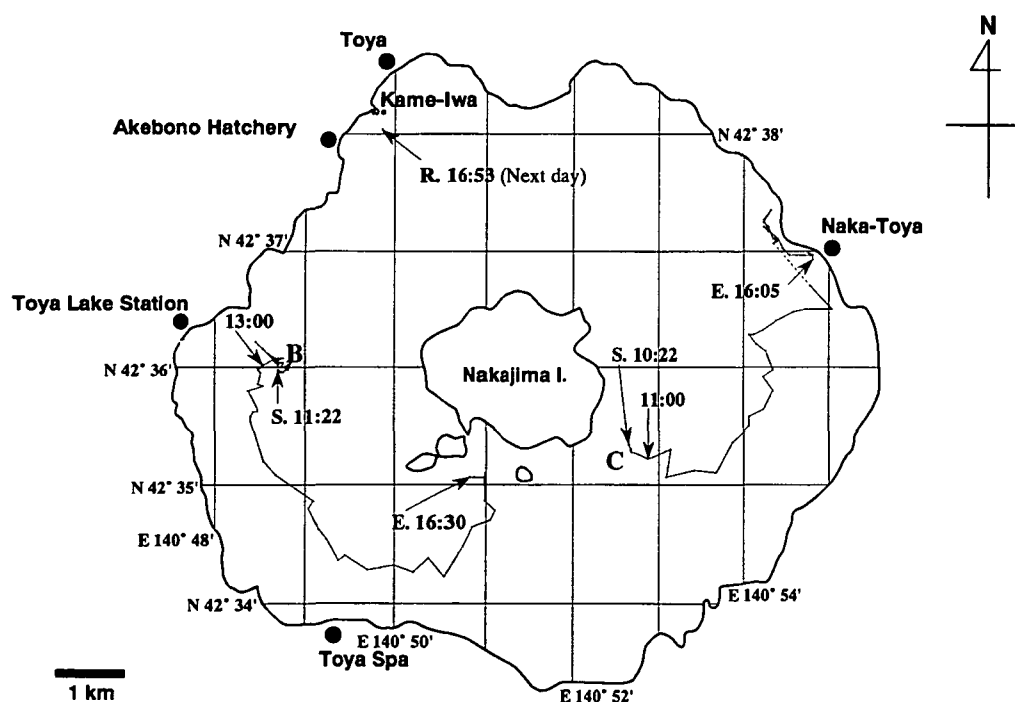


Figure 3 Tracks of mature male lacustrine sockeye salmon whose visual and magnetic cues were blocked. A magnetic ring was attached to the head of a fish whose vision was blocked to interfere with its magnetic and visual senses. This fish was released at point B area at 11:22 on October 26 (cloudiness, 4/10). The fish moved randomly for ~1.5 h, moved in a direction opposite to the natal area at 13:00 and reached south of Nakajima island by 16:30. This fish was rediscovered in the natal area at 16:53 on October 27. The vision-blocked fish was released at point C at 10:22 on October 27 (cloudiness, 0/10–3/10). The fish moved randomly and finally reached the shore of the Naka-Toya far from the natal area at 16:05. S, start of tracking; E, end of tracking; R, rediscovery of fish by ultrasonic signal.

September significantly shortened the homing duration. These results suggest that sex and degree of maturation are important factors for homing duration. In the present study, male fish captured in October were used for the tracking experiment. The fish captured in September did not show a straight return to the natal area.

It is surprising that the fish identifies his position in open water and the direction of the natal area with such a high degree of accuracy at a point 6.8 km distance from the natal area. As shown in Figure 2, both mature fish released south and southeast of their natal area returned directly. This suggests that rheotaxis to the water current does not contribute to the open water orientation in Lake Toya. It seems unlikely that fish use their olfactory cue in long-distance migration because odorants in the natal area are too diluted at a long distance (e.g. 6.8 km) from the natal area. This notion is further supported by the results that the blinded fish did not return directly. The random movement of the blinded fish suggests that lacustrine sockeye salmon return to the vicinity of natal area using their visual cue.

It is possible that fish use the olfactory cue for orientation even in open water not far from the natal area, because one fish selected a more direct course to the natal area at the point 1.1 km distance from the natal area. The present results also suggest that the fish do not primarily use a magnetic cue in the selection of the natal area in this species because fish with magnetic rings attached to their head returned directly. The tracking experiments were carried out during the daytime on sunny days and hence the visual cue might play a primary role in the return to the natal area. It is possible that a geomagnetic cue is also used for their open water orientation, especially on cloudy days or at night. In this sense, it is interesting to note that rainbow trout have magnetoreceptor cells in the nose (Walker *et al.*, 1997).

Tracking experiments of fish were carried out with the white bass, *Roccus chrysops*, by Hasler *et al.* (1969). Although the open water movement of the white bass was of a non-random nature, the fish did not show the direct movement seen in lacustrine sockeye salmon. The present results demonstrating the direct return of lacustrine sockeye salmon suggest that they have an amazing ability to precisely identify their position in open water and the direction of their natal area. This paper is the first report to demonstrate that ability. It is possible that the fish use a 'sun-compass' (Hasler and Wisby, 1951; Hasler and Schwassmann, 1960), polarized skylight patterns (Waterman and Forward, 1970, 1972) or the memory of landmarks (Guilford, 1993) to identify the position and direction, but further study is needed to more precisely clarify the mechanism of open water orientation in lacustrine sockeye salmon.

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