

The current propagation systems and physiological studies of Japanese chum salmon

Hiroshi Ueda

Received: 29 October 2014 / Accepted: 21 December 2014
© Japanese Society of Fisheries Science 2014

Abstract In Japan, chum salmon *Oncorhynchus keta* is mainly propagated via artificial insemination, the release of juveniles from their natal river to the ocean, and the recapture of homing adults along the coast and within the natal river. The biomass of Japanese chum salmon increased steadily from 1970 to 1996 because of the successful improvement of propagation systems. However, the returning rate of homing adults has become unstable, and the aftermath of the 2011 Tohoku earthquake and tsunami caused a major decrease in the number of juveniles released in the Tohoku area. It is now widely accepted that specific factors in the natal stream are imprinted on the nervous system of juvenile chum salmon during downstream migration and that adults use these factors to recognize the natal stream during their upstream homing migration. Recent physiological studies from behavioral to molecular biological approaches to elucidate mechanisms of imprinting and homing migration in chum salmon are useful for developing new chum salmon propagation systems to enhance the survival rates of juveniles in coastal areas and stabilize the returning rate of homing adults. This review introduces a semi-closed recirculating aquaculture system to estimate the health condition and improve the olfactory imprinting capability of juvenile chum salmon.

Keywords Japanese chum salmon · Propagation system · Imprinting · Homing · Aquaculture system

Introduction

In Japan, the chum salmon *Oncorhynchus keta* is the most abundant Pacific salmon species and has been used as an important protein source since the prehistoric period, especially in Hokkaido, where the Ainu people (an indigenous people) might use these fish for autumn and winter food. The precise ability of chum salmon to home in on their natal river for spawning was recognized approximately 250 years ago in Niigata [1]. Artificial salmon/trout propagation techniques were introduced from Western countries in the late 1870s, and artificial chum salmon propagation systems began to be implemented in the late 1880s. Enormous efforts to improve techniques of egg incubation, fry feeding, and juvenile release caused the numbers of released juveniles and returning adults to increase steadily from 0.5 to 2 billion and from 10 to 90 million, respectively, from the late 1970s to the 1990s. However, likely due to an inability to prevent fish disease in juveniles, a regime shift in the North Pacific Ocean ecosystem, and global warming, a sharp decline in adult returns with an approximately 8-year interval was observed from 1992 to 2008, despite an almost constant number of juveniles released. In addition, the aftermath of the Tohoku earthquake and tsunami in 2011 caused a major decrease in the number of juveniles released in the Tohoku area.

The present review provides an overview of the historic and current status of chum salmon propagation systems in Japan. I describe recent findings from three research approaches examining the physiological mechanisms underlying the imprinting and homing abilities of chum salmon: physiological biotelemetry studies on chum salmon homing migration, endocrinological studies on hormone profiles during imprinting and homing migration, and neurophysiological studies on olfactory imprinting and

H. Ueda (✉)
Field Science Center for Northern Biosphere, Hokkaido
University, Sapporo 060-0809, Japan
e-mail: hueda@fsc.hokudai.ac.jp

discriminating functions. Finally, a summary of new trials is presented with a focus on introducing new chum salmon propagation systems based on the findings of these research approaches.

History of Japanese chum salmon propagation systems

The homing ability of chum salmon related to spawning was recognized in the Miomote River, Murakami, Niigata, approximately 250 years ago by Buheiji Aoto, who established a system to protect homing adults. He created artificial channels known as “Tanegawa” where adults could spawn and fishing was prohibited [1]. In 1876, the first trial juvenile chum salmon release was conducted in the Nakagawa River, Ibaragi by Akikiyo Sekizawa, who had been impressed with artificial salmon/trout propagation techniques he had observed in 1873 in Weltausstellung, Wien, Austria, and at the International Exhibition of 1876 in Philadelphia, USA. Japanese chum salmon propagation began in 1888, when the first governmental hatchery was built in the Chitose River, Hokkaido, mainly due to the efforts of Kazutaka Ito, who had studied an artificial salmon propagation system at the Bucksport hatchery in Maine, USA, from 1886 to 1887 [2].

Due to the commencement of the Fisheries Resource Protection Law in 1951 and the enormous effort to establish juvenile release techniques in the 1960s, such as employing Atkins incubators for large numbers of artificially fertilized eggs, the number of returning adult chum salmon reached 3–5 million by 1965. Coastal surveys of juveniles were first conducted in 1969 and showed that timing juvenile release to match when the coastal sea surface temperature (SST) is approximately 5–10 °C leads to the highest survival rate of juveniles [3]. This favorable timing of juvenile release as well as improved rearing techniques for producing many healthy juveniles by feeding dry pellets to fry following yolk absorption in the late 1970s caused steady increases in the numbers of both juveniles released (from 0.5 to 2 billion) and adults returning (from 10 to 90 million) from the late 1970s to 1996 (Fig. 1).

Despite the almost constant release of approximately 1.8–2 billion juveniles, a sharp decline in adult returns was observed with an approximately 8-year interval from 1992 to 2008. The mechanisms underlying the 8-year interval between juvenile release and adult return are not yet clarified; however, salmon biomass is considered to be negatively affected by long-term climate change in the North Pacific Ocean, which has experienced climate change within decadal oscillation [4]. Recent global warming has also positively affected the survival rate of juvenile chum salmon in the Okhotsk Sea and caused a population

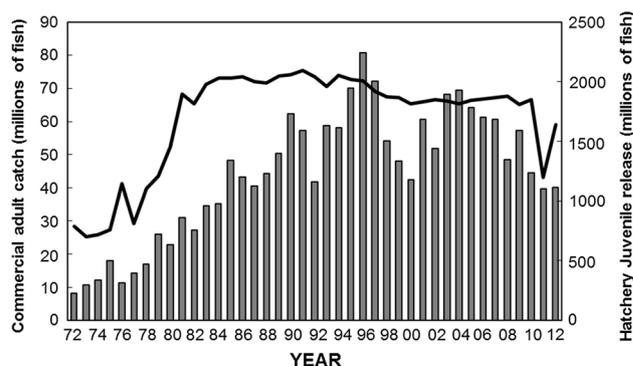


Fig. 1 Annual changes in the numbers of juveniles released from hatcheries (line) and the commercial adult catch (bars) of chum salmon in Japan from 1972 to 2012. The data is provided by the Hokkaido National Fisheries Research Institute

density-dependent effect on growth from ages 2 to 4 years and maturation in the Bering Sea [5]. Kitada [6] has reviewed the present status of the Japanese chum salmon stock enhancement program, and suggested the importance of juvenile quality and the vital roles of escapements in enhanced and non-enhanced rivers. In 2003, an amendment to the Pharmaceutical Affairs Law prohibited the use of formaldehyde, which had been quite effective for protection against fish diseases such as bacterial gill disease and ichthyobodosis. No other efficacious methods for protection against various fish diseases have been developed to date. Moreover, a major decrease in juvenile release was caused by the aftermath of the Tohoku earthquake and tsunami in 2011 (Fig. 1).

Current status of Japanese chum salmon propagation

The current system used for chum salmon propagation is illustrated in Fig. 2. Artificially fertilized eggs are stocked for 1 month in box-type incubators that can hold half a million eggs and which are supplied with clean cool spring water. Dead eggs are removed with a picking machine after the eyed stage, and live eggs are disinfected with an iodine solution to prevent viral and bacterial diseases. Eyed eggs are incubated to induce otolith thermal marking with cooled spring water at approximately 4 °C at the hatchery of the Hokkaido National Fisheries Research Institute. Several days before hatching, eyed eggs are placed on hatchery trays in gravel raceways, where the hatchery trays are set to maintain convective water exchanges. The hatchery trays are removed from the gravel raceways after hatching. The hatched alevins are left in the gravel raceways for approximately 2 months at 8 °C to absorb nutrients in their yolk sac. Chum salmon fry are transferred from the gravel raceways to outdoor

Fig. 2 The current chum salmon propagation system used in Japan, showing the cycle of the salmon enhancement program operated by the Hokkaido Salmon Propagation Association

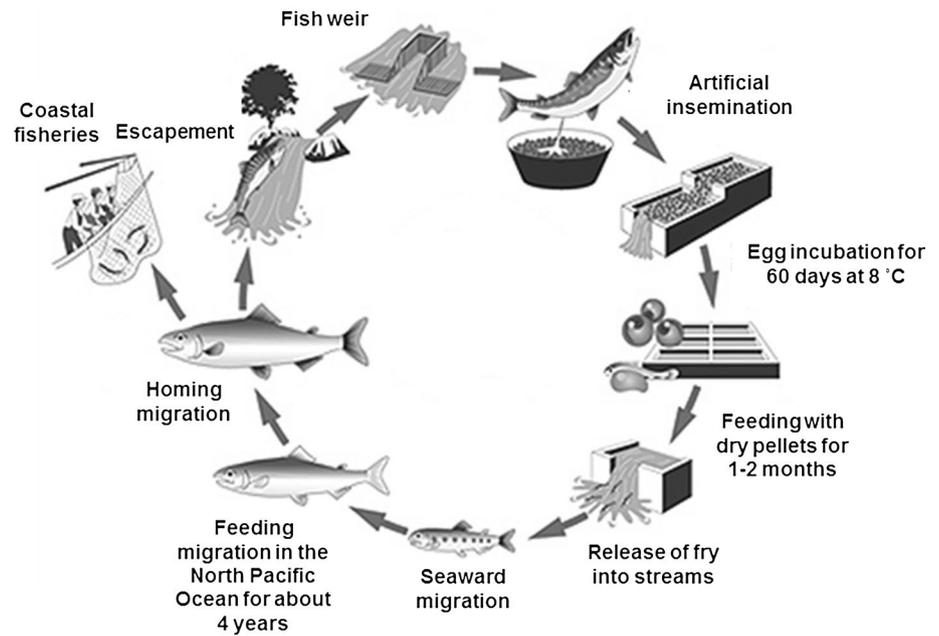
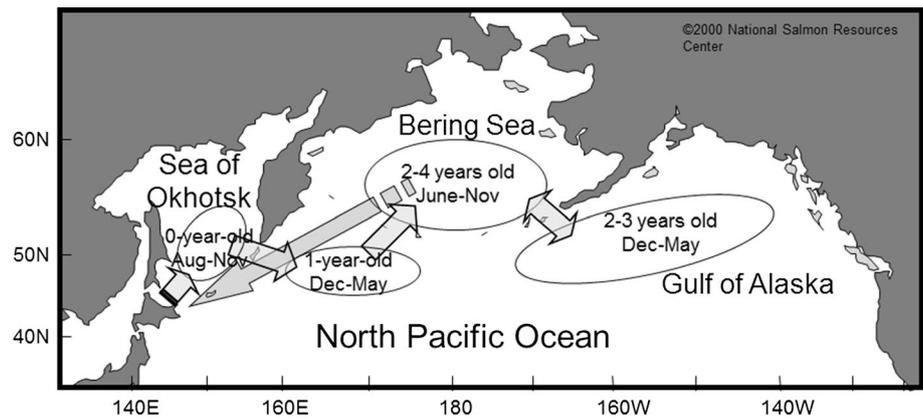


Fig. 3 Seasonal migration model for Japanese chum salmon in the ocean estimated through fish abundance and genetic stock identification by Urawa (2003)



feeding ponds following yolk absorption, approximately 2 months after hatching, and are fed with dry pellets for 1–2 months. At a body weight of approximately 1–2 g, juveniles are released into rivers between late March and mid-April. The juveniles then migrate to the sea after a short stay in the river [3].

The migration route of the Japanese chum salmon was estimated using information on fish abundance and data from the genetic stock identification of stocks sampled in the open ocean from 1993 to 1999 (Fig. 3) [7]. Juveniles less than 1-year-old are distributed in the Okhotsk Sea from August to November but are confined to a narrow band (SST 4–6 °C) of the western North Pacific from December to May. One-year-old salmon enter the Bering Sea from June to November. In the late fall, they travel southeast to the Gulf of Alaska, where they stay from December to May. They migrate between their summer feeding grounds in the

Bering Sea and their winter habitat in the Gulf of Alaska for 3–4 years until they begin their homing migration for spawning, triggered by the onset of gonadal maturation in the Bering Sea and western North Pacific.

Adult salmon are caught using set nets in coastal fisheries along the coastline of Hokkaido and northern Honshu in both the Japanese Sea and the Pacific Ocean. Escaped adults continue an upstream migration and are caught in weirs, usually at the mouths of rivers. The fish are then transferred to the hatchery, reared until final gonadal maturation occurs, and used for artificial insemination. New chum salmon propagation techniques await development to improve both the survival rate of juveniles and the returning rate of adult chum salmon. It is important to clarify the mechanisms of imprinting and homing migration in chum salmon to improve the survival rates of juveniles and returning rates of adults.

Physiological studies of imprinting and homing migration in chum salmon

Biotelemetry study on homing migration

Ultrasonic telemetry has made it possible to continually observe the migratory behavior of Pacific salmon in coastal areas [8, 9] and the central Bering Sea [10]. Ultrasonic tracking has been used in conjunction with sensory ablation experiments blocking visual olfactory cues [11] or magnetic senses [12].

In June 2000, Japanese chum salmon were attached to data loggers recording swimming speed, depth, and temperature, and they were released into the central Bering Sea (56°30'N, 179°00'E). In total, 27 chum salmon were released, and one logger was recovered from a set net in September on the east coast of Hokkaido, Japan (43°20'N, 145°46'E). The first recorded swimming profiles of homing chum salmon in the oceanic phase were collected over a period of 67 days covering a linear distance of 2,750 km [13]. The data obtained from the salmon indicated an average swimming speed, depth, and temperature of 62 ± 12 cm/sec, 10.4 ± 14.7 m, and 9.2 ± 0.2 °C, respectively. These results indicated that homing chum salmon exhibit navigational abilities in the homeward direction and that the salmon employ ocean current transport to reduce energy expenditure during migration. To accurately return home in open water, the salmon must recognize both exact locations (map) and compass direction (orientation) during migration, in addition to harboring an internal biological clock tracking the passage of time.

In Lake Toya, Japan, adult lacustrine sockeye salmon *O. nerka* display straight homing movements using visual cues, potentially without the involvement of magnetic cues, and adult lacustrine masu salmon *O. masou* exhibit coastal homing movements using both visual and olfactory cues [14]. Magnetoreceptor cells have been identified in the nose of rainbow trout *O. mykiss* [15], and empirical evidence of geomagnetic imprinting in sockeye salmon has recently been reported [16, 17]. Hasegawa [18] suggested that chum salmon use moonlight to navigate at night during homing migration. New research approaches combining neurophysiological studies of visual systems and magnetoreceptor cells with physiological biotelemetry behavioral analyses are necessary to investigate the involvement of visual and magnetic cues during oceanic imprinting and homing migration in chum salmon.

Endocrinological study on hormone profiles during imprinting and homing migration

Chum salmon imprinting and homing migration are closely related to downstream migration seaward and gonadal

maturation in the natal stream, respectively. Downstream migration is closely associated with smoltification (parr-smolt transformation, PST), which is under the complex regulation of several endocrine hormones, such as the growth hormone-releasing hormone (GHRH), the corticotropin-releasing hormone (CRH), and the thyrotropin-releasing hormone (TRH) in the brain; the growth hormone (GH), adrenocorticotropic (ACTH), and thyrotropin (TSH) in the pituitary gland; and insulin-like growth factor I, cortisol, and thyroid hormones [thyroxine (T_4) and triiodothyronine (T_3)] in many endocrine organs [19, 20]. In contrast, homing migration is directly connected to gonadal maturation, which is mainly controlled by the brain-pituitary-gonad (BPG) axis: the gonadotropin-releasing hormone (GnRH) in the brain controls gonadotropin (GTH), the luteinizing hormone (LH), and the follicle-stimulating hormone (FSH) synthesis and their release from the pituitary gland. In addition, GTH stimulates the release of steroid hormones: estradiol-17 β (E_2), testosterone (T), 11-ketotestosterone (11KT), and 17 α ,20 β -dihydroxy-4-pregnen-3-one (DHP) from the gonads [21]. It is important to investigate the hormone profiles of salmon during imprinting and homing migration.

Imprinting migration

No studies have investigated the hormonal changes that occur during imprinting migration in juvenile chum salmon; however, several have described the hormone profiles that occur during downstream migration and the artificial induction of downstream movement. A clear T_4 surge was observed during downstream migration, suggesting that T_4 plays an important role in the preparation for downstream migration; however, T_4 is not the sole factor identified as responsible for the onset of downstream migration [22, 23]. Ojima and Iwata [24] found that the central administration of GHRH, CRH, melatonin, and N-acetyl serotonin, and serotonin stimulated downstream movements, whereas only GHRH stimulated schooling behavior. In juvenile Chinook salmon *O. tshawytscha*, central administration of CRH was also found to induce downstream movement [25]. In fall-smolting coho salmon *O. kisutch*, central administration of GHRH and CRH stimulated downstream movement and T_4 secretion [26]. In the same species, the levels of TSH β mRNA and TSH in the pituitary, as well as TSH, T_4 and T_3 in plasma, have been assessed and found to show correlations with the PST [27]. In the brain of sockeye salmon, the mRNA encoding the TRH precursor has been studied via in situ hybridization [28], and the expression of cDNA encoding TRH receptor subtypes has been examined [29]. Recently, it was reported that T_3 determines the onset of the sensitive period for imprinting, and that it plays a critical role in later learning

in chicks *Gallus gallus domesticus* [30]. Although the onset of downstream migration, including smoltification, is under the complex regulation of several endocrine hormones, the brain-pituitary-thyroid (BPT) axis should have a critical role in imprinting during downstream migration. My research group is currently investigating the hormone profiles of TRH, TSH, and thyroid hormones in the BPT axis of chum salmon during imprinting migration in association with olfactory memory formation in the brain.

Homing migration

In chum salmon migrating from the Bering Sea to the spawning ground in the Chitose River, Hokkaido, Japan, the hormone profiles in the BPG axis have been measured using specific time-resolved fluoroimmunoassay systems [31]. The level of sGnRH in the olfactory bulbs of both sexes peaks when the fish are located between the coastal area and the river mouth of the Ishikari River, where the olfactory discriminating ability related to the natal stream should be important. Peak sGnRH levels in the telencephalon are observed when the fish are at the branch point of the Chitose River from the Ishikari River, where the olfactory functions should be highly activated. In the pituitary gland, sGnRH levels tend to increase in concert with LH levels in females from the coastal area and in males from the river mouth of the Ishikari River. In contrast, FSH levels do not show any clear correlations with sGnRH levels in the pituitary gland. Although the roles of cGnRH-II in these brain regions are currently unclear, cGnRH-II levels increase in the medulla oblongata of both sexes at their pre-spawning ground, and levels in the optic tectum increase in males. In the diencephalon and cerebellum, cGnRH-II levels show no significant changes during homing migration [21].

Immunoreactive sGnRH neurons exhibiting a pro-sGnRH mRNA signal have been observed in the dorsal olfactory nerve of chum salmon in the coastal area but not in fish at their spawning grounds [32]. Observations of changes in the levels of GTH subunit mRNAs in the pituitary glands of pre-spawning chum salmon show that the levels of GTH $\alpha 2$ and LH β increase when an individual enters freshwater, whereas no changes in the FSH β level are detected [33]. The serum steroid hormone levels in these fish show similar profiles to those observed in previous studies [34, 35]: E₂ levels in females and 11KT levels in males increase during vitellogenesis and spermatogenesis, respectively, while DHP levels increase dramatically at the time of final gonadal maturation in both sexes. Interestingly, sGnRH levels in the telencephalon and serum T levels show a coincidental peak at the branch point of the Chitose River from the Ishikari River in both sexes. These results suggest that sGnRH and cGnRH-II may play brain region-dependent roles in gonadal maturation and homing

migration in chum salmon. Endocrinological studies on hormone profiles in the BPT and BPG axes demonstrate that thyroid hormones and sGnRH play important roles in imprinting and homing migration, respectively. However, it is uncertain how the BPT and BPG hormones may control both the sensory systems and the central nervous systems during imprinting and homing migration, and so the sexually different influence of BPT and BPG hormones on the sensory and central nervous systems of males and females should also be studied.

Neurophysiological study of olfactory imprinting and homing

Since the olfactory hypothesis of salmon imprinting and homing to the natal stream was proposed by Hasler and Wisby [36] and Wisby and Hasler [37], the mechanisms underlying the olfactory imprinting and homing abilities of salmon have been intensively studied [38–48]. The pheromone hypothesis proposed by Nordeng [49, 50] based on studies in Arctic char *Salvelinus alpinus* and Atlantic salmon *Salmo salar* suggests that juvenile salmon in a stream release population-specific odors that guide homing adults. However, there are no juvenile chum salmon or pink salmon *O. gorbuscha* present at the time when the adults return. 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

In early studies, the natal stream odors were used to identify the olfactory bulbar response, and they have suggested that the odors of the natal stream are non-volatile [51–54]. A spectral analysis of the olfactory bulbar response indicated that the natal stream odors are absorbed by activated carbon and ion-exchange resin, insoluble in petroleum-ether, dialyzable, non-volatile, and heat stable [55]. In contrast to the olfactory organs of terrestrial animals, the olfactory organs of fish respond only to a limited number of dissolved chemical species, such as amino acids, steroids, bile acids, and prostaglandins [56].

Shoji et al. [57] analyzed the concentrations of dissolved free amino acids (DFAAs), inorganic cations, and bile acids in waters from three streams that flow into Lake Toya. The application of mixtures of inorganic cations or bile acids to the olfactory epithelium was found to induce only very small responses, whereas the application of mixtures of DFAAs induced large responses. The response to artificial stream water based on the composition of DFAAs and salts closely resembles the response to the corresponding natural stream water. Cross-adaptation experiments were carried out with three combinations of natural and artificial stream

water. Each combination of artificial stream water showed a very similar response pattern to that for the corresponding combination of natural stream water. We proposed that the DFAA composition of the natal stream water likely determines the natal stream odor, but that this odor may change seasonally or annually.

Yamamoto et al. [58] analyzed the concentrations and composition of DFAAs in water from the Teshio River in Hokkaido, Japan, where chum salmon return for spawning, during juvenile downstream migration in spring and adult upstream migration in autumn, in samples collected over a 4-year period. Among the 19 amino acids detected in the Teshio River water, the DFAA concentrations fluctuated greatly, but 5–7 compositions of stable DFAA were found between the spring and autumn samples within the 4-year span. Two types of artificial stream water (ASW) were prepared using the DFAA concentrations found in the Teshio River during the time of juvenile imprinting in spring (jASW) and adult homing in autumn (aASW) over a 4-year period. In behavioral experiments examining selective upstream movement in a 2-choice test tank (Y-maze) consisting of two water inlet arms and one pool, 4-year-old mature male chum salmon captured in the Teshio River showed a significant preference for either jASW or aASW compared to control water, with no preference being observed between jASW and aASW. These findings indicate that the long-term stability of the DFAA composition of natal streams might be crucial for olfactory homing in chum salmon.

Changes in the DFAA composition of stream water are attributed mainly to complicated biological processes in the watershed ecosystem. There are many possible factors affecting the DFAA concentrations in the stream environment, such as the soil, vegetation, litter, pollen, dew, and various microbial activities [59]. Among these factors, the roles of complex microbial communities referred to as biofilms have been intensively investigated [60, 61]. A biofilm consists of various microorganisms and is embedded in a matrix of extracellular polymeric substances. We investigated the origin of DFAAs in stream water focusing on biofilms in the streambed via laboratory incubation experiments. Stones were placed in the Toyohira stream on Hokkaido for 3 months, allowing the formation of biofilms, and then incubated for 24 h in the laboratory at stream-water temperature. After incubation, the composition and concentrations of DFAAs in the incubation solution were measured via high-performance liquid chromatography. The DFAA concentration increased greatly in the biofilm incubation solution in the treatment group, whereas the DFAA composition showed little change after the 24-h incubation, remaining similar to that observed in stream water, suggesting that biofilms are a major source of DFAAs in stream water [62].

New trials of Japanese chum salmon propagation systems

To achieve long-term sustainable chum salmon production in Japan, high rates of both juvenile survival and adult return are crucial. To produce healthy juveniles with high survival rates, a new chum salmon propagation system should be developed by introducing a semi-closed recirculating aquaculture system, estimating the health condition of fish, and improving the olfactory imprinting capability of juvenile chum salmon.

Semi-closed recirculating aquaculture system

In most chum salmon hatcheries in Japan, chum salmon fry are reared by feeding them commercial pellets until they are released into the stream in square concrete ponds. These ponds are supplied with spring water at a constant flow rate of 0.8–1.1 cm/sec, usually creating dead water space at each corner, and are frequently prone to fish diseases, such as bacterial gill disease and ichthyobodosis. Moreover, the shortage of good quality spring water has become a serious problem at hatcheries in Japan [3]. To overcome these problems, we are developing a semi-closed recirculating aquaculture system (RAS) for juvenile chum salmon (Fig. 4). This RAS system consists of a bio-active filtration tank to maintain high-quality water, an air blower in the filtration tank, an ultraviolet sterilization system for the disinfection of water, two water pumps to control water circulation, two Coolnics circulators to control water temperature, and two auto feeders to feed pellets containing bio-active substances, all within an oval-shaped, fiber reinforced plastic (FRP) fish tank. Using this new system, we are now examining the culture of high-quality healthy juvenile chum salmon. Preliminary evaluation of water quality via NH_3 and HNO_2 levels showed no differences between the RAS system and standard salmon hatchery pond water. In addition, preliminary analysis of the growth rates of chum salmon revealed no differences between the RAS system and the standard salmon hatchery pond, suggesting that the RAS does not subject the salmon to chronic stress. We are now investigating the effects of the RAS system on the imprinting ability of juvenile chum salmon.

Estimation of health condition

Mizuno et al. [63, 64] examined the relationship between rearing conditions and the health of juvenile chum salmon using body adenosine triphosphate (ATP) contents and ATP synthesis transcript levels as health parameters and found that these parameters can be used to effectively evaluate the health conditions of juvenile chum salmon. The health conditions of these fish are strongly correlated with their

Fig. 4 A semi-closed aquaculture system for juvenile chum salmon consisting of a bio-active filtration tank, an air blower in the filtration tank, an ultraviolet sterilization instrument, two water pumps, two Coolnics circulators, and two auto feeders, all within an oval-shaped fiber reinforced plastic fish tank

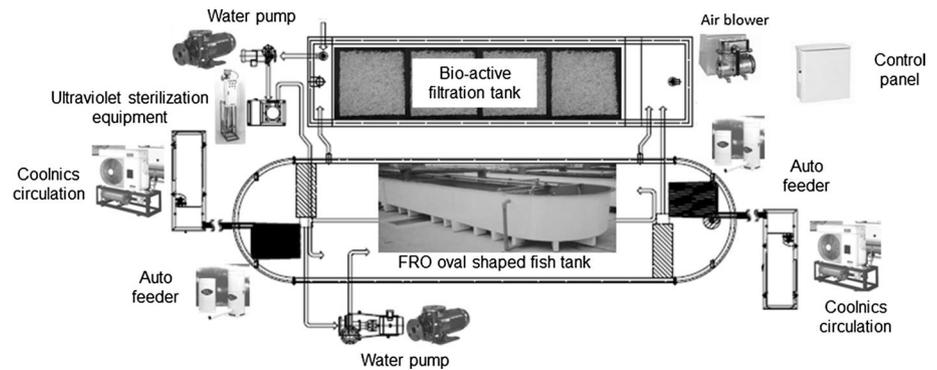
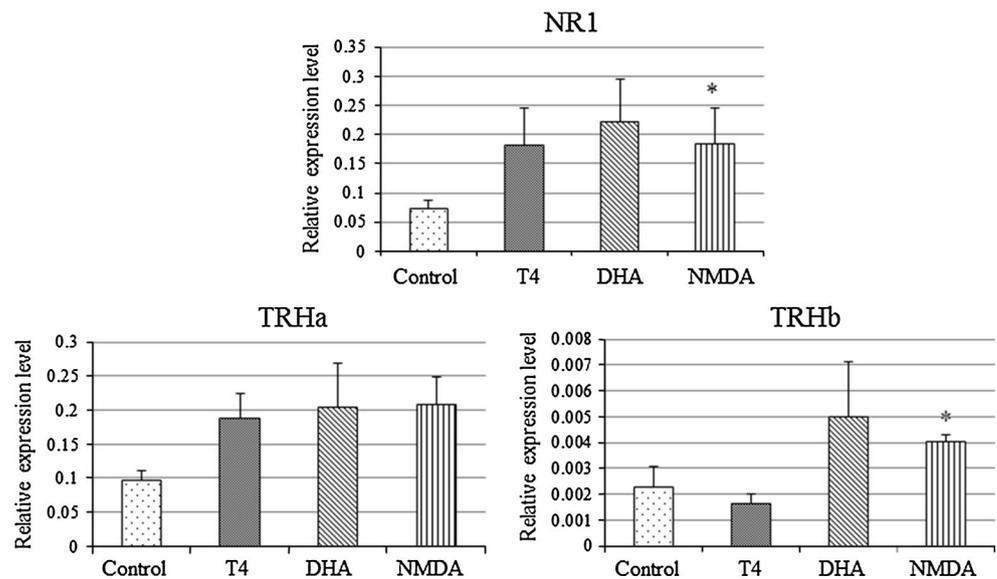


Fig. 5 Preliminary results of the effects of the oral administration of bioactive substances (T_4 , DHA, and NMDA) on gene expression levels of NMDA receptor essential subunit NR1 and TRHa/b in juvenile masu salmon. The asterisk indicates significant difference by the Steel–Dwass test ($*P<0.05$)



metabolism and swimming ability. Improvement of the metabolism and swimming ability of juvenile chum salmon can directly contribute to increased survival rates in coastal areas following downstream migration. Using the RAS system, we are investigating the effects of controlling the water circulation speed on improving the metabolism and swimming ability of juvenile chum salmon.

Improvement of the olfactory imprinting capability

Juvenile chum salmon can imprint the odor of their natal stream during imprinting downstream migration, which may involve the BPT axis. Changes in the BPT axis of juvenile chum salmon during downstream migration are currently being investigated in my laboratory. We are now attempting to improve the olfactory imprinting capability of juvenile chum salmon through oral administration of the following bioactive substances: docosahexaenoic acid (DHA), N-methyl-D-aspartate (NMDA), and thyroid hormone. DHA-linked phospholipids are reported to have the effect of improving memory learning in the mouse

brain [65]. NMDA is involved in the development of neural networks, learning, and memory in chicks [66]. Thyroid hormone determines the onset of the sensitive period for imprinting and plays a critical role in later learning [30]. A trial experiment has been conducted to improve the olfactory imprinting capability of juvenile masu salmon through the oral administration of these three bioactive substances, T_4 , DHA, and NMDA, and the subsequent evaluation of the gene expression levels of NMDA receptor essential subunit NR1 and TRHa/b genes. Preliminary results show that these three bioactive substances enhanced the gene expression levels of the NR1 and TRHa/b genes, with the exception of TRHb by T_4 administration (Fig. 5). These results suggested that these bioactive substances may affect the imprinting ability of juvenile masu salmon. In addition, DHA-administrated juvenile masu salmon have been released from the Shimoakka hatchery in Iwate Prefecture, which was severely damaged by the Tohoku earthquake and tsunami in 2011. We are awaiting the results of adult masu salmon return this fall. New experiments are also underway to evaluate how these bioactive substances affect

the olfactory imprinting ability of juvenile chum and sockeye salmon and adult returns to their natal river.

Conclusions

This review presents an overview of the current propagation system of chum salmon in Japan, physiological studies of Japanese chum salmon, and new trials of Japanese chum salmon propagation systems. Due to enormous efforts to improve juvenile release techniques as well as favorable oceanic environments, the biomass of Japanese chum salmon increased steadily from 1970 to 1996. However, a rapid decrease in returning rates has recently been observed in these fish, likely due to the lack of methods for preventing diseases in juvenile fish and the regime shift in the North Pacific ecosystem. Moreover, the aftermath of the 2011 Tohoku earthquake and tsunami caused severe damage to chum salmon hatcheries in Tohoku. Recent studies on the mechanisms involved in the imprinting and homing abilities of chum salmon have employed three approaches: physiological biotelemetry analyses of homing behavior, endocrinological analyses of hormone profiles during imprinting and homing migration, and neurophysiological analyses of olfactory discrimination abilities. Physiological biotelemetry studies show that salmon can navigate in open water using different sensory systems. Endocrinological studies demonstrate that the BPT and BPG hormones play important roles in imprinting and homing migration, respectively. Neurophysiological studies on olfactory function suggest that a stable DFAA composition in the natal streams is crucial for olfactory imprinting and homing of chum salmon. However, it is unclear how endocrinological changes may control both the sensory system and the central nervous systems. Further integrated studies should be conducted to clarify how these hormonal changes affect imprinting and homing migration in juveniles and adults, respectively. We are now developing the semi-closed RAS system to estimate the health condition and improve the olfactory imprinting capability of juvenile chum salmon. The Japanese chum salmon propagation system is believed to be one of the most successful fish propagation systems in the world. We aim to improve chum salmon propagation systems for long-term sustainable chum salmon production in Japan.

Acknowledgments I would like to thank the following collaborative researchers and students in my laboratory for their valuable contributions to the present study: Y. Naito, H. Tanaka, S. Urawa, H. Kudo, H. Yamada, M. Iwata, A. Urano, T. Shoji, M. Shimizu, S. Yanagi, K. Sato, H. Hino, Y. Yamamoto, S. Ishizawa, H. Bandoh, S. Mizuno, N. Katayama, and N. Koide. Special thanks are due to the Hokkaido National Fisheries Research Institute and the Hokkaido Salmon Propagation Association for providing valuable data for figures. The present study was supported in part by a Grant-in-Aid for

Scientific Research from the Ministry of Education, Culture, Sports, Science and Technology (MEXT), Japan; the Japan Society for the Promotion of Science (JSPS); Japan Science and Technology Agency (JST); the Hokkaido Foundation for the Promotion of Scientific and Industrial Technology; the Mitsubishi Foundation; the Mitsui & Co. Ltd, and Hokkaido University.

References

1. Akiba T (1988) Cultural history of salmon. The Hokkaido Shim-bun Press, Sapporo (In Japanese)
2. Nogawa H (2010) Development of artificial salmon propagation in Japan. *J Fish Technol* 3:1–8 (In Japanese with English abstract)
3. Seki J (2013) Development of hatchery techniques for releasing juvenile chum salmon in Japan. *J Fish Technol* 6:69–82 (In Japanese with English abstract)
4. Kaeriyama M, Seo H, Qin Y (2014) Effects of global warming on the life history and population dynamics of Japanese chum salmon. *Fish Sci* 80:251–260
5. Seo H, Kudo H, Kaeriyama M (2011) Long-term climate-related changes in somatic growth and population dynamics of Hokkaido chum salmon. *Environ Biol Fish* 90:131–142
6. Kitada S (2014) Japanese chum salmon stock enhancement: current perspective and future challenges. *Fish Sci* 80:237–249
7. Urawa S (2003) Stock identification studies of high seas salmon in Japan: a review and future plan. *N Pac Anadr Fish Comm Tech Rep* 5:9–10
8. Quinn TP, Groot C (1984) Pacific salmon (*Oncorhynchus*) migrations: orientation vs. random movement. *Can J Fish Aqua Sci* 41:1319–1324
9. Quinn TP, Terjart BA, Groot C (1989) Migratory orientation and vertical movements of homing adult sockeye salmon, *Oncorhynchus nerka*, in coastal waters. *Anim Behav* 37:587–599
10. Ogura M, Ishida Y (1994) Homing behavior and vertical movements of four species of Pacific salmon (*Oncorhynchus* spp.) in the central Bering Sea. *Can J Fish Aquat Sci* 52:532–540
11. Yano K, Nakamura A (1992) Observations of the effect of visual and olfactory ablation on the swimming behavior of migrating adult chum salmon, *Oncorhynchus keta*. *Jpn J Ichthyol* 39:67–83
12. Yano A, Ogura M, Sato A, Sakaki Y, Ban M, Nagasawa K (1996) Development of ultrasonic telemetry technique for investigating the magnetic sense of salmonids. *Fish Sci* 62:698–704
13. Tanaka H, Naito Y, Davis ND, Urawa S, Ueda H, Fukuwaka M (2005) Behavioral thermoregulation of chum salmon during homing migration in coastal waters. *Mar Ecol Prog Ser* 291:307–312
14. Ueda H (2004) Recent biotelemetry research on lacustrine salmon homing migration. *Mem Nat Inst Polar Res Spec Issue* 58:80–88
15. Walker MM, Diebel CE, Haugh CV, Pankhurst PM, Montgomery JC, Green CR (1997) Structure and function of the vertebrate magnetic sense. *Nature* 390:371–376
16. Putman NF, Lohmann KJ, Putman EM, Quinn TP, Klimley AP, Noakes DLG (2013) Evidence for geomagnetic imprinting as a homing mechanism in Pacific salmon. *Curr Biol* 23:312–316
17. Putman NF, Scanlan MM, Billman EJ, O’Neil JP, Couture RB, Quinn TP, Lohmann KJ, Noakes DLG (2014) An inherited magnetic map guides ocean navigation in juvenile Pacific salmon. *Curr Biol* 24:1–5
18. Hasegawa EI (2012) Chum salmon *Oncorhynchus keta* respond to moonlight during homeward migration. *J Fish Biol* 81:632–641
19. Björnsson BT, Stefansson SO, McCormick SD (2011) Environmental endocrinology of salmon smoltification. *Gen Comp Endocrinol* 170:290–298
20. Björnsson BT, Einarsdottir IE, Power D (2012) Is salmon smoltification an example of vertebrate metamorphosis? Lessons

- learnt from work on flatfish larval development. *Aquaculture* 362–363:264–272
21. Ueda H (2011) Physiological mechanisms of homing migration in Pacific salmon from behavioral to molecular biological approaches. *Gen Comp Endocrinol* 170:222–232
 22. Iwata M, Tsuboi H, Yamashita T, Amemiya A, Yamada H, Chiba H (2003) Function and trigger of thyroxine surge in migrating chum salmon *Oncorhynchus keta* fry. *Aquaculture* 222:315–329
 23. Ojima D, Iwata M (2007) The relationship between thyroxine surge and onset of downstream migration in chum salmon *Oncorhynchus keta* fry. *Aquaculture* 273:185–193
 24. Ojima D, Iwata M (2009) Central administration of growth hormone-releasing hormone triggers downstream movement and schooling behavior of chum salmon (*Oncorhynchus keta*) fry in an artificial stream. *Comp Biochem Physiol Part A* 152:293–298
 25. Clements S, Schreck CB (2004) Central administration of corticotropin-releasing hormone alters downstream movement in an artificial stream in juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Gen Comp Endocrinol* 137:1–8
 26. Ojima D, Iwata M (2010) Central administration of growth hormone-releasing hormone and corticotropin-releasing hormone stimulate downstream movement and thyroxine secretion in fall-smolting coho salmon (*Oncorhynchus kisutch*). *Gen Comp Endocrinol* 168:82–87
 27. Larsen DA, Swanson P, Dickhoff WW (2011) The pituitary-thyroid axis during the parr-smolt transformation of coho salmon, *Oncorhynchus kisutch*: quantification of TSH β mRNA, TSH, and thyroid hormones. *Gen Comp Endocrinol* 171:367–372
 28. Ando H, Ando J, Urano A (1998) Localization of mRNA encoding thyrotropin-releasing hormone precursor in the brain of sockeye salmon. *Zool Sci* 15:945–953
 29. Saito Y, Mekuchi M, Kobayashi N, Kimura M, Aoki Y, Masuda T, Azuma T, Fukami M, Iigo M, Yanagisawa T (2011) Molecular cloning, molecular evolution and gene expression of cDNAs encoding thyrotropin-releasing hormone receptor subtypes in a teleost, the sockeye salmon (*Oncorhynchus nerka*). *Gen Comp Endocrinol* 174:80–88
 30. Yamaguchi S, Aoki N, Kitajima T, Iikubo E, Katagiri S, Matsushima T, Homma K (2012) Thyroid hormone determines the start of the sensitive period of imprinting and primes later learning. *Nat Commun* 3:1081
 31. Yamada H, Amano M, Okuzawa K, Chiba H, Iwata M (2002) Maturation changes in brain contents of salmon GnRH in rainbow trout as measured by a newly developed time-resolved fluoroimmunoassay. *Gen Comp Endocrinol* 126:136–143
 32. Kudo H, Hyodo S, Ueda H, Hiroi O, Aida K, Urano A, Yamauchi K (1996) Cytophysiology of gonadotropin-releasing-hormone neurons in chum salmon (*Oncorhynchus keta*) forebrain before and after upstream migration. *Cell Tissue Res* 284:261–267
 33. Kitahashi T, Ando H, Ban M, Ueda H, Urano A (1998) Changes in the levels of gonadotropin subunit mRNAs in the pituitary of pre-spawning chum salmon. *Zool Sci* 15:753–760
 34. Ueda H, Hiroi O, Hara A, Yamauchi K, Nagahama Y (1984) Changes in serum concentrations of steroid hormone, thyroxine, and vitellogenin during spawning migration of chum salmon, *Oncorhynchus keta*. *Gen Comp Endocrinol* 53:203–211
 35. Ueda H (1999) Artificial control of salmon homing migration and its application to salmon propagation. *Bull Tohoku Nat Fish Res Inst* 62:133–139
 36. Hasler AD, Wisby WJ (1951) Discrimination of stream odors by fishes and relation to parent stream behavior. *Am Nat* 85:223–238
 37. Wisby WJ, Hasler AD (1954) Effect of olfactory occlusion on migrating silver salmon (*Oncorhynchus kisutch*). *J Fish Res Board Can* 11:472–478
 38. Hasler AD, Scholz AT (1983) Olfactory imprinting and homing in salmon. Springer, New York
 39. Døving KB (1989) Molecular cues in salmonid migration. In: Maruani J (ed) *Molecules in physics, chemistry, and biology*. Kluwer Academic Publishers, Amsterdam, pp 299–329
 40. Stabell OB (1992) Olfactory control of homing behaviour in salmonids. In: Hara TJ (ed) *Fish chemoreception*. Chapman and Hall, London, pp 249–270
 41. Dittman AW, Quinn TP (1996) Homing in Pacific salmon: mechanisms and ecological basis. *J Exp Biol* 199:83–91
 42. Bertmar G (1997) Chemosensory orientation in salmonid fishes. *Adv Fish Res* 2:63–80
 43. Nevitt GA, Dittman AH (1998) A new model for olfactory imprinting in salmon. *Integr Biol* 1:215–223
 44. Quinn TP (2005) *The behavior and ecology of Pacific salmon and trout*. University of Washington Press, Seattle
 45. Ueda H, Yamamoto Y, Hino H (2007) Physiological mechanisms of homing ability in sockeye salmon: from behavior to molecules using a lacustrine model. *Am Fish Soc Symp* 54:5–16
 46. Hino H, Miles NG, Bandoh H, Ueda H (2009) Molecular biological research on olfactory chemoreception in fishes. *J Fish Biol* 75:945–959
 47. Ueda H (2012) Physiological mechanisms of imprinting and homing migration in Pacific salmon *Oncorhynchus* spp. *J Fish Biol* 81:543–558
 48. Ueda H (2014) Homing ability and migration success in Pacific salmon: mechanistic insights from biotelemetry, endocrinology, and neurophysiology. *Mar Ecol Prog Ser* 496:219–232
 49. Nordeng HA (1971) Is the local orientation of anadromous fishes determined by pheromones? *Nature* 233:411–413
 50. Nordeng HA (1977) A pheromone hypothesis for homeward migration in anadromous salmonids. *Oikos* 28:155–159
 51. Fagerlund UHM, McBridge JR, Smith M, Tomlinson N (1963) Olfactory perception in migrating salmon III. Stimulants for adult sockeye salmon (*Oncorhynchus nerka*) in home stream waters. *J Fish Res Board Can* 20:1457–1463
 52. Cooper JC, Lee GF, Dizon AE (1974) An evaluation of the use of the EEG technique to determine chemical constituents in homestream water. *Trans Wis Acad Sci Arts Lett* 62:165–172
 53. Cooper JC, Scholz AT, Horrall RM, Hasler AD, Madison DM (1976) Experimental confirmation of the olfactory hypothesis with artificially imprinted homing coho salmon (*Oncorhynchus kisutch*). *J Fish Res Board Can* 33:703–710
 54. Bodznick D (1978) Calcium ion: an odorant for natural water discriminations and the migratory behavior of sockeye salmon. *J Comp Physiol* 127:157–166
 55. Ueda K (1985) An electrophysiological approach to the olfactory recognition of homestream waters in chum salmon. *NOAA Tech Rep NMFS* 27:97–102
 56. Hara TJ (1994) The diversity of chemical stimulation in fish olfaction and gustation. *Rev Fish Biol Fish* 4:1–35
 57. Shoji T, Ueda H, Ohgami T, Sakamoto T, Katsuragi Y, Yamauchi K, Kurihara K (2000) Amino acids dissolved in stream water as possible homestream odorants for masu salmon. *Chem Senses* 25:533–540
 58. Yamamoto Y, Shibata H, Ueda H (2013) Olfactory homing of chum salmon to stable compositions of amino acids in natal stream water. *Zool Sci* 30:607–612
 59. Thomas JD (1997) The role of dissolved organic matter, particularly free amino acids and humic substances, in freshwater ecosystems. *Fresh Biol* 38:1–36
 60. Costerton JW, Lewandowski Z, DeBeer D, Caldwell D, Korber D, James G (1994) Biofilms, the customized microniche. *J Bacteriol* 176:2137–2142
 61. Nosyk O, Haseborg ET, Metzger U, Frimmel FH (2008) A standardized pre-treatment method of biofilm flocs for fluorescence microscopic characterization. *J Microbiol Methods* 75:449–456

62. Ishizawa S, Yamamoto Y, Denboh T, Ueda H (2010) Release of dissolved free amino acids from biofilms in stream water. *Fish Sci* 76:669–676
63. Mizuno S, Nakajima M, Naito K, Koyama T, Saneyoshi H, Kobayashi M, Koide N, Ueda H (2010) Physiological impacts on high rearing density on chum salmon *Oncorhynchus keta* fry. *Aquacult Sci* 58:387–399
64. Mizuno S, Hatakeyama M, Nakajima M, Naito K, Koyama T, Saneyoshi H, Kobayashi M, Koide N, Misaka N, Ueda H (2010) Relationship between rearing condition and health in chum salmon (*Oncorhynchus keta*) fry. *Aquacult Sci* 58:529–531
65. Hiratsuka S, Koizumi K, Ooba T, Yokogoshi H (2009) Effects of dietary docosahexaenoic acid connecting phospholipids on the learning ability and fatty acid composition of the brain. *J Nutr Sci Vitaminol* 55:374–380
66. Nakamori T, Maekawa F, Sato K, Tanaka K, Ohki-Hamazaki H (2013) Neural basis of imprinting behavior in chicks. *Dev Growth Differ* 55:198–206