

SPECIAL ISSUE REVIEW PAPER

Sensory mechanisms of natal stream imprinting and homing in *Oncorhynchus* spp.

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Juvenile *Oncorhynchus* spp. can memorise their natal stream during downstream migration; juveniles migrate to feed during their growth phase and then they migrate long distances from their feeding habitat to their natal stream to reproduce as adults. Two different sensory mechanisms, olfaction and navigation, are involved in the imprinting and homing processes during short-distance migration within the natal stream and long-distance migration in open water, respectively. Here, olfactory functions are reviewed from both neurophysiological studies on the olfactory discrimination ability of natal stream odours and neuroendocrinological studies on the hormonal controlling mechanisms of olfactory memory formation and retrieval in the brain. These studies revealed that the long-term stability of dissolved free amino-acid composition in the natal stream is crucial for olfactory imprinting and homing. Additionally, the brain-pituitary-thyroid and brain-pituitary-gonadal hormones play important roles in olfactory memory formation and retrieval, respectively. Navigation functions were reviewed from physiological biotelemetry techniques with sensory interference experiments during the homing migration of anadromous and lacustrine *Oncorhynchus* spp. The experiments demonstrated that *Oncorhynchus* spp. used compass navigation mechanisms in the open water. These findings are discussed in relation to the sensory mechanisms involved in natal stream imprinting and homing in *Oncorhynchus* spp.

KEYWORDShoming, imprinting, natal stream, navigation, olfaction, *Oncorhynchus* spp

1 | INTRODUCTION

Oncorhynchus spp. are recognised for their precise ability to memorise their natal stream during downstream migration as juveniles. They migrate to the Pacific Ocean to feed during their growth phase and then, as adults, they migrate thousands of km from the Pacific Ocean to their natal stream to reproduce. Two different sensory mechanisms, olfaction and navigation, are believed to be involved in the natal stream imprinting and homing processes of *Oncorhynchus* spp. during short-distance migration within the natal stream and long-distance migration in open water, respectively. This review offers further knowledge about the physiological mechanisms of imprinting and homing migration in *Oncorhynchus* spp. (Ueda, 2012) by summarising two different research topics on the natal stream imprinting and homing in four *Oncorhynchus* (Suckley 1861) species in Japan: the anadromous pink salmon *Oncorhynchus gorbuscha* (Walbaum 1792) and chum salmon *Oncorhynchus keta* (Walbaum 1792) and the

anadromous and lacustrine sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) and masu salmon *Oncorhynchus masou* (Brevoort 1856). The first topic brings together studies on olfactory functions to reveal the olfactory discrimination ability of natal stream odours of the four Japanese *Oncorhynchus* species, using neurophysiological techniques. Additionally, the hormonal controlling mechanisms of olfactory memory formation and retrieval in the brains of anadromous *O. keta* and lacustrine *O. nerka* are reviewed, where studies have used neuroendocrinological techniques. The second topic brings together studies on navigation functions to reveal migratory ability in open water using physiological biotelemetry techniques with sensory interference experiments during the homing migration of the anadromous *O. keta* from the Bering Sea to Hokkaido, Japan. Experiments were used to assess the homing migration of the lacustrine *O. nerka* and *O. masou* in Lake Toya in Hokkaido, Japan, where the lake serves as a model ocean. These research findings are discussed in relation to olfactory natal-stream imprinting and homing mechanisms. The

findings are discussed in terms of their relation to compass-navigation mechanisms in open water in the anadromous and lacustrine *Oncorhynchus* spp. of Japan.

2 | RESEARCH ON OLFACTORY FUNCTIONS

To date, three different olfactory hypotheses have been proposed to explain how salmonids home to their natal stream. The first hypothesis is the olfactory imprinting hypothesis, which was proposed by Wisby and Hasler (1954) using coho salmon *Oncorhynchus kisutch* (Walbaum 1792). This hypothesis states that odour specific to the natal stream is imprinted to the olfactory system before juvenile salmonids migrate to the sea and the adults retrieve this odour information as a cue for homing when they migrate through the home-stream network back to their home tributary (Hasler & Scholz, 1983). Harden-Jones (1968) developed the sequential imprinting hypothesis, which states that juvenile salmonids are imprinted to sequential way points located between the spawning area and the river mouth. The second hypothesis is called the pheromone hypothesis, which was developed by Nordeng (1971, 1977) using Arctic char *Salvelinus alpinus* (L. 1758) and Atlantic salmon *Salmo salar* (L. 1758). This hypothesis states that homing adults are guided by population-specific odours or pheromones released from juvenile salmonids. Finally, the third hypothesis is the hierarchical navigation hypothesis, which was recently proposed by Bett and Hinch (2015), which states that the migrating adult salmonids rely on imprinted odours as a primary directional cue, conspecific odours as a secondary directional cue and non-olfactory environmental indicators as a tertiary directional cue.

The pheromone hypothesis is not applicable for *Oncorhynchus* spp. because juveniles of *O. gorbuscha* and *O. keta* are not present during the period when adults return. The imprinting hypothesis, which states that certain specific odorant factors in the natal stream are imprinted on the olfactory system of juvenile salmonids during downstream migration and that migrating adults rely on these factors in the natal stream to attract them during the process of homing upstream migration, is the most applicable hypothesis for *Oncorhynchus* spp. (Dittman & Quinn, 1996).

3 | NEUROPHYSIOLOGICAL STUDIES ON OLFACTION

In early studies, the olfactory bulbar response was used to identify the natal-stream odours and demonstrated that the application of natal-stream water to the olfactory epithelium of homing salmonids induced a large electroencephalographic response (Hara *et al.*, 1965). However, later it was determined that this large olfactory bulbar response was not only induced by natal-stream waters but also by other stream waters (Hara, 1970). The natal-stream odour was presumed to be absorbed on activated carbon and ion-exchange resin, insoluble in petroleum-ether, dialyzable, non-volatile and heat-stable by spectral analysis of the olfactory bulbar response of anadromous *O. keta* and lacustrine *O. nerka* (Ueda, 1985).

In North America, artificial chemical odours, β -phenylethyl alcohol (PEA) or morpholine, were used in imprinting experiments of *O. kisutch* during smoltification and these fish were then lured into unfamiliar streams scented with these odours during their homing migration several years later (Cooper *et al.*, 1976; Scholz *et al.*, 1976). The olfactory receptor cells of adult *O. kisutch* that were imprinted with PEA during smoltification were more sensitive to PEA than were those in the non-imprinted fish (Nevitt *et al.*, 1994). It was reported that it took 10 days for *O. kisutch* exposed to PEA during smoltification to develop an imprinted memory (Dittman *et al.*, 1996). Also, the stimulation of guanylyl cyclase activity by PEA was significantly greater in olfactory cilia isolated from PEA-imprinted fish than in PEA-naïve fish at the time of the homing migration, which occurred 2 years after exposure to PEA (Dittman *et al.*, 1997). Havey *et al.* (2017) presented experimental evidence for olfactory imprinting to a mixture of odorants containing amino acids and PEA in *O. nerka* at the embryonic and smolt stages. However, there have been few attempts to identify the properties of natal-stream odours in salmonid populations of the eastern Pacific Ocean.

It has been shown that the olfactory organs of fish discriminate only specific dissolved chemical species in water, such as amino acids, steroids, bile acids, prostaglandins and nucleotides (Hara, 1994). The specific odours of each natal stream should be unique and distinct, should not vary between the spawning ground and the stream mouth and should be stable during the several years between juvenile imprinting and adult homing. The compositions of dissolved free amino acids (DFAA) and bile acids were analysed in waters from the streams that flow into Lake Toya (Shoji *et al.*, 2000). The electrophysiological olfactory nerve response of lacustrine *O. masou* to artificial stream water (ASW) caused by the composition of DFAA induced large responses, but the application of bile-acid mixtures induced only very small responses. The olfactory nerve response pattern for each combination of ASW closely resembled that of the corresponding combination of natural stream water in cross-adaptation experiments. These results revealed that the compositions of DFAA in the natal-stream water are assumed to be the natal-stream odours.

The olfactory nerve responses of lacustrine *O. masou* and *O. nerka* were examined to determine their olfactory discrimination ability of various fresh waters; the results confirmed that both species elicited different responses, regardless of sex or gonadal maturity (Sato *et al.*, 2000). In cross-adaptation experiments, the secondary response to stream water was abolished by lake water, but the secondary response to lake water was not abolished by stream water. This result is reasonable because both species migrate from lake to stream. The threshold (*i.e.*, minimum concentration) that induced the olfactory nerve response to stream water after adaptation to lake water occurred between 0.1 and 1.0% in lacustrine *O. nerka* and *O. masou*, revealing that the olfactory discriminatory ability can be exerted only within a limited distance from the natal stream.

The upstream selective movements of the four *Oncorhynchus* spp. species (*i.e.*, *O. gorbuscha*, *O. keta*, *O. nerka* and *O. masou*) were compared using artificial natal-stream water (ANW) that was prepared to have the same composition and concentration of DFAA as those found in their natural natal streams and the experiment took place in a two-choice test tank (*i.e.*, a Y-maze) that consisted of two water inlet

arms and one pool. Two different types of water (ANW and control lake water) were added to the water inlet of either the left or the right arm and fish movement was monitored to determine the number of fish that moved into each arm. Among the four *Oncorhynchus* spp. species, *O. gorbuscha* showed the highest percentage of upstream movement, but showed the lowest level of selectivity for the arm with ANW. However, *O. keta*, *O. nerka* and *O. masou* showed significant selectivity for the arm with ANW (Ueda, 2011; Yamamoto *et al.*, 2008).

If salmonids always accurately homed to the streams where they were born, there would be a potential for reduced genetic diversity, along with a restricted distribution and small population size. Thus, it is quite interesting to investigate the relationship between salmonid evolution and homing accuracy from an evolutionary perspective. Compared with *O. gorbuscha*, *O. masou* have a restricted distribution and small population size (Kaeriyama & Ueda, 1998) (Figure 1(a)). They also return to their natal stream with the highest precision, whereas *O. gorbuscha* are more likely to stray into a non-natal stream. *Oncorhynchus gorbuscha* may have evolved the capacity to adapt to non-natal-stream odours, enabling this expansion in distribution. Retropositional genome analyses have revealed that *O. gorbuscha* are phylogenetically the most advanced *Oncorhynchus* species, while *O. masou* are more primitive (Murata *et al.* 1996) (Figure 1(b)).

Using an electro-olfactogram (EOG), the olfactory discrimination ability of stream odours in juvenile *O. keta* was measured during downstream migration from the Chitose Hatchery in Hokkaido, Japan (site A, Figure 2) to Ishikari Bay (site F, Figure 2). Fish were collected at the second bridge of the River Chitose (site B; the first collection site after release from the hatchery) and the confluence point with the River Old Yubari (site D). Fish that encountered streams with water that differed from that in the hatchery showed significantly greater responses to the River Ishikari water than to the River Chitose and River Toyohira waters (Ueda *et al.*, 2016). This phenomenon supports the sequential imprinting hypothesis developed by Harden-Jones (1968). The EOG responses of adult male *O. keta* collected at the Indian waterwheel, on the River Chitose (site H) were significantly higher for both the River Ishikari and the River Chitose, *i.e.* their natal-stream waters, than for the River Toyohira, which is a nearby tributary that is not part of their migratory path (Ueda *et al.*, 2016). These data suggest that the olfactory memory retrieval abilities regarding natal-stream odours increase during the upstream migration of adult *O. keta*.

The concentration and composition of DFAA in stream water may change seasonally and annually. In the River Teshio in Hokkaido, Japan, juvenile *O. keta* conduct their downstream migration in spring and adults conduct their upstream migration in autumn; there is a 4 year span between the downstream and upstream migrations. The River Teshio water contained 15 DFAA and the concentrations of these DFAA fluctuated greatly. However, the compositions (mole %) of 5–7 DFAA were stable between the spring and autumn samples within a 4 year span. The same concentrations of DFAA as those found in the River Teshio during the time of juvenile imprinting in spring (jASW) and adult homing in autumn (aASW) were prepared after a 4 year period. Behavioural experiments of upstream selective movement were conducted in a Y-maze (Yamamoto *et al.*, 2013).

Four-year-old mature *O. keta* males captured in the River Teshio showed a significant preference for either jASW or aASW over control water, but they did not display a preference between jASW and aASW. These results confirm that the long-term stability of the compositions of DFAA in the natal stream is crucial for olfactory imprinting and homing in *O. keta*. Furthermore, Chen *et al.* (2017) monitored the homing behaviours of *O. keta* to river-specific DFAA profiles using a PIT-tag system in a Y-maze. The majority of *O. keta* that homed to the River Chitose showed a preference for the River Chitose ASW and tended to stay in this arm of the maze for a longer period. These results confirmed the ability of *O. keta* to identify and discriminate ASW that contained natural levels of DFAA.

Within a catchment's ecosystems, complicated biological processes, such as soil, vegetation, litter, pollen, dew and various microbial activities cause changes in the compositions of DFAA (Thomas, 1997). Moreover, the roles of complex microbial communities called biofilms, which consist of various microorganisms that are embedded into a matrix of extracellular polymeric substances, have been intensively studied (Costerton *et al.*, 1994; Nosyk *et al.*, 2008). The origin of DFAA in stream water was investigated by focusing on biofilms in the stream bed via incubation experiments in the laboratory (Ishizawa *et al.*, 2010). Stones were placed in the River Toyohira for 3 months to allow the formation of biofilms and were then incubated in the laboratory at stream-water temperature for 24 h. The composition and concentration of DFAA in the incubation solution were measured after incubation. Although the concentration of DFAA increased greatly in the biofilm incubation solution, the composition of DFAA showed little change after the 24 h incubation. These results revealed that biofilms are a primary source of DFAA in stream water.

4 | NEUROENDOCRINOLOGICAL STUDIES ON HORMONES AND MEMORIES

For *Oncorhynchus* spp., the imprinting migration of juveniles and the homing migration of adults are closely related to seawater adaptation and gonadal maturation, respectively. Juvenile imprinting during downstream migration is associated with smoltification and smoltification is a complex process that is regulated by several endocrine hormones, such as growth hormone-releasing hormone (GHRH), corticotropin-releasing hormone (CRH) and thyrotropin-releasing hormone (TRH) in the brain; growth hormone (GH), adrenocorticotrophic hormone (ACTH) and thyrotropic hormone (TSH) in the pituitary gland; insulin-like growth factor I (IGF-I), cortisol and thyroid hormones (thyroxine:T4 and triiodothyronine: T3) in many of the endocrine organs (Björnsson *et al.*, 2011, 2012; McCormick, 2001). Specifically, the brain-pituitary-thyroid (BPT) hormones (*i.e.*, TRH in the brain, TSH in the pituitary gland and T4/T3 in the thyroid gland) are thought to play critical roles during the imprinting process that occurs during downstream migration. In contrast, adult homing migration is regulated mainly by the brain-pituitary-gonadal (BPG) hormones. Two gonadotropin-releasing hormones (GnRH), *i.e.*, salmonid GnRH (sGnRH; commonly named GnRH3) and chicken GnRH-II (cGnRH-II; commonly named GnRH2), exist in various regions of the brains of salmonids (Amano *et al.*, 1997). Specifically, the sGnRH

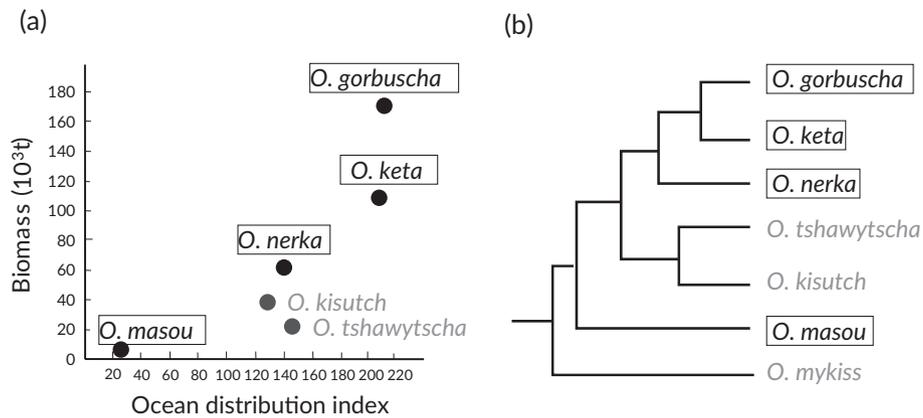


FIGURE 1 (a) The mean (1952–1975) total recorded catch biomass of *Oncorhynchus* spp. and the ocean distribution index that indicates the matrix numbers of an area of 2° latitude × 5° longitude where salmon were caught until 1985 (after Kaeriyama & Ueda, 1998). (b) Phylogenetic division of seven *Oncorhynchus* spp. using retropositional genome analyses (after Murata *et al.*, 1996). The four *Oncorhynchus* spp. occurring in Japan are framed

neurons that have two different precursor genes, *i.e.* *sgnrh-I* and *sgnrh-II*, are found in the olfactory bulb (OB), the terminal nerve (TN) and the preoptic area (POA) and these neurons are considered to play different roles in salmonid homing migration, but their exact roles have not yet been clarified. Mainly, sGnRH in the POA is believed to control the synthesis and release of gonadotropic hormone (GTH), luteinizing hormone (LH) and follicle-stimulating hormone (FSH). GTHs induce steroidogenesis in the gonads and steroid hormones stimulate gametogenesis and final gameto-maturation. Furthermore, oestradiol-17 β (E2) and testosterone (T) are active during vitellogenesis, T and 11-ketotestosterone (11KT) are active during spermatogenesis and 17 α ,20 β -dihydroxy-4-pregnen-3-one (DHP) are active during final gameto-maturation in both sexes (Nagahama, 1997). It is very

important to investigate the BPT and BPG hormone profiles in salmonids during juvenile imprinting and adult homing migration to clarify how these hormones control or mediate imprinting migration and homing migration, respectively. However, until now, it was impossible to link hormonal control mechanisms to imprinting and homing because molecular markers that permitted the evaluation of olfactory memory formation and retrieval in the brains of salmonids were unknown.

Synaptic plasticity is believed to underlie the formation of memory in the brains of vertebrates. In the critical period, the formation of a complex neural network by synaptic contact between the axons and dendrites of neurons produce the synaptic plasticity that promotes the ability of chemical synapses to change synaptic strength. As

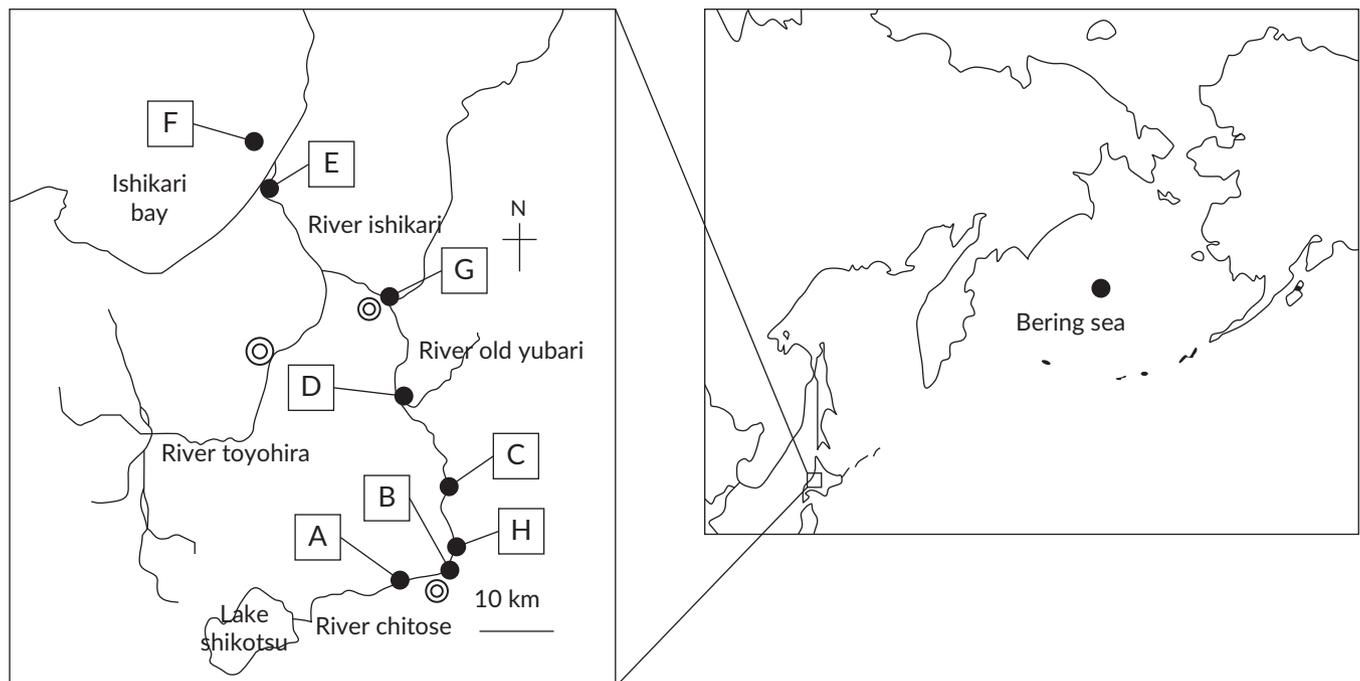


FIGURE 2 The study area with the sampling sites (●) of *Oncorhynchus keta* during juvenile downstream migration and adult homing migration. Site A, Chitose hatchery; B, second bridge on the river Chitose; C, river Chitose in Kamakura Ward; D, confluence point of the river Chitose and old Yubari rivers; E, mouth of the main stem of the river Ishikari; F, Ishikari Bay; G, confluence point of the Ishikari and Chitose rivers; and H, Indian waterwheel, on the river Chitose

memory is thought to be encoded by modifications in synaptic strength, long-term potentiation (LTP), which is the persistent strengthening of synaptic activity that produces a long-lasting increase in the signal transmission between two neurons, is widely considered as one of the major cellular mechanisms that underlies memory (Kotaleski & Blackwell, 2010). LTP has been studied with a specific focus on the *N*-methyl-D-aspartate receptor (NMDAR), which induces LTP (Martin *et al.*, 2000). The NMDAR is a glutamate receptor channel subtype that mediates most of the fast-excitatory synaptic transmission in the central nervous system. The NMDAR plays an important role in memory formation and retrieval in mammals (Park *et al.*, 2013) and in fishes (Cox *et al.*, 2005; Gómez *et al.*, 2006; Kinoshita *et al.*, 2005; Nam *et al.*, 2004; Sison & Gerlai, 2011; Tzeng *et al.*, 2007). Furthermore, the NMDAR is composed of two subunits: the essential NR1 subunit and the differentially expressed NR2A-D subunit (Shipton & Paulsen, 2013). The *nr1* gene of *O. keta* has been cloned and characterised (Yu *et al.*, 2014) and the effects of changes in salinity on *nr1* expression have been reported (Kim *et al.*, 2015). However, there have been no reports addressing how *nr1* might be involved in olfactory memory formation and retrieval in *Oncorhynchus* spp.

Several studies have described the hormone profiles that exist during downstream migration as well as the artificial induction of downstream movement in juvenile *Oncorhynchus* spp. A clear T4 surge was observed during the downstream migration of *O. keta* fry, suggesting that T4 plays an important role in the preparation for downstream migration. However, T4 has not been identified as the sole factor responsible for the onset of downstream migration (Iwata *et al.*, 2003; Ojima & Iwata, 2007). Ojima and Iwata (2009) reported that the central administration of GHRH, CRH, melatonin, N-acetyl serotonin and serotonin stimulated downstream movements, while only GHRH stimulated schooling behaviours. In juvenile Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792), the central administration of CRH was also found to induce downstream movements (Clements & Schreck, 2004). Additionally, treatments that affect the thyroid hormones have been shown to prompt olfactory cellular proliferation in *O. kisutch* (Lema & Nevitt, 2004). In fall-smolting *O. kisutch*, the central administration of GHRH and CRH stimulated downstream movement and T4 secretion (Ojima & Iwata, 2010). In the same species, the levels of TSH β messenger (m)RNA and TSH in the pituitary gland and the levels of TSH, T4 and T3 in the plasma have been assessed and were found to be correlated with smoltification (Larsen *et al.*, 2011). In the brains of *O. nerka*, the mRNA that encodes the TRH precursor has been studied by *in situ* hybridization (Ando *et al.*, 1998) and the expression of complementary (c)DNA encoding TRH receptor subtypes has been examined (Saito *et al.*, 2011). It was reported that T3 determined the onset of the sensitive period for imprinting and it is known that T3 plays a critical role in the later learning in chicks *Gallus gallus domesticus* (Yamaguchi *et al.*, 2012). Although the onset of downstream migration, which includes smoltification, is regulated by a complex set of several endocrine hormones, the BPT hormones are considered to play a critical role in imprinting during downstream migration (Dittman & Quinn, 1996).

Under-yearling juvenile *O. keta* were reared in the Chitose hatchery (site A, Figure 2) and then released into the River Chitose, where

they migrated to Ishikari Bay (site F, Figure 2). The relationship between the BPT hormones and natal-stream odour imprinting was investigated based on the whole-brain mRNA expression of *trha/b* and *tsh β* in the upper head that contains the pituitary gland, the levels of T4 and T3 isolated in the lower jaw that contains the thyroid glands and the whole-brain mRNA expression of *nr1*. Ueda *et al.* (2016) analysed the gene expression profiles of *trha/b* and *tsh β* in juvenile *O. keta* and revealed that the environmental changes experienced by fish during the release from the hatchery to the natal stream significantly enhanced the *trha/b* and *tsh β* expression levels and T4/T3 levels significantly increased during downstream migration towards the sea. Ueda *et al.* (2016) also demonstrated that the *nr1* expression levels showed a significant initial peak that was correlated with larval brain development in the hatchery (Pouwels, 1978); additionally, there was a gradual significant increase that immediately followed a significant *trha/b* expression surge at the River Chitose in Kamaka Ward (site C) and there was a second significant peak at the mouth of the River Ishikari (site E). The results of *in situ* hybridization confirmed that, compared to the results in the hatchery (site A), *nr1* mRNA localisation increased prominently in the ventral telencephalon (TE) at the River Chitose in Kamaka Ward (site C) immediately after the fish were released into the river (site B). Moreover, in experiments that included the oral administration of T4 (2 mg g⁻¹ pellet) to juvenile *O. keta*, Ueda *et al.* (2016) found increases in the levels of T4/T3 in the whole body and significant increases in the *nr1* gene expression in the whole brain for 4 days. Interestingly, the T4/T3 levels increased for 14 days, but no significant difference was observed in the *nr1* expression; thus, these results revealed that the critical period of imprinting is limited to fewer than 7 days. These results clarified that, at the initiation of juvenile *O. keta* downstream migration, the environmental changes involved in the release from the hatchery into the river induced the activation of the BPT hormones, which then stimulated the upregulation of *nr1* and induced the induction of LTP, which ultimately enhanced the olfactory memory formation capability of natal stream-specific odours (Figure 3(a)). Further research should investigate how T4/T3 may activate the imprinting abilities of natal-stream odours in the olfactory epithelium.

The BPG hormone profiles were measured in adult *O. keta* that were migrating from the Bering Sea to the natal hatchery in the River Chitose (site A, Figure 2) using specific time-resolved fluoro-immunoassay systems (Yamada *et al.*, 2002). The level of sGnRH in the OB of both sexes peaked when the fish were located between Ishikari Bay (site F) and the mouth of the River Ishikari (site E), which was a location where the olfactory discriminating ability of the natal stream was expected to be important. The sGnRH also peaked in the TE when the fish reached the point where the River Chitose joined the River Ishikari (site G); at this point, the olfactory functions should be highly activated, as individuals must determine which branch to enter. In the pituitary gland, the sGnRH levels tended to increase in concert with the LH levels around Ishikari Bay (sites F) and the mouth of the River Ishikari (site E). In contrast, the FSH levels did not show any clear correlations with the sGnRH levels in the pituitary gland (Ueda, 2011).

The sGnRH neurons, which showed signals for pro-sGnRH mRNA, were observed in the dorsal olfactory nerve of *O. keta* at Ishikari Bay

(site F), but these signals were not observed in fish at the natal hatchery (site A) (Kudo *et al.*, 1996). Changes in the levels of the GTH subunit mRNAs in the pituitary gland of pre-spawning *O. keta* demonstrated that the levels of GTH α 2 (there are two distinct α subunit proteins, with only the α 2 subunit utilised as the composer of LH β) and LH β increased when an individual entered fresh water; however, no changes were observed in the FSH β levels at this point (Kitahashi *et al.*, 1998a). It was interesting to note that in both sexes the sGnRH levels in the TE and the serum T levels showed a coincident peak at the point where the River Chitose joined the River Ishikari (site G). Ueda *et al.* (2016) showed that the mRNA expression levels of *sgnrh-I* and *II* and *nr1* in the OB and TE appeared to increase and there were certain differences between males and females that might be related to sex-specific gonadal maturation. The increased *nr1* expression in the OB showed that the olfactory memory retrieval abilities of adult *O. keta* increased during upstream homing migration. Interestingly, the *sgnrh-II* expression in the hypothalamus of males was also high in the Bering Sea (Ueda *et al.*, 2016). These results revealed that sGnRH was involved in brain region-dependent roles that affected gonadal maturation and olfactory memory retrieval in adult *O. keta*.

The serum steroid hormone levels showed the following profiles: during vitellogenesis and spermatogenesis, E2 increased in females and 11KT increased in males, respectively, during homing migration from the Bering Sea to the River Chitose. Although E2 in males and 11KT in females showed interesting small peaks during upstream migration to the natal hatchery, the exact meanings of these peaks were unknown. Additionally, T, which is a precursor of both E2 and 11KT, showed peaks that resembled those of E2 and 11KT. Furthermore, DHP increased dramatically in both sexes at the time of final gonadal maturation (Ueda, 2011; Ueda *et al.*, 1984).

Due to the differences in salinity between seawater and fresh water, it is difficult to manipulate endocrinological functions in anadromous salmonids using experimental treatments. In contrast, lacustrine salmonid populations offer a model system for studying the hormonal control mechanisms of salmonid homing. In Lake Shikotsu,

Hokkaido, Japan (surface area 78 km²; average and maximum depths of 265 and 363 m, respectively), lacustrine *O. nerka* are artificially produced by hatchery propagation. During the spawning season between September and November, adults were captured adjacent to their natal hatchery prior to spawning, tagged and released in the centre of the lake. Blood samples were collected at both capture and recapture to measure changes in the steroid hormone levels in individual migrants as well as to monitor the homing duration and precision during each month (Sato *et al.*, 1997). Homing duration significantly decreased from September to October in males and from October to November in females. All males returned more quickly than females in September and October, but half of the males had not returned to the natal hatchery by November. In contrast, 78–90% of females returned to the natal hatchery between September and November. Since there was no difference in sex in terms of the total number of homing individuals, there was an average of 83% homing of both sexes for the 3 month periods. These results clearly showed that the sexual differences between males and females differed in terms of gonadal maturity. Those individuals that did not return to the natal site may have possibly migrated elsewhere and widened their distribution area.

The GnRH analogue (GnRHa) treatment has been reported to be highly effective for inducing the release of GTH and the onset of ovulation and spermiation in teleosts (Zohar & Mylonas, 2001). To investigate the effects of the GnRHa treatment on the homing duration of lacustrine *O. nerka* in Lake Shikotsu, Sato *et al.* (1997) investigated the effects of GnRHa intramuscular implantation on both the homing profiles and the serum steroid hormone levels of fish in September. Although no gonadectomies were conducted in this experiment, GnRHa implantation was highly efficient in shortening homing duration. Kitahashi *et al.* (1998b) confirmed the efficiency of GnRHa implantation in shortening the homing duration of lacustrine *O. nerka* in Lake Shikotsu and demonstrated that this efficiency differed based on gonadal maturity; specifically, the shortening effect of GnRHa was observed in maturing fish in September but not in matured fish in October. GnRHa implantation also caused dramatic increases in the

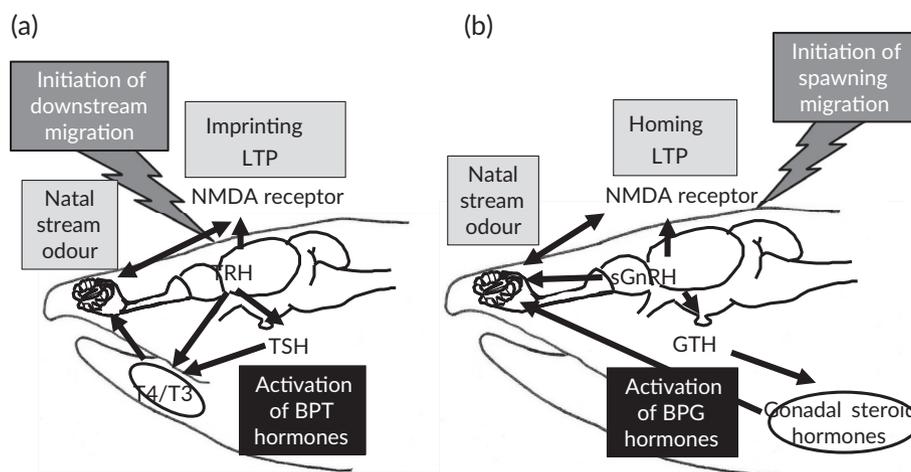


FIGURE 3 Schematic illustrations of (a) olfactory imprinting in juvenile salmonids. Initiation of downstream migration of juveniles induces the expression of the brain-pituitary-thyroid (BPT) hormones, which then stimulate the upregulation of *nr1*, inducing long-term potentiation (LTP) that enhances the olfactory memory formation capability of natal stream-specific odours. (b) Olfactory homing in adult salmonids. Initiation of homing migration of adult salmon induces the activation of the brain-pituitary-gonadal (BPG) hormones, which then stimulate the upregulation of *nr1*, inducing LTP that enhances the olfactory memory retrieval capability of natal stream-specific odours

serum DHP levels in both sexes. A discrepancy was observed between males that returned rapidly and those that returned slowly, *i.e.* the rapidly returning males had higher serum T levels and lower serum DHP levels than did the slowly returning males. The direct actions of T and DHP on homing duration were investigated by T and DHP implantation in fish in September. T-implantation tended to reduce homing duration in both males and females, but there was no statistically significant difference between the two sexes. Furthermore, though DHP did not have any significant effect in males, DHP-implantation significantly shortened homing duration in females. Although DHP is known to be 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 salmonid homing migration should be further investigated and special attention should be focused on their influence on the sensory and central nervous systems.

To investigate the involvement of the NMDAR on the homing duration of lacustrine *O. nerka* in Lake Shikotsu, the effect of NMDAR antagonists (*i.e.*, APV and MK-801) on homing duration was investigated in late October. Although there were no rescue experiment using agonists, the homing duration of male lacustrine *O. nerka* was significantly prolonged by both blockers (Fukaya, 1999; Ueda, 2014). These results suggested that the NMDAR is deeply involved in the retrieval of the imprinting memory in *O. nerka*.

These results demonstrated that the sGnRH neurons in the POA must be involved in gonadal maturation and those in the OB and TN may have olfactory-related functions that are related to olfactory-guided homing migration. The initiation of homing migration in adult *Oncorhynchus* sp. induced the activation of the BPG hormones, which then stimulated the upregulation of *nr1* and induced the induction of LTP, which subsequently enhanced the olfactory memory retrieval capability of natal stream-specific odours (Figure 3(b)). Further research should investigate the sexually different roles of the BPG hormones as well as the brain region-specific roles of sGnRH in the sensory systems and the central nervous system.

5 | RESEARCH ON NAVIGATION FUNCTIONS

The geomagnetic imprinting hypothesis has been used to propose that *O. tshawytscha* may migrate from their ocean habitats to their natal streams in a narrow migration corridor along a magnetic field isoline (Bracis & Anderson, 2012). A collective navigation hypothesis has been proposed for homeward migration in both anadromous *Oncorhynchus* and *Salmo* (L. 1758) species that states they are thought to use geomagnetic, celestial and olfactory cues (Berdahl *et al.*, 2014). An inherited magnetic map has been proposed as a navigational solution that enables salmonids to migrate to oceanic foraging grounds without prior experience or guidance from older conspecifics (Putman, 2015). Population-specific strategies (Byron & Burke, 2014) and social interactions (Berdahl *et al.*, 2017) have also been demonstrated as mechanisms of oceanic spawning migration in anadromous salmonids.

In contrast to the long history of research on the roles of the olfactory functions on natal-stream imprinting and homing in

salmonids, research on the navigation functions have just started involving intensive investigations due to the development of biotelemetry techniques. Biotelemetry technologies, such as ultrasonic and radio telemetry, data logging and pop-up satellite telemetry, have rapidly developed in recent years and it is now possible to continuously observe the underwater behaviour of salmonids in open water (Cooke *et al.*, 2004; Hussey *et al.*, 2015). Several ultrasonic tracking attempts have been employed to evaluate the migratory behaviour of *Oncorhynchus* spp. in coastal seas (Quinn & Groot, 1984; Quinn *et al.*, 1989) and in the central Bering Sea (Ogura & Ishida, 1994). In addition, some ultrasonic tracking experiments have been conducted with sensory ablation treatments. The behaviour of anosmic *S. salar* was studied using ultrasonic tracking in a fjord and demonstrated the capability of olfactory discrimination of fine-scale hydrographic features (Døving *et al.*, 1985). The effects of visual and olfactory ablation on the swimming behaviour of adult *O. keta* were examined using ultrasonic tracking along the Okhotsk coast of Hokkaido, Japan and this study reported vertical and horizontal zigzag movements in both types of ablated fish (Yano & Nakamura, 1992). Ultrasonic telemetry techniques were developed to investigate the magnetic sense of maturing *O. keta* in the western North Pacific Ocean and there were no significant differences observed in horizontal and vertical movements or in swimming speeds between the magnetically disturbed fish and the control fish (Yano *et al.*, 1996). However, magnetoreceptor cells have been identified in the nasal cavity of rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) (Walker *et al.* 1997) and empirical evidence for geomagnetic imprinting has been reported for *O. tshawytscha* (Bracis & Anderson, 2012), *O. gorbuscha* and *O. nerka* (Putman *et al.*, 2013). Azumaya *et al.* (2016), studied the Earth's magnetic forces during *O. keta* homing migration from the Bering Sea to Japan using magnetic archival tags that can record the magnetic force. Their results demonstrated that the homing migration route approximately followed the isoline of magnetic intensity.

6 | O. KETA HOMING BEHAVIOUR FROM THE BERING SEA TO HOKKAIDO

A seasonal migration model for Japanese *O. keta* in the Pacific Ocean has been proposed using genetic stock identification techniques and it has been suggested that they start homing migration from the Bering Sea to Japan in summer (Urawa, 2004). Tanaka *et al.* (2005) examined *O. keta* homing behaviour from the Bering Sea to Hokkaido, Japan. Japanese *O. keta* were collected by longline in June 2000 in the central Bering Sea (56° 30' N, 179° 00' E) and the fish were identified as having Japanese origin based on scale analysis; specifically, this was possible because most of the Japanese *O. keta* were released from hatcheries and the width of their scale rings during the fry stage was wider than those seen in wild *O. keta* from other countries. Twenty-seven *O. keta* were released with an external propeller data logger, which recorded swimming speed, depth and temperature, was attached externally through the dorsal musculature of the fish anterior to the dorsal fin. Only one logger was recovered from a set net in September along the eastern coast of Hokkaido (43° 20' N, 145° 46' E). The first recorded swimming profiles of *O. keta* homing from the

Bering Sea to Hokkaido were collected over a period of 67 days and these profiles covered a linear distance of 2,750 km. The *O. keta* had travelled with an average swimming speed, depth and temperature of (mean \pm s.d.) 62 ± 12 cm s⁻¹, 10.4 ± 14.7 m and $9.2 \pm 0.2^\circ\text{C}$, respectively. Both swimming speed and depth trimodally peaked around dawn and dusk, with an additional small peak around midnight. The fish showed sequential up-and-down movements near the thermocline during twilight and daytime that could be thermoregulation behaviours. These diurnal migratory patterns suggested that homing *O. keta* allocated a proportion of their time to foraging and their foraging strategy differed between daytime and night-time. These results indicated that the homing *O. keta* have homeward-bound navigation abilities from the central Bering Sea to Japan. Along the coast of Hokkaido and north mainland of Japan, the swimming depth of *O. keta* was recorded using archival tags; the results indicated that swimming depth was related to moonlight during homeward migrations (Hasegawa, 2012).

7 | LACUSTRINE *O. NERKA* AND *O. MASOU* HOMING BEHAVIOURS IN LAKE TOYA, HOKKAIDO

It is difficult to implement physiologically controlled and manipulated experiments using anadromous salmonids as fish migrate from seawater in coastal seas to fresh water in their natal streams once they reach gonadal maturation. On the other hand, lacustrine salmonid populations offer a good model system for studying homing behaviours during the migration from open waters to natal areas for reproduction through the use of sensory ablation treatments. The homing migrations of mature lacustrine *O. nerka* (Ueda *et al.*, 1998) and lacustrine *O. masou* (Ueda *et al.*, 2000), whose sensory cues were impaired by ablations, were compared and the fish were tracked from the centre of Lake Toya, which is a large caldera lake (surface area 71 km², average and maximum depths of 116 and 179 m, respectively), to their natal areas using an ultrasonic tracking system. A mature *O. nerka* male whose magnetic cues were interfered with by a strong NdFe magnetic ring that was attached to its head returned straight to the natal area after 1 h of random movement. A mature *O. nerka* male, whose visual cues were blocked by the injection of carbon toner and corn oil and whose magnetic cues altered via a magnetic ring, moved in a direction opposite from its natal area. In contrast, a mature control *O. masou* male moved constantly along the coast and stopped his movement at the mouth of stream. In contrast, a blinded mature *O. masou* female was released and moved randomly away from the coast and a mature *O. masou* male, whose olfactory cue was blocked by petroleum jelly, moved first along the coast and eventually moved towards the open water.

The comparison between the straight movements of *O. nerka* and the coastal movement behaviours of *O. masou* is quite informative. It has been reported that *O. nerka* are widely distributed in the North Pacific Ocean, while *O. masou* are narrowly distributed in the western North Pacific Ocean (Kaeriyama & Ueda, 1998). These data suggest some evolutionary aspects of successful homing migration in *Oncorhynchus* spp., where the narrowly distributed *O. masou* required only

coastal recognition ability for successful migration using olfactory and visual cues, while the widely distributed *O. nerka* required the development of open-water orientation ability to return successfully to their natal streams with high precision using visual and magnetic cues (Ueda, 2014). The roles of each sensory system should be further investigated including how each sensory system could control coastal recognition and open water orientation.

The spawning migration of lacustrine *O. masou* with attached depth and temperature data loggers was monitored in Lake Toya (Matsushita, 2001; Ueda, 2016). A clear diurnal movement was observed after they first encountered the mouth of river at the beginning of the spawning season; this change was detected by the difference in the ambient temperature between the mouth of the river (14–20°C) and the surface of the lake (20–22°C). After this encounter, fish swam vertically around the thermocline depth during the day and stayed near the water surface at night, showing clear diurnal movement that could be thermoregulation behaviour. This movement gradually disappeared towards the peak of the spawning season, when they migrated upstream to the spawning ground. These behavioural changes observed in *O. masou* during the spawning season showed that *O. masou* were able to calculate the day length with an innate biological clock; furthermore, this circadian rhythm after encountering cool temperatures at the river mouth was useful for calculating the timing of upstream migration to their spawning river.

To accurately home in open water, salmonids must recognise exact locations (map) and compass directions (orientation) during migration and they must have an internal biological clock to calculate the duration of migration from the feeding ground to the spawning ground. New research approaches that reveal how salmonids can navigate in open water using compasses, maps and biological clocks are necessary to identify which sensory systems are involved (and how) in the oceanic imprinting and homing migration of *Oncorhynchus* spp.

8 | CONCLUSIONS

This review synthesises findings on the physiological mechanisms of imprinting and homing migration in *Oncorhynchus* spp. (Ueda, 2012) and describes the importance of two different sensory mechanisms, *i.e.* olfaction and navigation, on the natal-stream imprinting and homing, primarily by studying the migration of anadromous *O. keta* from the Bering Sea to Hokkaido, Japan and by studying the migration of lacustrine *O. nerka* and *O. masou* in Lake Toya and Lake Shikotsu in Hokkaido, Japan. Olfactory functions were investigated using both neurophysiological studies on the olfactory discriminating ability of natal-stream odours and neuroendocrinological studies on the hormonal controlling mechanisms of olfactory memory formation and retrieval in the brains of *Oncorhynchus* spp. The neurophysiological studies demonstrated that the long-term stability of DFAA composition that comprise natal-stream odours and are produced by biofilms in the natal stream are crucial for the olfactory discriminating abilities during imprinting and homing migration. The neuroendocrinological studies revealed that the BPT and BPG axes played leading roles during juvenile olfactory imprinting and adult homing migration, respectively; additionally, the NMDAR was useful for studying brain

molecular markers related to olfactory memory formation and retrieval. However, the olfactory mechanisms of straying are still unclear and the relationship between salmonid evolution and homing accuracy must be understood to explain the mechanisms of straying (Keefer & Caudill, 2014). Navigation functions were examined using physiological biotelemetry techniques with sensory interference experiments during the homing migration of anadromous and lacustrine *Oncorhynchus* spp. The results indicated that *Oncorhynchus* spp. can navigate in open water using several sensory systems. The role of magnetic sensory systems should be further examined during the oceanic imprinting and homing migration of *Oncorhynchus* spp. Despite the inherent difficulties in the temporally limited imprinting and homing, neurophysiological, neuroendocrinological and physiological biotelemetry studies using model anadromous and lacustrine *Oncorhynchus* spp. can provide new explanations for the precise sensory mechanisms of natal-stream imprinting and homing migration in Pacific and Atlantic salmon.

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