REVIEW

Homing ability and migration success in Pacific salmon: mechanistic insights from biotelemetry, endocrinology, and neurophysiology

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ABSTRACT: Salmon have precise abilities to migrate long distances from the ocean to their natal streams for reproduction. Using chum salmon *Oncorhynchus keta* in the North Pacific Ocean as well as sockeye salmon *O. nerka* and masu salmon *O. masou* in Lake Toya and Lake Shikotsu (Hokkaido, Japan), mechanisms of homing ability and migration success were investigated using 3 different approaches: biotelemetry studies of behavior, endocrinology studies on the brain-pituitary-gonadal (BPG) axis, and neurophysiological studies on olfactory function. Physiological biotelemetry techniques were used to compare homing behavior of adult chum salmon from the Bering Sea to Hokkaido with lacustrine sockeye and masu salmon within Lake Toya, demonstrating that salmon can navigate in open water using different sensory systems. Hormone profiles in the BPG axis were analyzed in both chum salmon and sockeye salmon during their homing migration, and showed that salmon gonadotropin-releasing hormone is an important factor facilitating homing during migration. The olfactory functions of salmon were investigated using electrophysiological, behavioral, and biochemical techniques, suggesting that dissolved free amino acid compositions in natal streams are crucial for olfactory imprinting and homing. These topics are discussed in terms of mechanisms of homing ability in Pacific salmon with special reference to navigation abilities in open water, hormonal controlling mechanisms during homing migration, and olfactory discriminating abilities of natal stream odors — all necessary to successfully reach spawning grounds.

KEY WORDS: Pacific salmon · Homing ability · Reproduction · Olfaction · Biotelemetry · Endocrinology · Neurophysiology

INTRODUCTION

Salmon are recognized for their ability to precisely migrate thousands of kilometers from their feeding habitat in the ocean to their natal stream for reproduction. The homing ability allowing them to make the journey with such precision is one of the most interesting aspects of the salmon life cycle, but also one of the most challenging to study. It is now widely accepted that a specific odor signature characterizing the natal stream is imprinted in the olfactory systems of juvenile salmon during downstream migration, and that adult salmon recall this signature and recognize the natal river during the homing migration (Hasler & Scholz 1983, Ueda 2012). Recently, evidence of geomagnetic imprinting has been reported in sockeye salmon *Oncorhynchus nerka* and been used to explain their migration precision (Putman et al. 2013). However, there are still many uncertainties regarding which sensory systems play important roles in open water orientation, which hormones control homing migration, and how olfactory systems discriminate among natal stream odors to identify the natal stream — all of which are necessary for adult salmon to succeed in their reproductive migration.
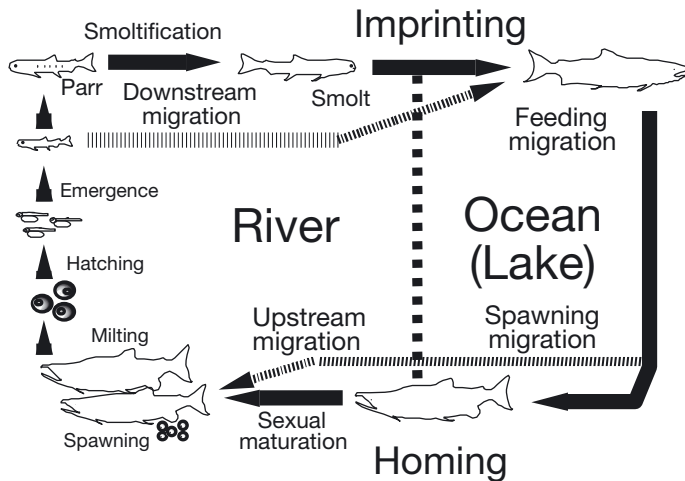
Fig. 1. Life history of 2 different types of Pacific salmonid species in Japan. Dotted line: chum and pink salmon; solid line: sockeye and masu salmon

There are 4 Pacific salmon in Japan: pink salmon *Oncorhynchus gorbuscha*, chum salmon *O. keta*, sockeye salmon, and masu salmon *O. masou*. The life cycles of pink and chum salmon are similar to one another, and different from those of sockeye and masu salmon (Fig. 1). All juvenile pink and chum salmon fry undertake downstream migration within a few months of emergence, returning to carry out upstream migration a few weeks prior to final gonadal maturation. Conversely, sockeye and masu salmon smolts remain in their natal streams or lakes for a year and a half before undertaking downstream migration, and adult sockeye and masu salmon return for upstream migration at least several months before reproduction. Unlike pink and chum salmon, sockeye and masu salmon may persist in landlocked systems, never going to sea (Groot & Margolis 1991). Retropositional genome analyses have revealed that pink salmon are phylogenetically the most advanced salmon species in Japanese waters, while masu salmon are considered to be the more primitive species (Murata et al. 1996). Pink salmon are also the most widely distributed species and have the largest population size, while masu salmon appear to have the most restricted distribution and the smallest population (Kaeriyama & Ueda 1998). Although the homing accuracy of these salmon has not been compared in detail, it is believed that masu salmon return to their natal stream with the highest precision, and that pink salmon are more likely to stray into a non-natal stream.

In this review, the results of 3 different research approaches are used to clarify mechanisms of hom-

ing ability in Pacific salmon: physiological biotelemetry studies on salmon homing behavior, endocrinological studies focused on the brain-pituitary-gonadal (BPG) axis, and neurophysiological studies on olfactory function. These topics are discussed with reference to mechanisms of homing ability in Pacific salmon with special focus on navigation abilities in open water, hormonal control mechanisms during homing migration, and olfactory imprinting and discriminating abilities of natal stream odors.

PHYSIOLOGICAL BIOTELEMETRY STUDIES

The recent rapid development of biotelemetry technology and methods, such as ultrasonic and radio telemetry, data logging, and pop-up satellite telemetry, make it possible to continually observe the underwater behavior of salmon in open water (Cooke et al. 2004). In particular, ultrasonic transmitters that emit pulsed signals have been useful for investigating the migratory behavior of salmon in coastal seas (Quinn & Groot 1984, Quinn et al. 1989) and the central Bering Sea (Ogura & Ishida 1995). Moreover, ultrasonic tracking has been used in conjunction with sensory ablation experiments, which block visual and olfactory cues or magnetic senses, permitting insight into the relative importance of individual senses to salmon homing (Døving et al. 1985, Yano & Nakamura 1992, Hansen et al. 1993, Yano et al. 1996).

Chum salmon from the Bering Sea to Hokkaido, Japan

Japanese chum salmon were collected by longline in June 2000 in the central Bering Sea (56° 30′ N, 179° 00′ E) in healthy condition. Individuals were determined to be of Japanese origin by scale analysis, as most Japanese chum salmon have been released from hatcheries and the width of their scale ring during fry stage is wider than wild salmon from other countries. A propeller data logger, which recorded swimming speed (5 s sampling interval), depth (5 s sampling interval), and temperature (1 min sampling interval) was attached externally through the dorsal musculature of the fish anterior to the dorsal fin (Tanaka et al. 2005). In total, 27 chum salmon were released with external data loggers, with one logger recovered from a set net on September on the east coast of Hokkaido, Japan (43° 20′ N, 145° 46′ E). This was the first recorded

swimming profile of a homing chum salmon in the oceanic phase, collected over a period of 67 d covering a straight distance of 2750 km. The salmon had travelled an average of 62 ± 12 cm s^{-1} at a depth of 10.4 ± 14.7 m and at a temperature of $9.2 \pm 0.2°$C. Horizontal swimming speed was 36.4 ± 15.2 km d^{-1}, but the fish sometimes moved at speeds of <10 km d^{-1} during the initial 10 d after tagging. Excluding this less active 10 d period from the analysis, mean horizontal speed was 42.3 ± 11.5 km d^{-1}. Both swimming speed and depth trimodally peaked around dawn and around sunset, with an additional small peak around midnight. The fish showed sequential up-and-down movements near the thermocline during the twilight and the daytime. These diurnal migratory patterns suggest that the homing chum salmon allocated a proportion of their time to foraging, and also that the foraging strategy differed in the daytime and the nighttime (Tanaka et al. 2005). Although we could not calculate energy expenditures of chum salmon during the long distance migration, these foraging behaviors must be related to massive energy expenditures during migration. These results indicated that the homing chum salmon had navigation abilities in the homeward direction, and that salmon used ocean current transport to reduce energy expenditure during migration. To accurately navigate home in open water, salmon must recognize both exact locations (map) and compass direction (orientation) during migration, and must have an internal biological clock tracking the passage of time.

Lacustrine sockeye and masu salmon in Lake Toya, Hokkaido, Japan

For anadromous salmon research, it is difficult to carry out physiologically controlled and manipulated experiments as fish move from the sea in their pre-maturation phase to their natal stream where they become mature. In contrast, lacustrine salmon populations offer a model system for studying homing behaviors from open water to natal areas for reproduction. The homing migrations of mature lacustrine sockeye salmon, whose sensory cues were impaired by ablations, were tracked from the center of the Lake Toya, a large caldera lake in Hokkaido, Japan (surface area 71 km^2, average depth 116 m and max. depth 179 m) to their natal area via ultrasonic tracking system (Ueda et al. 1998). A mature male sockeye salmon (control fish) with a brass ring attached to the head (Fig. 2A, fish a) as well as a similar mature male sockeye salmon whose magnetic cues were interfered with by attachment of a strong NdFe magnetic ring on the head (Fig. 2A, fish b) returned straight to the natal area after 1 h of random movement. A mature male sockeye salmon, whose visual cues were blocked by injection of carbon toner and corn oil and whose magnetic cues were interfered with via a magnetic ring, moved in the direction opposite to the natal area, but was eventually rediscovered in the natal area on the following evening, suggesting the possible involvement of olfactory cues, in the absence of visual and magnetic senses, in finding the natal
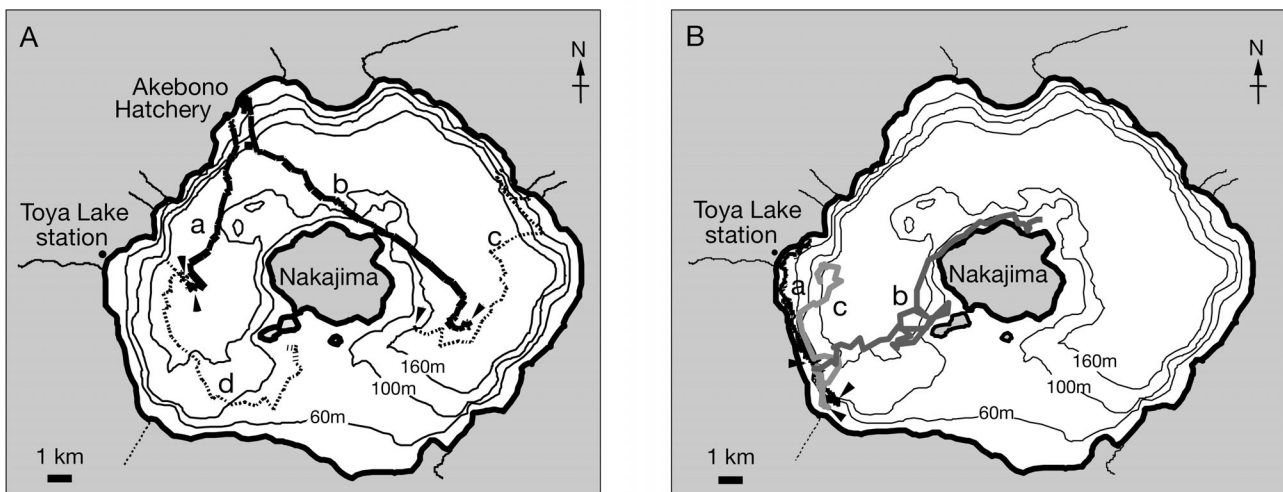

Fig. 2. Tracks of (A) 4 mature male lacustrine sockeye salmon (a: control fish; b: magnetic cue-interfered fish; c: visual cue-interfered fish; d: visual and magnetic cue-interfered fish) and (B) 3 mature lacustrine masu salmon in Lake Toya (a: control fish; b: visual cue-interfered fish; c: olfactory cue-interfered fish) during the spawning season. Arrowheads indicate the release point of each fish

area (Fig. 2A, fish c). A blinded male sockeye salmon was also moved to the shore of Naka-Toya far from the natal area in the evening, where it stayed for a few days (Fig. 2A, fish d). These data suggest that visual cues are critical to the straight homing of sockeye salmon, while magnetic cues do not appear to be necessary for successful return to the natal area. However, magnetoreceptor cells have been identified in the nose of rainbow trout *Oncorhynchus mykiss* (Walker et al. 1997) and empirical evidence for geomagnetic imprinting in sockeye salmon has recently been reported (Putman et al. 2013). New research approaches combining neurophysiological studies of magnetoreceptor cells with physiological biotelemetry behavioral studies are necessary to investigate the involvement of magnetic cues during oceanic imprinting and homing migration in salmon.

The homing behaviors of mature lacustrine masu salmon were also tracked in Lake Toya (Ueda et al. 2000). A mature control male masu salmon moved constantly along the coast, and stopped his movement at the mouth of stream (Fig. 2B, fish a), while a blinded mature female masu salmon was released and moved randomly away from the coast (Fig. 2B, fish b), and a mature male masu salmon, whose olfactory cue was blocked by Vaseline, moved randomly along the coast, eventually moving towards open water (Fig. 2B, fish c). Moreover, lacustrine masu salmon in Lake Toya with depth and temperature data loggers attached showed obvious diurnal movement after they encountered the mouth of river for the first time at the beginning of spawning season. They swam vertically around thermocline depth in the daytime and stayed at the water surface during the nighttime. This diurnal movement disappeared gradually toward the peak of the spawning season, at which point they carried out upstream migration to the spawning ground. These behavioral changes in masu salmon during the spawning season suggested that masu salmon are able to calculate the day length with an innate biological clock, because the diurnal movement after entering river might be useful to estimate the timing of upstream migration in their spawning river.

It is informative to compare the straight movements of sockeye salmon with the coastal movement behaviors of masu salmon (Ueda 2004). These 2 species show large differences in ocean distribution: sockeye salmon are widely distributed in the North Pacific Ocean, while masu salmon are narrowly distributed in the west North Pacific Ocean (Kaeriyama & Ueda 1998). These data suggest some evolutionary aspects of successful homing migration of salmonids where the narrowly distributed masu salmon only require coastal recognition ability for successful migration, while the widely distributed sockeye salmon required the development of open water orientation ability in order to successfully return to their natal streams with high precision.

ENDOCRINOLOGY STUDIES

Salmon homing is closely related to gonadal maturation, which is regulated mainly by the brain-pituitary-gonadal (BPG) axis (see Table 1 for a complete list of abbreviations used in this paper). Two gonadotropin-releasing hormones (GnRH), salmon GnRH (sGnRH) and chicken GnRH-II (cGnRH-II), exist in various regions of the salmon brain (Amano et al. 1997). In particular, sGnRH in the olfactory system, the terminal nerve, and the preoptic area are considered to play important roles in salmon homing

Table 1. Abbreviations used in this paper

Abbrev.	Definition
aASW	artificial stream water at the time of adult homing in autumn
ASW	artificial stream water
BPG	brain-pituitary-gonad
cGnRH-II	chicken gonadotropin-releasing hormone-II
DFAA	dissolved free amino acid
DHP	17α,20β-dihydroxy-4-pregnen-3-one
E2	estradiol-17β
EOG	electro-olfactogram
FSH	follicle-stimulating hormone
Glu	L-glutamic acid
GnRH	gonadotropin-releasing hormone
GnRHa	gonadotropin-releasing hormone analog
GTH	gonadotropin
11KT	11-ketotostosterone
jASW	artificial stream water at the time of juvenile imprinting in spring
LH	luteinizing hormone
LPT	long-term potentiation
MOR	main olfactory receptor
N24	olfactory system-specific protein of 24 kDa
nASW	artificial natal stream water
NLW	natural lake water
NMDA	N-methyl-D-aspartate
OR	olfactory receptor
PEA	β-phenylethyl alcohol
Pro	L-proline
sGnRH	salmon gonadotropin-releasing hormone
SOIG	salmon olfactory imprinting-related gene
T	testosterone
VOR	vomeronasal olfactory receptor

migration. sGnRH in the preoptic area controls synthesis and release of gonadotropin (GTH), luteinizing hormone (LH), and follicle-stimulating hormone (FSH). GTHs induce steroidogenesis in the gonads, and steroid hormones stimulate gametogenesis and final gameto-maturation; estradiol-17β (E_2) and testosterone (T) are active in vitellogenesis, T and 11-ketotestosterone (11KT) in spermatogenesis, and 17α, 20β-dihydroxy-4-pregnen-3-one (DHP) in final gameto-maturation in both sexes (Nagahama 1999). It is very important to investigate hormone profiles in the BPG axis of salmon during homing migration as well as gonadal maturation (Ueda & Yamauchi 1995, Ueda 1999) in order to clarify how these hormones control/mediate homing migration and gonadal maturation.

Hormone profiles of chum salmon during homing migration

The hormone profiles in the BPG axis of chum salmon migrating from the Bering Sea to the spawning ground in the Chitose River, Hokkaido, Japan, were measured using specific time-resolved fluoroimmunoassay systems (Yamada et al. 2002). The level of sGnRH in the olfactory bulb of both sexes peaked when the fish was located between the coastal sea and the river mouth of the Ishikari River; a location where the olfactory discriminating ability of the natal stream is expected to be important. Peak sGnRH in the telencephalon was observed when the fish was at the branch point of the Chitose River from the Ishikari River, where the olfactory functions should be highly activated as individuals attempt to determine which branch to enter. In the pituitary gland, sGnRH levels tended to increase in concert with LH levels from the coastal sea in females to the river mouth of the Ishikari River in males. In contrast, FSH levels did not show any clear correlations with sGnRH levels in the pituitary gland. Although the roles of cGnRH-II in these brain regions are yet unclear, levels increased in the medulla oblongata of both sexes at the pre-spawning ground, and levels in the optic tectum increased in males. In the diencephalon and cerebellum, cGnRH-II levels showed no significant changes during homing migration (Ueda 2011).

Immunoreactive sGnRH neurons, which showed signals for pro-sGnRH mRNA, were observed in the dorsal olfactory nerve of chum salmon in the coastal sea, but not in fish at the spawning grounds (Kudo et al. 1996a). Changes in the levels of GTH subunit mRNAs in the pituitary gland of pre-spawning chum salmon demonstrated that the levels of GTHα2 and LHβ increased when an individual entered freshwater, but showed no change in FSHβ level (Kitahashi et al. 1998a). Serum steroid hormone levels showed similar profiles to those observed in previous studies (i.e. Ueda et al. 1984, Ueda 1999): E_2 in females and 11KT in males increased during vitellogenesis and spermatogenesis, respectively, while DHP increased dramatically at the time of final gonadal maturation in both sexes. It is interesting to note that both sGnRH levels in the telencephalon and serum T levels in both sexes showed a coincident peak at the branch point of the Chitose River from the Ishikari River. These results suggest that sGnRH and cGnRH-II may be involved in brain region-dependent roles on gonadal maturation and homing migration in chum salmon.

Homing profiles in lacustrine sockeye salmon

Since it is difficult to carry out experimental treatments to manipulate endocrinological functions in anadromous salmon owing to the salinity differences between seawater and freshwater, lacustrine salmon populations offer a model system for studying hormonal control mechanisms of salmon homing. In Lake Shikotsu (surface area 78 km^2, average depth 265 m, max. depth 363 m), lacustrine sockeye salmon are artificially produced by hatchery propagation. Adult sockeye salmon were captured between September and November adjacent to their natal hatchery prior to spawning, sampled for serum steroid hormones, tagged, and released in the center of the lake. Fish were resampled at recapture to characterize changes in steroid hormone levels in individual migrants as well as to monitor homing duration and precision in each month (Sato et al. 1997). Homing duration was significantly truncated from September to October in males and from October to November in females (Fig. 3A). 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 to 90% of females returned over the entire 3 mo sampling period (Fig. 3B). It is interesting to note that the average homing percentage of both sexes for 3 mo is 83%, with no sex difference in the total number of homing individuals. Although male salmon do not display territorial behavior, they are highly aggressive in order to compete for access to females, sug-
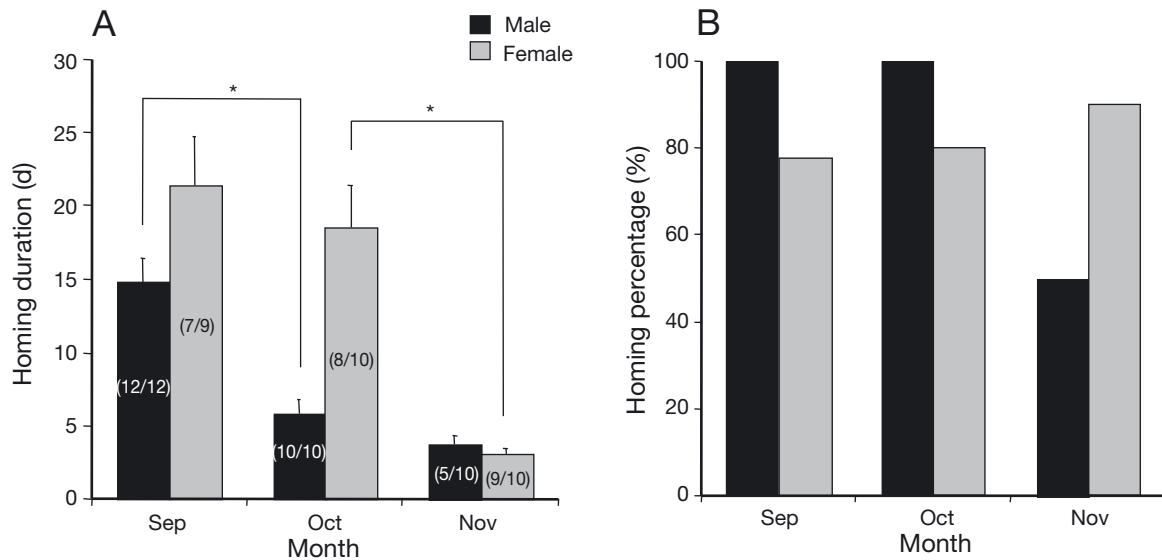
Fig. 3. Changes in homing (A) duration and (B) percentage of lacustrine sockeye salmon in Lake Shikotsu from September to November. Numbers in parentheses indicate the number of released fish/number of returned fish. *Significant differences between months (p ≤ 0.05)

gesting that early returning males might accrue some benefits in securing females for breeding. It has been reported that increased T levels are correlated with compromised immune function (Harris & Bird 2000), suggesting a tradeoff where by faster migration may be advantageous even with the risk of disease.

Hormone implantation treatment in sockeye salmon

Since GnRH treatment is highly effective in inducing GTH release, ovulation and milting in teleost fishes (Zohar 1996), we investigated the effect of GnRH analog (GnRHa) implantation on both homing profiles and serum steroid hormone levels of fish in September (Sato et al. 1997, Kitahashi et al. 1998c). The 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 males: rapidly returning males had higher serum T levels and lower serum DHP levels than slowly returning males. To examine the direct action of T and DHP on homing duration, T and DHP were implanted in fish in September. T implantation tended to reduce homing duration in both males and females, but there was no statistical significance. DHP implantation significantly shortened homing duration in females, but it did not have any significant effect on males (Fig. 4). These steroid

hormone implantations did not affect serum T and DHP levels. It is 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). Andro-
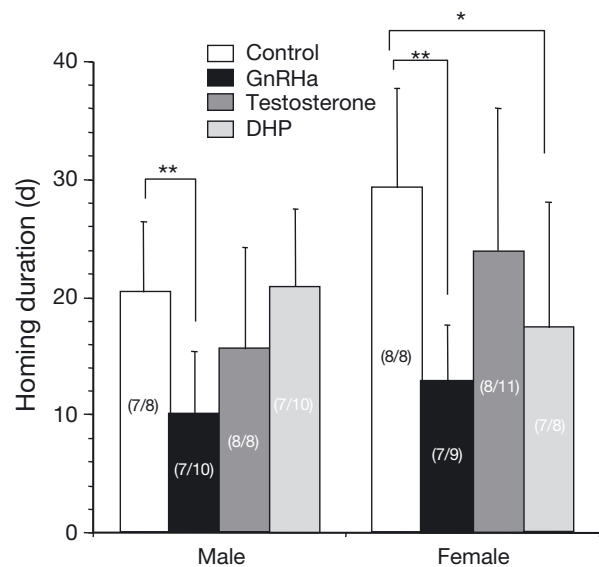

Fig. 4. Effects of GnRH analog (GnRHa), testosterone and 17α, 20β-dihydroxy-4-pregnen-3-one (DHP) implantation on homing duration of lacustrine sockeye salmon in Lake Shikotsu in September. Numbers in parentheses indicate the number of released fish/number of returned fish. Asterisks indicate significant differences from controls (*p ≤ 0.05, **p ≤ 0.01)

gens are involved in stimulating aggressive behavior in teleost fishes (Villars 1983), and serum T and 11KT are the 2 major androgens that influence spawning behaviors, downstream and upstream migration, and the social dominance hierarchy (Kindler et al. 1989, Cardwell & Liley 1991, Pankhurst & Barnett 1993, Brantley et al. 1993, Cardwell et al. 1996, Munakata et al. 2001a,b). Although DHP is a maturation-inducing steroid in salmonids (Nagahama & Adachi 1985), its function in the central nervous system has not yet been clarified. The functional roles of T and DHP on salmon homing migration should be further investigated with special attention to their action on the sensory and 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 GTHα and LHβ mRNAs in GnRHa-implanted fish were higher than those in control fish, but the levels of FSHβ mRNA showed no change (Kitahashi et al. 1998b). 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_2 and T in females (Fukaya et al. 1998). These data suggest sGnRH in the brain stimulates LH release from the pituitary gland, and then LH enhances serum DHP levels in both sexes during the final phase of gamete maturation as well as the latter part of homing migration. GnRH is believed to play a prominent role in the homing migration of both sexes, but gonadal steroids, especially T and DHP, seem to differently affect the homing migration of males and females. The different sex-dependent effects of BPG hormones on the sensory systems and the central nervous systems should be examined in future studies.

NEUROPHYSIOLOGICAL STUDIES

Since the olfactory hypotheses for salmon imprinting and homing to their natal stream was proposed by Hasler's research group in 1950s (Hasler & Wisby 1951, Wisby & Hasler 1954), mechanisms of olfactory imprinting and homing abilities in salmon have been intensively studied (Hasler & Scholz 1983, Døving 1989, Stabell 1992, Hara 1994, Dittman & Quinn 1996, Bertmar 1997, Nevitt & Dittman 1998, Quinn 2005, Ueda et al. 2007, Hino et al. 2009, Ueda 2011, 2012), beginning with the pheromone hypothesis proposed by Nordeng (1971, 1977), in which, using

Arctic char *Salvelinus alpines* and Atlantic salmon *Salmo salar*, it was suggested that juvenile salmon in a stream released population-specific odors that guided homing adults. Several subsequent investigations of olfactory imprinting have also suggested that juvenile salmonids produce population-specific odors or pheromones (Groot et al. 1986, Quinn & Tolson 1986, Courtenay et al. 1997). It has also been demonstrated that sex steroids and prostaglandins that affect the olfactory epithelium of salmonids may act as sex pheromones (Moore & Scott 1992, Moore & Warning 1996). Recently, the amino acid L-kynurenine was identified as a sex pheromone in the urine of ovulated female masu salmon (Yambe et al. 2006). However, there are no juveniles of chum salmon or pink salmon present when adults return. Nonetheless, it is now widely accepted that some specific odors in the natal stream are important for olfactory imprinting and homing in salmon.

Properties of natal stream odors

Several attempts to identity the natal stream odor were made based on the olfactory bulbar response, suggesting that the natal stream odors were non-volatile (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, non-volatile, and heat-stable (Ueda 1985). Unlike olfactory organs of terrestrial animals, fish olfactory organs respond only to a limited suite of dissolved chemical species, such as amino acids, steroids, bile acids, and prostaglandins (Hara 1994).

Shoji et al. (2000) analyzed the compositions of dissolved free amino acid (DFAA), inorganic cations and bile acids in waters from 3 streams that 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 DFAA induced large responses. The response to artificial stream water based on the composition of DFAA and salts closely resembled the response to the corresponding natural stream water. Cross-adaptation experiments with 3 combinations of natural and artificial stream waters were carried out. The response pattern for each combination of artificial stream water closely resembled that of the corresponding combination of natural stream water. Accordingly, we proposed that DFAA

compositions in the natal stream water are likely natal stream odors, but these odors may change seasonally or annually.

Yamamoto et al. (2013) analyzed DFAA concentration and composition of water from the Teshio River in Hokkaido, Japan, where chum salmon returned for spawning, during juvenile downstream migration in spring and adult upstream migration in autumn with a 4 yr difference. Among the 19 amino acids found in the Teshio River water, DFAA concentrations fluctuated greatly, but 5 to 7 stable DFAA compositions (mole %) were found between the spring and autumn samples within a 4 yr span. Two kinds of artificial stream water (ASW) were prepared using the same DFAA concentration in the Teshio River during the time of juvenile imprinting in spring (jASW) and adult homing in autumn (aASW), after a 4 yr period. In behavioral experiments of upstream selective movement in a 2-choice test tank (Y-maze) consisting of 2 water inlet arms and one pool, 4-yr-old mature male chum salmon captured in the Teshio River showed significant preference for either jASW or aASW when compared to control water, with no preference for jASW or aASW — although in electro-olfactogram (EOG) experiments adults were able to discriminate between jASW and aASW. These findings indicate that the long-term stability of the DFAA compositions in natal streams might be crucial for olfactory homing in chum salmon.

Changes in the DFAA compositions in stream water are attributed mainly to complicated biological processes in the watershed ecosystem. There are many possible factors affecting the DFAA compositions both within and beyond the stream environment, such as soils, vegetation, litter, pollen, dew, and various microbial activities (Thomas 1997). Among these factors, the roles of complex microbial communities called biofilms have been intensively investigated (Costerton et al. 1994, Nosyk et al. 2008). A biofilm consists of various microorganisms, and is embedded into a matrix of extracellular polymeric substances. Ishizawa et al. (2010) investigated the origin of DFAA in stream water focusing on biofilms in the stream bed via incubation experiments in the laboratory. Stones were placed in the Toyohira stream, Hokkaido, for 3 mo, allowing formation of biofilms, and then incubated for 24 h in the laboratory at stream water temperature. After incubation, the composition and concentrations of DFAA in the incubation solution were measured by high-performance liquid chromatography. The DFAA concentration increased greatly in the biofilm incubation solution of the treatment group, but the DFAA composition (mole %) showed little change after the

24 h incubation (i.e. similar to the stream water), suggesting that biofilms are a major source of DFAA in stream water.

Artificial imprinting studies using amino acids

Imprinting experiments have been used to demonstrate the reliance of salmon on olfactory cues. Coho salmon were experimentally imprinted with β-phenylethyl alcohol (PEA) or morpholine during smoltification and lured into unfamiliar streams scented with these odors during homing migration a few years later (Cooper et al. 1976, Scholz et al. 1976). The olfactory receptor cells of coho salmon that had been imprinted with PEA had a higher sensitivity to PEA compared with non-imprinted fish (Nevitt et al. 1994), and only fish that were exposed to PEA or natural stream odors during smoltification formed an imprinted memory (Dittman et al. 1996). Using electrophysiological and behavioral experiments, Yamamoto et al. (2010) showed that 1-yr-old lacustrine sockeye salmon can be imprinted at smoltification by a single amino acid, 1 µM L-proline (Pro) or L-glutamic acid (Glu). The EOG responses of test fish exposed to Pro in March (before smoltification) and April to June (during smoltification) for 2 wk were significantly greater than those of non-exposed control fish, but not those of test fish exposed in July (after smoltification). When Pro and control water were added to the water inlets of the Y-maze during the spawning season 2 yr after the test water exposure, 80% of maturing and mature test fish exposed before and during smoltification showed a preference for Pro, whereas those exposed after smoltification displayed no preference. The EOG response of test fish exposed to Pro or Glu for 1 h, 6 h, 1 d, 7 d, or 14 d in May revealed that only the response after 14 d of exposure was significantly greater than the control. Yamamoto et al. (2010) concluded that 1-yr-old sockeye salmon could be imprinted by a single amino acid before and during smoltification, and that imprinting requires exposure for at least 14 d in the artificial rearing environment. In a natural stream environment, however, smolts should be imprinted immediately by different odors when they encounter a branch stream that flows into a main stream during downstream migration as in the sequential imprinting hypothesis proposed by Harden Jones (1968). Further experiments using e.g. artificial raceway tanks should be designed to clarify how smolts are imprinted when they encounter odors for a short time during downstream migration.

Comparison of olfactory discriminating abilities among four Pacific salmon species

Behavior experiments were compared to test attractant effects on upstream selective movement among the 4 Pacific salmon (pink, chum, sockeye, and masu salmon) using artificial natal stream water (nASW) prepared to the same composition and concentration of DFAA in their natural natal stream in the Y-maze. Either nASW or natural lake water (NLW) was added to the water inlet of either left or right arms and the fish movement monitored to determine the number of fish that moved to each arm. In both nASW and NLW, pink salmon showed the highest percentage of upstream movement among the 4 Pacific salmon species, but showed the least selectivity (59.3%) in the arm running nASW, whereas the other 3 Pacific salmon species (chum, sockeye, and masu salmon) showed significant selectivity (85.7, 75.9, and 81.3%, respectively) in the arm running nASW (Fig. 5). It is interesting to note the significant selectivity to the test water of about 80% in the experimental conditions. The difference of olfactory discriminating ability merits further investigation to determine the source of error among the 20% of fish that select the wrong path.
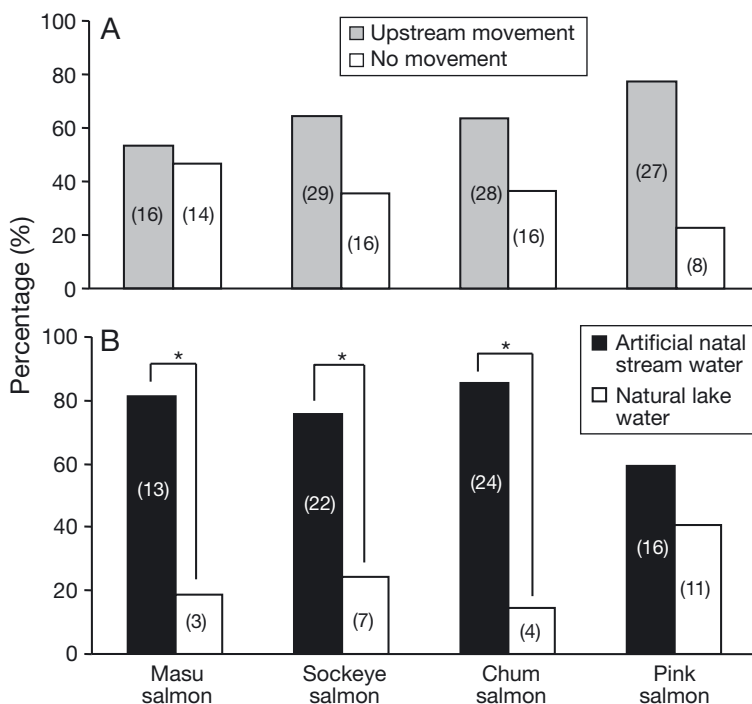

Fig. 5. (A) Upstream movement and (B) selectivity in each artificial natal stream water of 4 mature male Pacific salmon in the 2-choice test tank. Numbers in parentheses indicate the number of fish. *Significant differences between responses (p ≤ 0.05)

If salmon always demonstrate accurate homing to their natal stream, there would be little chance of widening their distribution area or of increasing their population size; in addition, there is the dangerous possibility that this may reduce genetic diversity. Pink salmon, which have the widest distribution of the salmon species in Japan, may have evolved the capacity to adapt to non-natal stream odors and hence possess an expanded distribution. The relationship between salmon evolution and homing accuracy should be investigated from an evolutionary perspective to determine the adaptive significance to homing inaccuracy.

Biochemical and molecular biological studies on salmon olfactory functions

Using sodium dodecyl sulfate-polyacrylamide gel electrophoresis, an olfactory system-specific protein of 24 kDa (N24) was identified in lacustrine sockeye salmon by electrophoretic comparison of proteins restricted to the olfactory system with those found in other parts of the brain (Shimizu et al. 1993). In various species of teleosts, N24 immunoreactivity was found in the olfactory system of species migrating between the sea and freshwater streams, such as Japanese eel *Anguilla japonica*, but not in non-migratory species, such as carp *Cyprinus carpio* (Ueda et al. 1994). Interestingly, N24 immunoreactivity was also observed in the testicular germ cells, spermatids and spermatozoa, suggesting its involvement in sperm chemotaxis (Ueda et al. 1993). Immunocytochemical and immunoelectronmicroscopic observations revealed that N24 positive immunoreactivity occurred in ciliated and micovillar olfactory receptor cells and the glomerular layer near the mitral cells in the olfactory bulb (Kudo et al. 1996b, Yanagi et al. 2004). cDNA encoding N24 was isolated and sequenced, and this cDNA contained a region encoding 216 amino acid residues. Protein and nucleotide sequencing demonstrated the existence of a remarkable homology between N24 and glutathione S-transferase class pi enzymes (Kudo et al. 1999). Northern blot analysis showed that N24 mRNA with a length of 950 base pairs was expressed in lacustrine sockeye salmon olfactory epithelium. The functional roles of N24 during salmon homing

migration are still unclear, but N24 is a useful molecular marker for studying olfactory functions in salmonids.

Salmon olfactory imprinting-related gene (SOIG) from the olfactory system of lacustrine sockeye salmon has been identified by subtractive hybridization technique of cDNA representational difference analysis using fish at smoltification as a tester and fish at the feeding migration term as a driver (Hino et al. 2007). SOIG mRNA was shown to be expressed in olfactory receptor cells and basal cells of the olfactory epithelium. The expression levels of SOIG mRNA in the olfactory epithelium have been analyzed during several lifecycle stages of lacustrine sockeye salmon and chum salmon, such as ontogeny, smoltification, and homing. During ontogeny, the expression levels of SOIG mRNA were significantly higher in alevin (juvenile fry) than in embryos at 43 and 60 d after fertilization in chum salmon. During smoltification, SOIG mRNA levels increased before and during smoltification, and decreased after smoltification in sockeye salmon. These changes coincided with serum thyroxine changes during smoltification (Yamamoto et al. 2010). During homing migration, SOIG mRNA levels in the olfactory epithelium of chum salmon were elevated at the estuary and pre-spawning ground. It is thought that SOIG might be related to olfaction or cell proliferation during both smoltification and the final stage of homing.

Olfactory chemoreception is accomplished via binding of the odorant substance to an olfactory receptor (OR), which is reportedly encoded by 100 to 200 genes (Alioto & Ngai 2005) in the olfactory epithelium with subsequent propagation of the information to the central nervous system. There are 2 types of OR genes, main olfactory receptors (MORs), which are expressed in ciliated olfactory receptor cells, and vomeronasal olfactory receptors (VORs), which are expressed in microvillous olfactory receptor cells. MOR genes have also been identified in a number of salmonids (Wickens et al. 2001, Dukes et al. 2004, 2006, Morinishi et al. 2007). Recently, OR expression was investigated in different life stages of Atlantic salmon, demonstrating that 7 V2R-like (*OlfC*) genes were expressed at higher levels in juveniles (parr and smolts) than in adults (Johnstone et al. 2011). Although many MORs and VORs have been identified from several vertebrates owing to the progress of whole genome analysis, many ligands remain uncharacterized. Further intensive molecular biological studies must be performed to clarify the olfactory chemoreception during imprinting and homing migration in salmon.

Bandoh et al. (2011) applied blood oxygenation level-dependent functional magnetic resonance imaging to investigate the odor information processing of natal stream in the brain of lacustrine sockeye salmon, and found that strong responses to odors of natal stream were mainly observed in the lateral area of dorsal telencephalon, which is homologous to the medial pallium (hippocampus) in terrestrial vertebrates. Olfactory memory plays a key role in imprinting and recalling natal stream odor information in salmon. In the formation of memory, the possible role of long-term potentiation (LTP) has been studied with a focus on *N*-methyl-D-aspartate (NMDA) receptors, which induce LTP (Martin et al. 2000). LTP occurs in the brain of zebrafish *Danio rerio* (Nam et al. 2004), rainbow trout (Kinoshita et al. 2005), and common carp (Satou et al. 2006). Effects of NMDA receptor blockers (APV and MK-801) on homing duration of male lacustrine sockeye salmon in Lake Shikotsu in late October was investigated, revealing that homing duration was significantly prolonged by both blockers (Fig. 6). These results suggest that NMDA receptors might be deeply involved in recalling the imprinting memory in sockeye salmon, and the exact roles of NMDA during imprinting migration should be investigated.

CONCLUSIONS

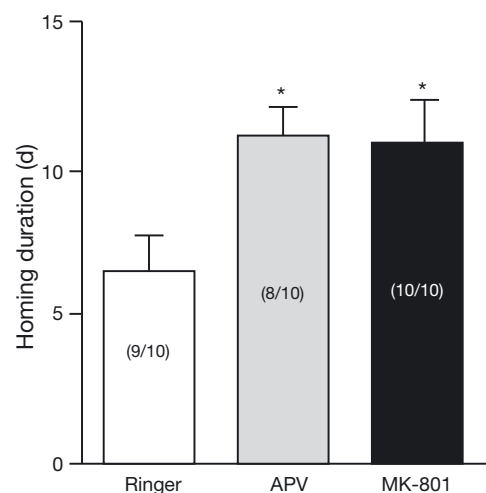This review describes recent studies on mechanisms of homing ability mainly in anadromous chum

Fig. 6. Effects of MNDA blockers (APV and MK-801) on homing duration of male lacustrine sockeye salmon in Lake Shikotsu in October. Numbers in parentheses indicate the number of released fish/number of returned fish. *Significant differences from control (Ringer; $p \leq 0.05$)

salmon from the Bering Sea to Japan as well as in lacustrine sockeye and masu salmon in Lake Toya and Lake Shikotsu by means of 3 different approaches: physiological biotelemetry studies on salmon homing behavior, endocrinological studies on hormone profiles in the BPG axis, and neurophysiological studies on olfactory discrimination abilities. Physiological biotelemetry studies show that salmon can navigate in open water using different sensory systems, but the sensory mechanisms of open water orientation remain unknown. The role of magnetic sensory systems should be further examined during oceanic imprinting and homing migration in salmon. Endocrinology studies demonstrate that sGnRH plays an important role in homing migration. However, it is uncertain how the BPG hormones may control both the sensory systems and the central nervous systems during homing migration in males and females, and so the different influence of BPG hormones on the sensory and central nervous systems of both males and females should also be studied. Neurophysiological studies on olfactory function suggest that stable DFAA compositions in natal streams are crucial for olfactory imprinting and homing of individual salmon, but the origins of inaccurate homing are unclear. The relationship between salmon evolution and homing accuracy should be further investigated to better understand this phenomenon. Despite of the difficulties of a temporally limited spawning season, studies from molecular biology and behavioral biology using these model salmon species will provide new explanations for the precise imprinting and homing phenomenon among Pacific salmon. In addition, biotelemetry coupled with other approaches will provide insight into the factors that influence the individual fitness and hence success of Pacific salmon migration.

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