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# Physiological Mechanisms of Homing Ability in Sockeye Salmon: From Behavior to Molecules Using a Lacustrine Model

Hiroshi Ueda, Yuzo Yamamoto, and Hiroshi Hino

**ABSTRACT** 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 much remains unknown because of the difficulties in following the whole life cycle, especially the oceanic migration. Kokanee *Oncorhynchus nerka* (lacustrine sockeye salmon), offer promise as systems for studying the physiological mechanisms of homing ability in salmon. Three types of physiological study, from behavior to molecules, were conducted using Lake Toya and Lake Shikotsu, Hokkaido, Japan, as model “oceans” and are reviewed here. The first study examined homing behavior of mature sockeye salmon in Lake Toya using ultrasonic tracking systems, testing for use of visual cues and magnetic orientation. Visual cues, but not magnetic orientation, appeared to be important in straight homing behavior. The second study examined the effect of hormonal controlling mechanisms, in relation to sexual differences, on homing duration (the time required to home) and homing accuracy during the spawning season in Lake Shikotsu. Administering gonadotropin-releasing hormone (GnRH) analog shortened homing duration. The third study examined the olfactory discriminating ability of home stream odorants using a two-choice test tank. Sockeye salmon exhibited preferential upstream selective movement toward artificial home stream water that had been prepared to mimic the composition of amino acids and related substance of the home stream. These results demonstrate the suitability of the lacustrine model for studying the physiological mechanisms of homing ability in sockeye salmon.

Salmon have an amazing ability to migrate thousands of kilometers from the open ocean to their natal stream to reproduce after several years of oceanic feeding. It is widely accepted that specific cues associated with the natal stream are imprinted to particular areas of the nervous systems of juvenile salmon during downstream migration and that adult salmon utilize these cues to recognize the natal stream during the homing migration. Since the olfactory hypothesis for salmon homing was proposed by Wisby and Hasler (1954), the olfactory homing mechanism has been investigated in many behavioral, physiological, biochemical, and neurobiological studies (see reviews; Cooper

and Hirsch 1982; Hasler and Scholz 1983; Døving 1989; Stabell 1992; Ueda and Yamauchi 1995; Satou et al. 1996; Bertmar 1997; Nevitt and Dittman 1998; Ueda and

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Shoji 2002; Quinn 2005). The olfactory discriminating ability is believed to be exerted only within a short distance of the coast of the natal stream as it is impossible for salmon to use only this ability for a long distance migration from the feeding area to the natal area. For open water orientation, the contributions of a map and compass system have been discussed (Quinn and Groot 1984; Quinn et al. 1989; Hansen et al. 1993; Ogura and Ishida 1994; Dittman and Quinn 1996; Ueda 2004). However, it remains unclear both which sensory systems play leading roles in open water orientation and how the olfactory system discriminates stream odors. One of the reasons for this uncertainty is the lack of a suitable model system for intensively examining homing ability in salmon as they move from open water to the natal stream.

Lacustrine sockeye salmon offer a model system for studying homing ability. We review three studies, ranging from behavior to molecules, examining the physiological mechanisms of homing ability in lacustrine sockeye salmon. First, the homing behaviors of mature sockeye salmon whose sensory cues had been impaired were tracked from the center of the lake to the natal area using a conventional ultrasonic biotelemetry technique. Second, hormonal control mechanisms were compared between male and female sockeye salmon with reference to the changes in homing duration (the time required to home) and homing accuracy. The effects of hormone implantation on homing duration were also examined. Third, the olfactory discriminating ability of

sockeye salmon was studied using upstream selective movement toward artificial home stream water using a two-choice test tank. The results are reviewed and discussed with respect to open water orientation, sex-dependent hormone actions on homing migration, and olfactory mechanisms of freshwater discrimination.

### Study Areas and Populations

All studies were conducted in Lake Toya (surface area 71 km<sup>2</sup>, average and maximum depth 116 m and 179 m, respectively) or Lake Shikotsu (surface area 78 km<sup>2</sup>, average and maximum depth 265 m and 363 m, respectively), large caldera lakes in Hokkaido, Japan. Most lacustrine sockeye salmon in both lakes are spawned and released from hatcheries within a few months of emergence. Although the smolting process in lacustrine sockeye salmon is not well understood, adults attain maturity in 3–5 years and return to their natal hatchery for breeding (Figure 1). The active spawning season is the middle of October to early November in both lakes.

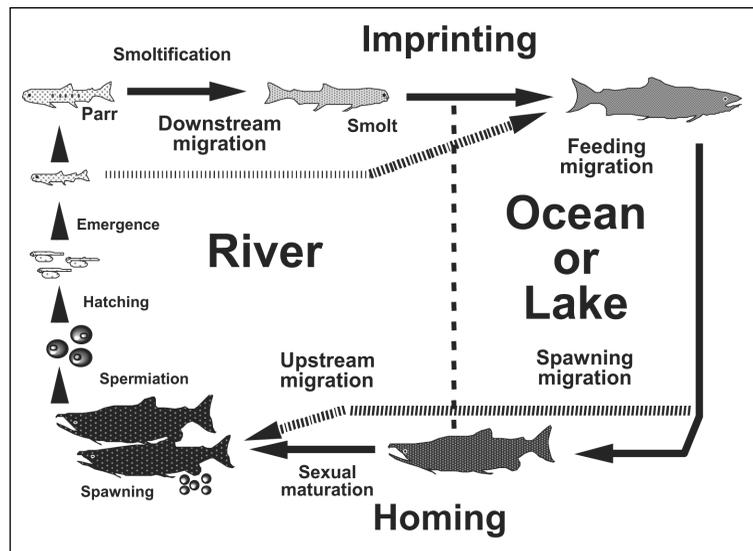


Figure 1. Life histories of lacustrine and anadromous sockeye salmon. Dotted line: lacustrine form; solid line: anadromous form.

## Biotelemetry of Homing Behavior

Salmon likely use their olfactory discriminatory ability during migration from coastal waters to the natal stream, but it is 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 detail (Cooke et al. 2004). In particular, ultrasonic transmitters have been used to investigate the migratory behavior of salmonids in the coastal eastern Pacific Ocean (Quinn et al. 1989) and the central Bering Sea (Ogura and Ishida 1994). Ultrasonic tracking has been used in combination with sensory ablation experiments, which blocked visual and olfactory cues or magnetic senses, to study oceanic migratory salmonids (Døving et al. 1985; Yano and Nakamura 1992; Yano et al. 1996). However, it is difficult to carry out controlled experiments on anadromous fish as they migrate from the sea, in their pre-maturation phase, to their natal stream, where they mature. Lacustrine forms offer a good model system for studying the homing mechanisms of salmon from open water to their natal area for reproduction.

## Methods

The sensory cues of mature sockeye salmon were impaired and then their homing migrations were tracked from the center of Lake Toya to the natal area using an ultrasonic tracking system (Ueda et al. 1998). Four treatments were each applied to a differ-

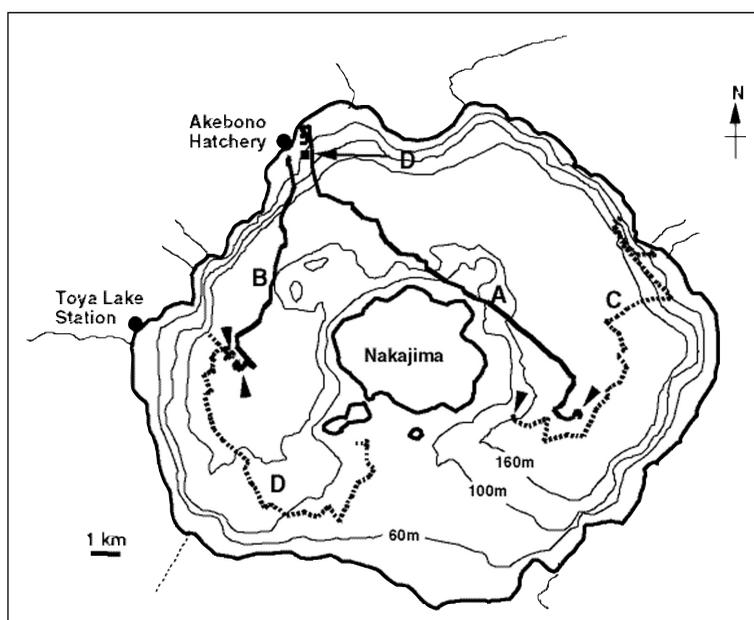
ent mature male sockeye salmon:

1. Experimental blocking of magnetic cues using a magnetic ring;
2. (Control) application of a surrogate brass ring with no influence on magnetic cues;
3. Experimental blocking of visual cues through blinding; and
4. Experimental blocking of magnetic and visual cues.

The experimental fish were then released near the center of the lake and their homing migrations tracked.

## Results

Sockeye salmon with the magnetic blocking and control treatments returned straight to the natal area after 1 h of random movement (Figure 2A, 2B). The blinded sockeye salmon



**Figure 2.** Tracks of four mature male lacustrine sockeye salmon in Lake Toya during the spawning season. Arrowheads indicate each fish's point of release: A—magnetic cue-interference fish, B—magnetic cue-interference control fish (brass ring), C—visual cue-interference fish, D—visual and magnetic cues-interference fish.

moved to the shore of Naka-Toya in the evening and stayed there for a few days, far from the natal area (Figure 2C). The sockeye salmon whose visual and magnetic cues were both blocked moved in a direction opposite to the natal area, and were rediscovered in the natal area on the following evening, suggesting the possibility of involvement of olfactory cues in finding the natal area (Figure 2D).

## Discussion

The ultrasonic location transmitters were combined with sensory ablation to evaluate homing capability, particularly orientation ability, of sockeye salmon. Visual cues appeared critical to the straight homing of sockeye salmon, while magnetic cues did not appear to be necessary. However, magnetoreceptor cells have been identified in the nose of rainbow trout *O. mykiss* (Walker et al. 1997).

Further investigation of the role of magnetic cues in salmon homing migration is required. Moreover, since lacustrine salmon experience the lake for their entire life cycle, they may be able to learn and exploit other sensory systems. Thus the lacustrine experiments may shed light on sensory systems available for use in open water orientation but may not necessarily reflect what is actually used in oceanic migrations.

## Hormonal Controlling Mechanisms

The salmon homing migration is closely related to gonadal maturation, which is regulated mainly by the brain–pituitary–gonadal axis. Briefly, gonadotropin-releasing hormone (GnRH) controls gonadotropin (GTH: LH and FSH) synthesis and release from the pituitary gland. Gonadotropins induce steroidogenesis in the gonads, and steroid hormones stimulate gametogenesis and final gameto-maturation; estradiol-17 $\beta$  (E<sub>2</sub>) and testosterone (T) are active in vitellogenesis, T and 11

ketotestosterone (11KT) in spermatogenesis, and 17 $\alpha$ ,20 $\beta$ -dihydroxy-4-pregnen-3-one (DHP) in final gameto-maturation in both sexes (Nagahama 1999). We investigated the hormone profiles in the brain–pituitary–gonadal axis in relation to homing migration and gonadal maturation of mature lacustrine sockeye salmon in Lake Shikotsu (Ueda 1999).

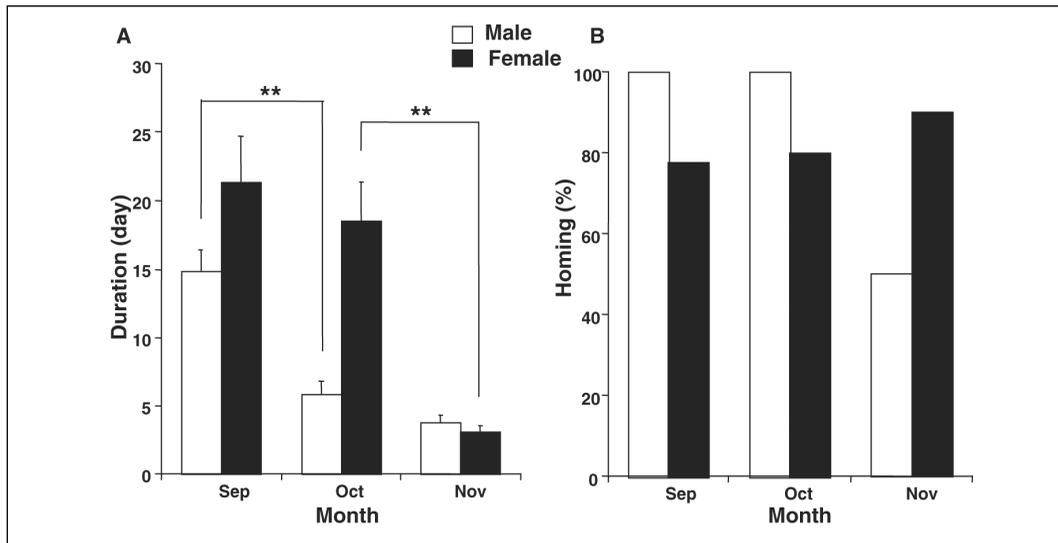
## Methods

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 sampled again at recapture to characterize changes in steroid hormone levels in individual migrants as well as homing duration and homing percentage by month (Sato et al. 1997).

## Homing Duration: Results and Discussion

Homing duration shortened significantly from September to October in males and from October to November in females (Figure 3A). All males returned faster than females early in September and October and half of the males did not return to the natal site in November. In contrast, 78–90% of females returned over the entire 3-month sampling period (Figure 3B). The average homing percentage of either sex for 3 months was 83%, indicating no differences in the total number of homing individuals between male and female.

The sex ratio of chum salmon on the spawning ground is predominated by males early and females late in the spawning run (Bakkala 1970). Quinn and Foote (1994) also demonstrated that sex-specific differential arrival timing on the spawning grounds and subsequent differences in reproductive success in sockeye salmon. The drastic reduction



**Figure 3. Changes in homing duration (A) and percentage (B) of lacustrine sockeye salmon in Lake Shikotsu from September to November. Error bars represent SE \*\*,  $P < 0.01$  by Student's  $t$ -test.**

of male homing percentage late in the season suggests, beyond differential survival, possibly less selection pressure on males for spawning at the natal site, and therefore increasing probability of straying to spawn as final maturation approaches.

The occurrence of relatively few nonhoming females throughout the sampling period may be related to the following two population-level hypotheses: 1) the conservative protection of these individuals' strain from the disruption of being captured at their natal spawning site and 2) the enhancement of their strain arising from a wild spawning distribution within the lake.

### Steroid Hormone Profiles: Results

The sexual differences in homing behavior are thought to be reflected by the different steroid hormone profiles between males and females (Sato et al. 1997). In males, the reduced homing duration coincided with increased serum 11KT levels. Reduction of homing percentage was associated with increased serum DHP levels (Figure 4A). In females, the reduced hom-

ing duration coincided with an increase of serum T and DHP levels, and a drop in serum  $E_2$  levels (Figure 4B).

### Steroid Hormone Implantation Studies: Results

Since GnRH treatment has been reported to be highly effective in inducing GTH release, ovulation and spermiation in teleost fishes (Zohar 1996), we investigated the effect of GnRH analog (GnRH<sub>a</sub>) implantation on both homing profiles and serum steroid hormone levels of fish in September (Sato et al. 1997). GnRH<sub>a</sub> implantation reduced homing duration and caused dramatic increases in serum DHP levels in both sexes (Figure 5). 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 GnRH<sub>a</sub>-implantation (Kitahashi et al. 1998b). GnRH<sub>a</sub>-implanted fish returned sig-

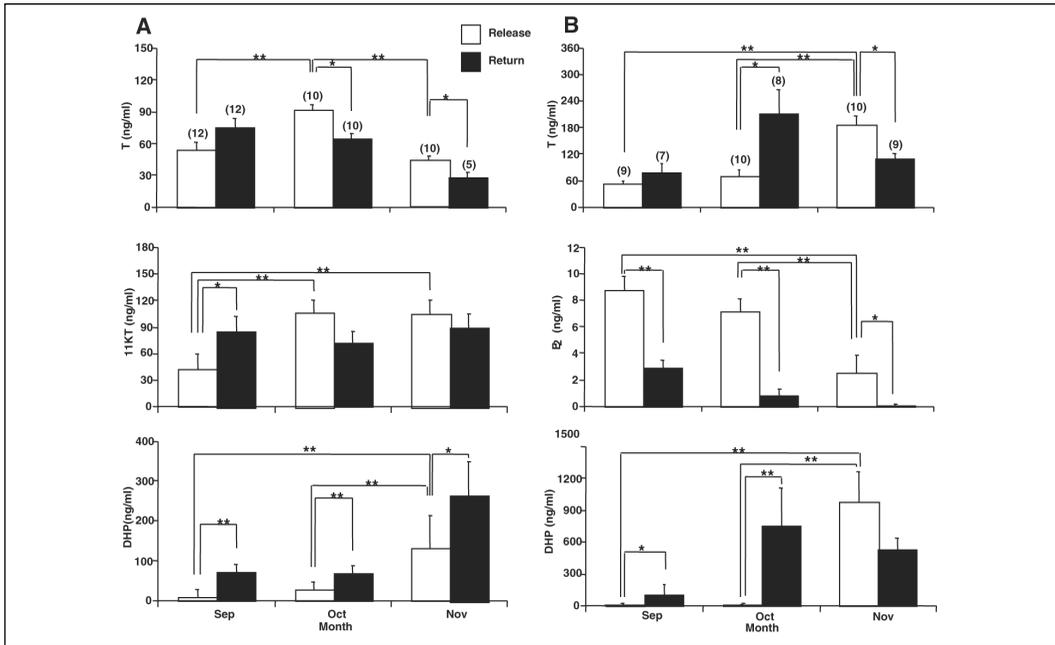


Figure 4. Changes in serum steroid hormone levels of male (A) and female (B) lacustrine sockeye salmon from September to November in Lake Shikotsu. White and black bars represent the mean  $\pm$  SE of the indicated number of samples shown in parenthesis at the time of release and return, respectively. \*,  $P < 0.05$ ; \*\*,  $P < 0.01$  by Student's *t*-test.

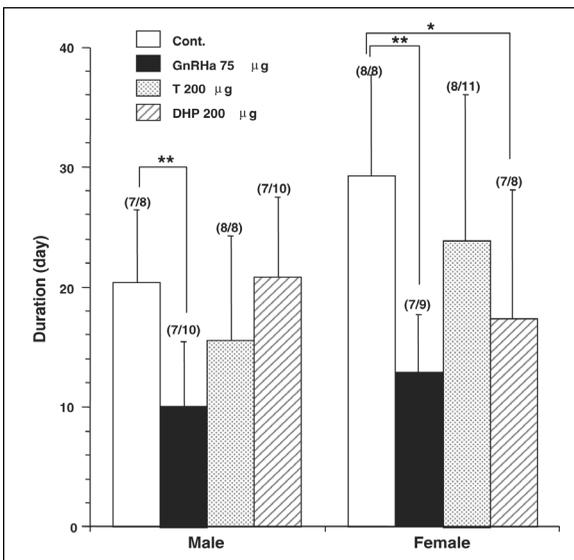


Figure 5. Effects of GnRH analog (75  $\mu$ g/fish) and steroid hormone (200  $\mu$ g/fish) implantation on homing duration of lacustrine sockeye salmon in Lake Shikotsu in September. Number in parentheses indicate returning fish/releasing fish. Error bars represent SE of the samples shown in parenthesis (number of return/number of release). \*,  $P < 0.05$ ; \*\*,  $P < 0.01$  by Student's *t*-test.

nificantly earlier than the control fish regardless of sex. T implantation tended to reduce homing duration in both males and females, but not to a statistically significant degree. 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.

### Discussion

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 lacustrine sockeye salmon of both sexes was observed at the time when they gathered at the mouth of their natal stream in Lake Chuzenji, Japan (Ikuta 1996). Androgens are well-known to be involved

in stimulating aggressive behavior in teleost fishes (Villars 1983), and serum T and 11KT are the two major androgens which influence spawning behavior as well as the social dominance hierarchy (Kindler et al. 1989; Cardwell and Liley 1991; Pankhurst and Barnett 1993; Brantly et al. 1993; Cardwell et al. 1996). Although DHP is known to be a maturation-inducing steroid in salmonids (Nagahama and Adachi 1985), its function to the central nervous system has not yet been clarified. 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.

GnRHa implantation was also highly effective in accelerating gonadal maturation in anadromous, maturing sockeye salmon of both sexes. Expression of GTH subunit genes in the pituitary gland was examined and revealed that the levels of GTH  $\alpha$  and LH $\beta$  mRNAs in GnRHa-implanted fish were higher than those in control fish, but the levels of FSH $\beta$  mRNA showed no change (Kitahashi et al. 1998a). Implantation of GnRHa caused a significant elevation of serum DHP levels in both sexes, but had no effect on levels of T and 11KT in males or E<sub>2</sub> and T in females (Fukaya et al. 1998).

This suggests GnRH in the brain stimulates LH release from the pituitary gland, and then LH enhances serum DHP levels in both sexes during the later part of the homing migration in salmonid fishes. GnRH is believed to play a leading role in the homing migration of both sexes (Urano et al. 1999), but gonadal steroids, especially T and DHP, seem to have sexually different influences on homing migration. Further study using our model systems may reveal sexual differences in hormonal control of the homing migration in salmonid fishes with special reference to the early part of the homing migration.

### Olfactory Discriminating Ability

Since the olfactory transduction mechanism in fish began to be examined by electrophysiological techniques, many studies have been carried out on the olfactory discriminating ability of salmon. The early studies reported that application of natal stream water to the olfactory epithelium of homing salmon induced a large olfactory bulbar response (Hara et al. 1965; Ueda et al. 1967; Hara 1970). Later, it was shown that not only the natal stream water but also waters from other streams induced olfactory bulbar responses in salmon (Oshima et al. 1969; Ueda et al. 1971; Dizon et al. 1973; Bodznick 1975). Using coho salmon *O. kisutch*, behavioral and electrophysiological studies reported that imprinting with a synthetic odor such as phenyl ethyl alcohol was possible (Nevitt et al. 1994; Dittman et al. 1996).

We examined the olfactory discriminatory ability of lacustrine sockeye 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 (1990). The olfactory organs elicited different response properties to various freshwaters regardless of sex or gonadal maturity (Sato et al. 2000). The source and effluent water from the culture pond evoked the minimum and maximum response magnitudes, respectively.

Various odorants are released from fish including amino acids, steroids, bile acids, and prostaglandins (Hara 1994). Several studies have suggested that juvenile salmonids produce population-specific odors or pheromones, which might be detectable by the adults during the homing migration (Nørdeng, 1971; Groot et al. 1986; Quinn and Tolson 1986; Courtenay et al. 1997). It has also been demonstrated that sex steroids and prostaglandins that have effects on the olfactory epithelium of salmonids may act as sexu-

al pheromones (Moore and Scott 1992; Moore and Warning 1996). These odors may modify the source water in such a way as to make the culture pond water more detectable to the olfactory system.

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.

Several attempts to identify the natal stream odor were made based on the olfactory bulbar response, and suggested that the natal river odors were nonvolatile (Fagerlund et al. 1963; Cooper et al. 1974; Bodznick 1978). Spectral analysis of the olfactory bulbar response suggested that the natal stream odor was absorbed on activated carbon and ion-exchange resin, insoluble in petroleum-ether, dialyzable, nonvolatile, and heat-stable (Ueda 1985). Unlike olfactory organs of terrestrial animals, only a limited number of chemicals are known to elicit an olfactory response in fish. Chemicals that elicit the response from the olfactory organs of salmon are amino acids, steroids, bile acids, and prostaglandins (Hara 1994).

We analyzed the compositions of amino acids and bile acids in waters from three streams which flow into Lake Toya. Application of bile acids, combined based on their compositions in stream waters, to the olfactory epithelium induced only very small responses. In contrast, application of mixtures of amino acids induced large responses (Shoji et al. 2000). 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 to each combination closely resembled the response to the corresponding combination of stream waters.

## Methods

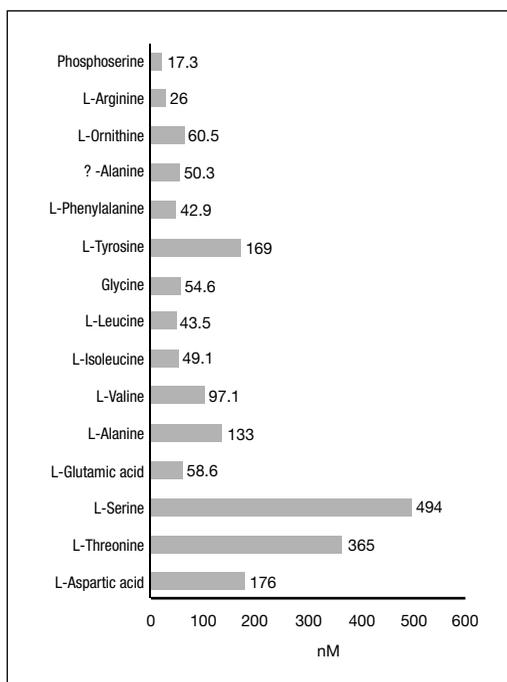
Upstream selective movement of lacustrine sockeye salmon, which were captured in the Lake Shikotsu Hatchery, was investigated in a two-choice test tank consisted of two water inlet arms and one pool. Two tests were run: one using natural lake water in each arm and one using natural lake water in one arm and artificial amino acid water in the other arm. The artificial amino acid water was prepared based on the compositions of amino acid and related substances in the Lake Shikotsu Hatchery water (Figure 6).

## Results

Of 227 sockeye salmon tested, 81 (35.6%) showed upstream movement to one of the choice arms. When natural lake water flowed from the two arms the moving fish exhibited no selectivity between left and right arms. When artificial home stream water flowed in one arm, the moving fish exhibited strong preference to that arm: 47 fish (75.8%) versus 15 (24.2%) (Table 1). There were no sexual differences in upstream selective movement: 77.1% of males and 74.1% of females were observed in the arm with the artificial home stream water (Table 1).

## Discussion

In our previous upstream selective movement of chum salmon *O. keta*, over 80% of male chum salmon showed upstream selective movement in the artificial home stream water (Shoji et al. 2003). Accordingly, we conclude



**Figure 6. The compositions and concentrations of amino acid and related substances in the Lake Shikotsu Hatchery water.**

that amino acids dissolved in the home stream water are home stream odorants. Further, these results strongly support the hypothesis that amino acids dissolved in stream waters are home stream substances for salmon homing. It is likely that amino acids in stream waters come from a variety of organisms, including plants. Amino acids in the mucus from the fish body surface may also contribute to the formation of the natal stream odors (Hara et al. 1984), but the large variation of amino acid compositions among the streams cannot simply be explained by the fish mucus amino acids.

**Conclusions**

We’ve reviewed our recent studies on the physiological mechanisms of the homing migration mainly in lacustrine sockeye salmon in Lake Toya and Lake Shikotsu,

**Table 1.**

Selectivity of lacustrine sockeye salmon in the two-choice test tank. Of 227 fish tested, 81 exhibited upstream movement (35.6%). Among those that moved, no selectivity was observed when natural water (NLW) flowed in both arms (NLW/NLW row). When artificial home stream water (AHW) flowed in the right arm (NLW/AHW row), fish preferentially selected that arm (\*\*,  $P < 0.01$ ). Among the fish exhibiting movement in the NLW/AHW test, the preference for AHW was similar in males (77.1%) and females (74.1%).

	Left Arm	Right Arm	Significance
NLW / NLW	10	9	
NLW / AHW	15	47	**
Males	8	27	**
Females	7	20	**

where the lakes serve as a model “ocean.” Using this model, valuable insights into salmon homing migration have been provided by three different approaches: physiological biotelemetry of homing behavior, hormonal control mechanisms, and olfactory discrimination ability. However, many aspects remain unknown, such as the imprinting mechanisms during downstream migration, the triggering mechanisms of the shift from feeding migration to spawning migration, the sensory mechanisms of open water orientation, and the hormonal control mechanisms for sensory systems as well as the central nervous system. Despite the difficulties in a temporally limited spawning season, studies of lacustrine models, from molecular biology to behavioral biology, provide a new concept for the physiological mechanisms of homing migration in salmon.

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## References

- Bakkala, R. G. 1970. Synopsis of biological data on the chum salmon, *Oncorhynchus keta* (Walbaum) 1792. FAO Fish Synopsis 4, US Fish and Wildlife Service Circular 315:1-89.
- Bertmar, G. 1997. Chemosensory orientation in salmonid fishes. *Advances in Fish Research* 2:63-80, Vedams, New Delhi.
- Bodznick, D. 1975. The relationship of olfactory EEG evoked by naturally-occurring stream waters to the homing behavior of sockeye salmon (*Oncorhynchus nerka*, Walbaum). *Comparative Biochemistry and Physiology* 52A:487-495.
- Bodznick, D. 1978. Calcium ion: an odorant for natural water discriminations and the migratory behavior of sockeye salmon. *Journal of Comparative Physiology* 127:157-166.
- Brantly, R. K., J. C. Wingfield, and A. H. Bass. 1993. Sex steroid levels in *Porichthys notatus*, a fish with alternative reproductive tactics, and a review of the hormonal bases for male dimorphism among teleost fishes. *Hormones and Behavior* 27:332-347.
- Cardwell, J. R., and N. R. Liley. 1991. Androgen control of social status in males of a wild population of stoplight parrotfish, *Sparisome viride* (Scaridae). *Hormones and Behavior* 25:1-18.
- Cardwell, J. R., P. W. Sorensen, G. J. Van Der Kraak, and N. R. Liley. 1996. Effect of dominance status on sex hormone levels in laboratory and wild-spawning male trout. *General and Comparative Endocrinology* 101:333-341.
- Cooke, S. J., S. G. Hinch, M. Wikelski, R. D. Andrews, L. J. Kuchel, T. G. Wolcott, and P. J. Butler. 2004. Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution* 19:334-343.
- Cooper, J. C., and P. J. Hirsch, P. J. 1982. The role of chemoreception in salmonid homing. Pages 343-362 in T. J. Hara, editor. *Chemoreception in fishes*. Elsevier, Amsterdam.
- Cooper, J. C., G. F. Lee, and A. E. Dizon. 1974. An evaluation of the use of the EEG technique to determine chemical constituents in homestream water. *Wisconsin Academy of Science, Arts, and Letters* 62:165-172, Madison.
- Courtenay, S. C., T. P. Quinn, H. M. C. Dupuis, C. Groot, and P. A. Larkin. 1997. Factors affecting the recognition of population-specific odours by juvenile coho salmon. *Journal of Fish Biology* 50:1042-1060.
- Dittman, A. W., and T. P. Quinn. 1996. Homing in Pacific salmon: mechanisms and ecological basis. *Journal of Experimental Biology* 199:83-91.
- Dittman, A. W., T. P. Quinn, and G. A. Nevitt. 1996. Timing of imprinting to natural and artificial odors by coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 53:434-442.
- Dizon, A. E., R. M. Horral, and A. D. Hasler, A. D. 1973. Olfactory electroencephalographic responses of homing coho salmon, *Oncorhynchus kisutch*, to water conditioned by conspecifics. *Fisheries Bulletin, Washington* 71:893-896.
- Døving, K. B. 1989. Molecular cues in salmonid migration. Pages 299-329 in J. Maruani, editor. *Molecules in physics, chemistry, and biology*. Kluwer Academic Publishers, Amsterdam.
- Døving, K. B., H. Westerberg, and P. B. Johnsen. 1985. Role of olfaction in the behavioral and neuronal responses of Atlantic salmon, *Salmo salar*, to hydrographic stratification. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1658-1667.
- Fagerlund, U. H. M., J. R. McBridge, M. Smith, and N. Tomlinson. 1963. Olfactory perception in migrating salmon III. Stimulants for adult sockeye salmon (*Oncorhynchus nerka*) in home stream waters. *Journal of Fisheries Research Board of Canada* 20:1457-1463.
- Fukaya, M., H. Ueda, A. Sato, M. Kaeriyama, H. Ando, Y. Zohar, A. Urano, and K. Yamauchi. 1998. Acceleration of gonadal maturation in anadromous maturing sockeye salmon by gonadotropin-releasing hormone analog implantation. *Fisheries Science* 64:948-951.
- Groot, C., T. P. Quinn, and T. J. Hara. 1986. Responses of migrating adult sockeye salmon (*Oncorhynchus nerka*) to population-specific odors. *Canadian Journal of Zoology* 64:926-932.
- Hansen, L. P., N. Jonsson, and B. Jonsson. 1993. Oceanic migration in homing Atlantic salmon. *Animal Behaviour* 45:927-941.
- Hara, T. J. 1970. An electrophysiological basis for olfactory discrimination in homing salmon: a review. *Journal of Fisheries Research Board of Canada* 27:565-586.
- Hara, T. J. 1994. The diversity of chemical stimulation in fish olfaction and gustation. *Reviews in Fish Biology and Fisheries* 4:1-35.
- Hara, T. J., K. Ueda, and A. Gorbman. 1965. Electroencephalographic studies of homing salmon. *Science* 149:884-885.

- Hara, T. J., S. Macdonald, R. E. Evans, T. Marui, and S. Arai. 1984. Morpholine, bile acids and skin mucus as possible chemical cues in salmonid homing: electrophysiological re-evaluation. Pages 363–378 in J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill, editors. *Mechanisms of migration in fishes*. Plenum, New York.
- Hasler, A. D., and A. T. Scholz. 1983. Olfactory imprinting and homing salmon. Springer-Verlag, New York.
- Ikuta, K. 1996. Effects of steroid hormones on migration of salmonid fishes. *Bulletin of National Research Institute for Aquaculture Supplement 2*:23–27.
- Kindler, P. W., D. P. Philipp, M. T. Gross, and J. M. Bahr. 1989. Serum 11-ketotestosterone and testosterone concentrations associated with reproduction in male bluegill (*Lepomis macrochirus*: Centrarchidae). *General and Comparative Endocrinology* 75:446–453.
- Kitahashi, T., D. Alok, H. Ando, M. Kaeriyama, Y. Zohar, H. Ueda, and A. Urano. 1998a. GnRH analog stimulate gonadotropin II gene expression in maturing sockeye salmon. *Zoological Science* 15:761–765.
- Kitahashi, T., Sato, A., Alok, D., Kaeriyama, M., Zohar, Y., Yamauchi, K., Urano, A., and Ueda, H. 1998b. Gonadotropin-releasing hormone analog and sex steroids shorten homing duration of sockeye salmon in Lake Shikotsu. *Zoological Science* 15:767–771.
- Moore, A., and A. P. Scott. 1992. 17 $\alpha$ ,20b-dihydroxy-4-pregnen-3-one 20-sulphate is a potent odorant precocious male Atlantic salmon (*Salmo salar* L.) parr which have been pre-exposed to the urine of ovulated females. *Proceedings of the Royal Society of London B* 249:205–209.
- Moore, A., and C. P. Warning. 1996. Electrophysiological and endocrinological evidence that F-series prostaglandins function as priming pheromones in mature male Atlantic salmon (*Salmo salar*) parr. *Journal of Experimental Biology* 199:2307–2316.
- Nagahama, Y. 1999. Gonadal steroid hormones: major regulators of gonadal differentiation and gametogenesis in fish. Pages 211–222 in B. Norberg, O. S. Kjesbu, G. L. Taranger, E. Andersson, and S. O. Stefansson, editors. *Proceedings of the 6th International Symposium on the Reproductive Physiology of Fish*, Bergen, Norway.
- Nagahama, Y., and S. Adachi. 1985. Identification of a maturation-inducing steroid in a teleost, the amago salmon (*Oncorhynchus rhodurus*). *Developmental Biology* 109:428–435.
- Nevitt, G. A., and A. H. Dittman. 1998. A new model for olfactory imprinting in salmon. *Integrative Biology* 1:215–223, Wiley-Liss Inc., New York.
- Nevitt, G. A., A. H. Dittman, T. P. Quinn, and W. J. Moody, Jr. 1994. Evidence for a peripheral olfactory memory in imprinted salmon. *Proceedings of National Academy of Science of the United States of America* 91:4288–4292.
- Nordeng, H. 1971. Is the local orientation of anadromous fishes determined by pheromones? *Nature* 233:411–413.
- Ogura, M., and Y. Ishida. 1994. Homing behavior and vertical movements of four species of Pacific salmon (*Oncorhynchus* spp.) in the central Bering Sea. *Canadian Journal of Fisheries and Aquatic Sciences* 52:532–540.
- Oshima, K., W. E. Hahn, and A. Gorbman. 1969. Olfactory discrimination of natural waters by salmon. *Journal of Fisheries Research Board of Canada* 26:2111–2121.
- Pankhurst, N. W., and C. W. Barnett. 1993. Relationship of population density, territorial interaction and plasma levels of gonadal steroids in spawning male demoiselles *Chromis dispulis* (Pisces: Pomacentridae). *General and Comparative Endocrinology* 90:168–176.
- Quinn, T. P. 2005. *The behavior and ecology of Pacific salmon and trout*. University of Washington Press, Seattle.
- Quinn, T. P., and C. J. Foote. 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon (*Oncorhynchus nerka*). *Animal Behaviour* 33:51–56.
- Quinn, T. P., and C. Groot. 1984. Pacific salmon (*Oncorhynchus*) migrations: orientation vs. random movement. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1319–1324.
- Quinn, T. P., and G. M. Tolson. 1986. Evidence of chemically mediated population recognition in coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Zoology* 64:84–87.
- Quinn, T. P., B. A. Terjart, and C. Groot. 1989. Migratory orientation and vertical movements of homing adult sockeye salmon, *Oncorhynchus nerka*, in coastal waters. *Animal Behaviour* 37:587–599.
- Sato, A., H. Ueda, F. Fukaya, M. Kaeriyama, Y. Zohar, A. Urano, and K. Yamauchi. 1997. Sexual differences in homing profiles and shortening of homing duration by gonadotropin-releasing hormone analog implantation in lacustrine sockeye salmon (*Oncorhynchus nerka*) in Lake Shikotsu. *Zoological Science* 14:1009–1014.
- Sato, K., T. Shoji, and H. Ueda. 2000. Olfactory discriminating ability of lacustrine sockeye and masu salmon in various freshwaters. *Zoological Science* 17:313–317.
- Satou, M., Y. Kudo, and S. Kitamura. 1996. Strategies for studying the olfactory mechanism in salmon homing. *Bulletin of National Research Institute for Aquaculture Supplement 2*, 49–57.
- Shoji, T., H. Ueda, T. Ohgami, T. Sakamoto, Y. Katsuragi, K. Yamauchi, and K. Kurihara. 2000. Amino acids dissolved in stream water as possible homestream odorants for masu salmon. *Chemical Senses* 25:533–540.
- Shoji, T., Y. Yamamoto, D. Nishikawa, K. Kurihara, and H. Ueda. 2003. Amino acids in stream water are essential for salmon homing migration. *Fish Physiology and Biochemistry* 28:249–251.
- Stabell, O. B. 1992. Olfactory control of homing behaviour in salmonids. Pages 249–270 in T. J. Hara, editor. *Fish chemoreception*. Chapman and Hall, London.
- Sveinsson, T., and T. J. Hara. 1990. Analysis of olfactory responses to amino acids in Arctic char (*Salvelinus alpinus*) using a linear multiple-receptor model. *Comparative Biochemistry and Physiology* 97A:279–287.
- Ueda, H. 1999. Artificial control of salmon homing migration and its application to salmon propagation. *Bulletin*

- of Tohoku National Fisheries Research Institute 62:133–39.
- Ueda, H. 2004. Recent biotelemetry research on lacustrine salmon homing migration. *Memoris of National Institute of Polar Research, Special Issue* 58:80–88.
- Ueda, H., and T. Shoji. 2002. Physiological mechanisms of homing migration in salmon. *Fisheries Science*, 68 (Supplement 1):53–56.
- Ueda, H., and K. Yamauchi. 1995. Biochemistry of fish migration. Pages 265–279 in P. W. Hochachka, and T. P. Mommsen, editors. *Environmental and Ecological Biochemistry*. Elsevier, Amsterdam.
- Ueda, H., M. Kaeriyama, K. Mukasa, A. Urano, H. Kudo, T. Shoji, Y. Tokumitsu, K. Yamauchi, and K. Kurihara. 1998. Lacustrine sockeye salmon return straight to their natal area from open water using both visual and olfactory cues. *Chemical Senses* 23:207–212.
- Ueda, K. 1985. An electrophysiological approach to the olfactory recognition of homestream waters in chum salmon. *NOAA Technical Report NMFS* 27:97–102.
- Ueda, K., T. J. Hara, and A. Gorbman. 1967. Electroencephalographic studies on olfactory discrimination in adult spawning salmon. *Comparative Biochemistry and Physiology* 21:133–143.
- Ueda, K., T. J. Hara, M. Satou, and S. Kaji. 1971. Electrophysiological studies of olfactory discrimination of natural waters by himé salmon, a land-locked Pacific salmon, *Oncorhynchus nerka*. *Journal of Faculty of Science University of Tokyo Section IV Zoology* 12:167–182.
- Urano, A., H. Ando, and H. Ueda. 1999. Molecular neuroendocrine basis of spawning migration in salmon. Pages 46–56 in H. B. Kwon, J. M. P. Joss, and S. Ishii, editors. *Recent progress in molecular and comparative endocrinology*. Academia Scinica, Taipei, Taiwan.
- Villars, T. A. 1983. Hormones and aggressive behavior in teleost fishes. Pages 407–433 in B. B. Svare, editor. *Hormones and aggressive behavior*. Plenum, New York.
- Walker, M. M., C. E. Diebel, C. V. Haugh, P. M. Pankhurst, J. C. Montgomery, and C. R. Green. Structure and function of the vertebrate magnetic sense. *Nature* 390:371–376, 1997.
- Wisby, W. J., and A. D. Hasler. 1954. Effect of olfactory occlusion on migrating silver salmon (*Oncorhynchus kisutch*). *Journal of Fisheries Research Board of Canada* 11:472–478.
- Yano, A., M. Ogura, A. Sato, Y. Sakaki, M. Ban, and K. Nagasawa. 1996. Development of ultrasonic telemetry technique for investigating the magnetic sense of salmonids. *Fisheries Science* 62:698–704.
- Yano, K., and A. Nakamura. 1992. Observations of the effect of visual and olfactory ablation on the swimming behavior of migrating adult chum salmon, *Oncorhynchus keta*. *Japanese Journal of Ichthyology* 39:67–83.
- Zohar, Y. 1996. New approaches for the manipulation of ovulation and spawning in farmed fish. *Bulletin of National Research Institute for Aquaculture Supplement* 2:43–48.