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Mechanisms of Homing in Salmonids

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Abstract—The article reviews modern concepts of the significance and mechanisms of homing and its complementary straying in salmonids. Homing is a fundamental, highly adaptive characteristic of salmon behavior. An intraspecific population structure formed in salmon on its basis, and it includes a great number of reproductively isolated populations, among which a small-scale migration is possible via straying. Straying allows salmon to colonize new habitats and recolonize empty ones after extinction of the local populations. The homing ability became the basis for large-scale artificial salmon reproduction. The following physiological mechanisms of homing are considered: the primary role of olfaction and the process of sequential imprinting of olfactory stimuli of a natal river which occurs in juveniles, mainly during the smoltification period, as well as in the earlier stages of life and during downstream migration; the use of olfactory "memory" by adult fish returning to spawn; the role of hormonal regulation in the imprinting process in juveniles and homing migration of adult fish. Data on the molecular and genetic bases of olfactory chemoreception are presented. It is shown that the rates of homing (and straying) vary among species and among populations of the same species, depending on their biological and ecological features, on a variety of environmental factors and conditions, and anthropogenic impact. The negative effects of straying of farmed and hatchery salmon into natural populations are discussed.

Keywords: homing, straying, olfactory imprinting, hormonal regulation, salmonids
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INTRODUCTION

Salmonids, Atlantic (the genus *Salmo*) and Pacific (the genus *Oncorhynchus*) salmon, char (the genus *Salvelinus*) and other closely related groups reproduce in fresh water of rivers and lakes, where their embryogenesis, larval and juvenile stages of development occur over several months or longer. The juvenile stage in pink salmon, chum salmon, and some populations of other species is short; in other species, it lasts from a year to several years and is completed when juveniles migrate to the ocean for feeding. In most species, except for pink and chum salmon, there are natural populations that stay in fresh water through their life (nonanadromous or resident forms). After feeding migrations in the ocean, anadromous salmon return to spawn to the same fresh water bodies where they were born (Ricker, 1972; Groot and Margolis, 1991; Altukhov et al., 1997; Hendry et al., 2004).

The ability to return to natal sites for reproduction, so-called homing or home instinct, is a fundamental behavioral trait of salmonids that is especially pronounced in them (Hasler and Scholz, 1983; Stabell, 1984), though many zoological species, particularly those associated with migrations, e.g., migratory birds, sea turtles, pinnipeds and many others, are known to have different degrees of this ability (Yablokov, 1987; Sokolov, 1991; Altukhov and Salmenkova, 1994; Pess, 2009). The alternative to exact homing is straying, i.e., the return not to the natal sites but to nonnatal waterbodies for reproduction. Homing is a highly adaptive feature that enhances salmon fitness, because, the return of adult fish to the natal site for spawning makes it possible to find mates and to locate in habitats favorable for reproduction and survival of juveniles (Quinn, 1993, 2005). Due to homing a great number of reproductively isolated (to a great extent), locally adapted populations that maximally use diverse conditions of the ranges have been formed in vast spawning areas of salmonids (Ricker, 1972; Konovalov, 1980; Altukhov et al., 1997; Waples et al., 2001). The homing ability is the basis for large-scale artificial salmon reproduction with the release of juveniles to natural waterbodies, from which they migrate to the open ocean and return as adults to "natal" streams, i.e. salmon hatcheries, to spawn. Straying in natural salmon populations, which is usually estimated as a small percentage of the total abundance of the return, is also a natural behavioral characteristic of salmon and is of great importance in their biology and evolution, thus supplementing homing. Straying makes it possible to buffer to a certain degree against

Table 1. Mean estimates of straying rates in salmon populations according to Pess, 2009; Keefer and Caudill, 2012

Species	Pess, 2009	Keefer and Caudill, 2012
Chum salmon *Oncorhynchus keta*	19.1	28.4
Pink salmon *O. gorbuscha*	15.4	8.4
Sockey salmon *O. nerka*	0.8	2.4
Coho salmon *O. kisutch*	7.8	9.8
Spring Chinook salmon (stream-type) *O. tshawytscha*	6.2	3.4
Fall Chinook salmon (ocean-type) *O. tshawytscha*	–	34.9
Steelhead *O. mykiss*	7.7	13.8
Atlantic salmon *Salmo salar*	7.7	10.1

unfavorable changes in habitat quality and to preserve the population; it enables colonization of new habitats (Bakhstansky, 1980; Milner and Bailey, 1989; Thorpe, 1994; Burger et al., 1997; Quinn et al., 2001) and recolonization of former habitats after the extinction of local populations (Withler, 1982; Pess, 2009; Pess et al., 2012). Quinn (1984) suggested considering straying and homing as evolutionary alternatives of the species: homing provides its maximal adaptation to a relatively stable environment, and straying allows species distribution and the avoidance of a catastrophically changing environment. There is a dynamic equilibrium between both types of life strategy, homing and straying, with the dominance of homing.

STRAYING RATES

The rate of straying decreases in a stable environment and increases in an unstable one. It varies within and among populations as a reaction to habitat stability. This is shown by experimental estimates of straying or homing rates obtained by different methods of juvenile tagging and the subsequent record of tagged fish return to the release site and to waterbodies of the nearby region. Fish tagging usually involves the procedure of cutting off a fin or a combination of fins, the use of parasitic marks, coded wire tags (CWTs), thermal marks in otoliths, genetic markers (e.g. allozymes and microsatellites) (Nielson, 1992). Estimates of straying range from a tenth of a percent to several tens of percents for different species and populations of salmon (Altukhov et al., 1997; Hendry et al., 2004; Pess, 2009; Keefer and Caudill, 2012, 2014) (Table 1). The authors report that the comparison of straying rates between different salmon species is not entirely correct, because the studies were conducted in different years, different streams, different spatial scales, and mainly under the conditions of hatcheries, but the artificial reproduction of salmon, especially when it involves the transplantation of eggs and juveniles between different hatcheries, usually enhances straying (Quinn, 1993; Keefer and Caudill, 2014). According to Pess (2009), estimates of homing for different salmon species and populations average 92% (S.D. ± 9.4%), while straying estimates average 8% (S.D. ± 9.5%); the minimum straying rates based on practically all estimates are typical for sockeye salmon, and the maximum straying rates are typical for ocean-type chinook salmon according to Table 1. It follows from the above that the estimates in natural populations may be somewhat different due to more precise homing and lower straying.

Many authors (Quinn, 1993; Thorpe, 1994; Hendry et al., 2004; Keefer and Caudill, 2014) report that pink and chum salmon have higher straying rates than other species of Pacific and Atlantic salmon. However, we should pay attention to the data from some authors that demonstrate rather strict homing in some populations of these species (Klyashtorin, 1989; Omelchenko and Vyalova, 1990; Mathisen, 1994; Gharret et al., 2001; Churikov and Gharret, 2002). Table 2 presents additional experimental estimates of straying for chum and pink salmon that confirm the above statements. It can be suggested that the especially high rates of straying obtained for American populations of chum and pink salmon are particularly due to the spawning of many of them in an unstable tidal zone of river estuaries (Brenner et al., 2012).

It should be taken into account that straying as physical migration always exceeds genetic migration (Altukhov et al., 1997; Hendry et al., 2004). For example, the gene exchange between two populations of sockeye salmon as estimated with allozyme markers proved to be less than 1%, which corresponded to the lowest estimates of straying obtained with parasites as biological markers (Quinn et al., 1987). The study of interaction between three populations of chum salmon demonstrated that the rate of straying of tagged fish was by an order of magnitude higher than gene flow (Tallman and Healey, 1994) (Table 2). In the authors' opinion, this indicates the lower reproductive success of "alien" fish.

Though direct estimates of the heritability of homing and straying behavior within the population are unknown, several facts and studies indicate the presence of a hereditary component (Hendry et al., 2004). Thus, successful homing is directly associated with the period of anadromous migration and sexual matura-

Table 2. Straying estimates of chum and pink salmon populations

Species	Straying estimates, %	Locality	Reference
Chum salmon *O. keta*	2–10	Hokkaido, Japan	Sakano, 1960 (cited according to Okazaki, 1982)
	5.3	British Columbia, Canada	McQuarrie and Bailey, 1980 (cited according to Quinn, 1980)
	0.2	Southeast Alaska	Smoker and Thrower, 1995
	37.9 (17.6–54.0)	Vancouver Island, British Columbia	Tallman and Healey, 1994: (1) CWT tagging method, (2) method of estimation of the genetic migration according to the data of allozyme analysis
	5	–	
Pink salmon *O. gorbuscha*	3–4	British Columbia, Canada	Bams, 1976
	0.1–11.5	Hatchery that did not transported alien eggs, Kuril Islands, Russia	Omelchenko and Vyalova, 1990
	34.1	Prince William Sound	Habicht et al., 1998 (cited according to Hendry et al., 2004
	3.4–7.1	Prince William Sound, Alaska	Wertheimer et al., 2000
	8–9	Lake Auke basin, Alaska	Gharrett et al., 2001
	4–7	Lake Auke basin, Alaska	Mortensen et al., 2002
	5.1 (3.7–9.2)	Southeast Alaska	Thedinga et al., 2000

tion, which are inheritable features (Hendry and Day, 2005; Quinn et al., 2011), so homing should has also certain hereditary basis (Keefer and Caudill, 2014). Bams (1976) compared the rates of homing (1) in the progeny of pink salmon transplanted from a distant river, (2) in the progeny of hybrid stock created by crossing females from the donor with males of the native stock, and (3) in the progeny of the native stock. The homing of pink salmon hybrids was found to be lower than that of native population but higher than in the pure transplanted group. The author concluded that the homing precision is controlled genetically. According to the data of Candy and Beacham (2000), the hybrids of native and transplanted Chinook salmon were three times more to stray than fish of the native population. The progeny of transplanted populations also strayed to the donor river for transplantation, from which there was no release. The other publication (McIsaak and Quinn, 1988) demonstrated that progeny of Chinook salmon from the natal population, which was reared and released from a hatchery, homed not only to the release site but to the spawning area of their ancestral population.

PHYSIOLOGICAL BASES OF HOMING

The homing of anadromous salmon species includes two stages: (1) a marine stage when salmon migrate for reproduction from feeding regions in the open ocean to the coastal areas to the mouths of their natal rivers, and (2) a fresh water stage, when salmon migrate upstream the natal river or to the tributaries of the river to the sites where they were born. It is suggested that salmon migrating to spawning areas are capable of using different natural cues for navigation in the open sea: rheotaxis with respect to a current flow, the Sun's position, polarized light patterns, the Earth's magnetic field and possibly other cues (Hansen et al., 1993; Dittman and Quinn, 1996; Quinn, 2005; Putman et al., 2013). Moreover, salmon must have a precise biological clock to calculate the timing of migration from feeding sea areas to natal rivers and from river mouths to spawning grounds (Ueda, 2012). It is still unknown which sensory systems play a crucial role in orientation in the open sea. With respect to orientation by the Earth's magnetic field, there is information that the olfactory system of salmon has cells containing magnetite crystals. Magnetite is an iron oxide with the chemical formula Fe_3O_4, which is the most magnetic of all naturally occurring minerals (Walker et al., 1988; Ogura et al., 1992). The ability to sense the Earth's magnetic field in salmon, as well as in other animals, is due to the connection of magnetite with ion channels in receptor cells of the olfactory system, where the geomagnetic information is converted into nerve signals. It is shown that, during the spawning migration from the ocean to the Frazer River around Vancouver Island, sockeye, salmon use either the northern or southern route depending on changes in the drifting magnetic field in the region (Putman et al., 2013).

The freshwater phase of salmon homing has been more extensively studied than the marine phase. When salmon reach the natal river, orientation mechanisms change simultaneously with changes in physiology, endocrine system, metabolism, behavior, etc. (Hasler and Scholtz, 1983; Dittman and Quinn, 1996). Numerous studies have proved that olfaction plays the primary role in the homing mechanism (Wisby and Hasler, 1954; Hasler and Scholtz, 1983; Dittman and Quinn, 1996). Hasler and Wisby (1951) hypothesized the occurrence of olfactory imprinting of odors of the natal river in juvenile salmon on the basis of experiments demonstrating that fish may differentiate between water of different streams with the sense of odors. The hypothesis postulated that (1) rivers differ in time-stable chemical properties; (2) salmon are able to recognize these differences; (3) salmon imprint on chemical properties of natal rivers before and during the downstream migration (from river to sea), memorize them during oceanic migrations, and respond to them when returning to spawn as adults.

Hasler and Scholtz (1983) suggested that processes of olfactory learning and homing are closely related to the level of hormones at different life stages. They established experimentally that the imprint of odors of the natal river in the juvenile coho salmon *Oncorhynchus kisutch* is more effective during the especially sensitive period of smoltification before the seaward migration, when parrs (the stage of juvenile fish before downstream migration) are transformed into smolts (the stage of juveniles during downstream migration) (parr–smolt transformation) . At the stage of smoltification, a very deep reorganization of fish physiology and behavior occurs, which prepares juveniles for the transition from freshwater to marine life. These processes are directly associated with the release of thyroid hormones, thyroxine and triiodothyronine, into the blood; they play a role in enhancing olfaction and are involved in olfactory imprinting (Hasler and Scholtz, 1983; Dickhoff and Sullivan, 1987). The activity of the thyroid gland in vertebrates is controlled by pituitary, and thyroid hormones regulate different processes from the rate of metabolism, growth, and maturation to neuron generation including the peripheral olfactory system (Dittman and Quinn, 1983). Kudo et al. (1994) showed that the olfactory epithelium in the masu salmon *Oncorhyncus masou* becomes enriched with thyroid hormone receptors during smolting as compared to the parr. Thus, surges of thyroid hormones in juvenile salmon stimulate cell growth of the olfactory epithelium in the nasal cavity and the development of olfactory receptor neurons facilitating olfactory imprinting (Nevitt et al., 1994).

Unlike the relatively stable experimental conditions under which the data on the role of the smoltification period in imprinting were obtained, the natural conditions encountered by wild salmon during their life history can strongly vary over time. So, natural processes of imprinting, as well as thyroid hormone surges caused by different environmental variations, are not single-phase but are distributed in time and develop as the memorization of a series of sequential olfactory signals.

In this way a sequential imprinting characteristic of natural conditions is formed. Dittman and Quinn (1996) consider the formation of imprinting in wild salmon as a complex system that varies in accordance with spatial and thermal differences of juvenile migration in different species and populations. The activity of the thyroid system, which participates in imprinting, is subject to the effect of different signals, both from endogenous processes of fish development (including smoltification) and from the environment. In the course of downstream migration, surges of thyroid hormones in juveniles occur as a response to such environmental factors as temperature and seasonal variations, photoperiod, current velocity, etc. All of these factors provide a complex relationship between juvenile migration, thyroxine level, and imprinting. As a result wild salmon have a flexible system of imprinting with which they imprint on key freshwater cues in certain moments associated both with endogenous development and with juvenile migration (Dittman and Quinn, 1996).

The process of sequential imprinting in some populations, e.g., in resident forms or in such species as pink and chum salmon with a very short period of smoltification, begins at earlier stages of the life. When returning to spawn, adult fish orient to a sequential (in reverse order) series of odors. The sequential imprinting theory is consistent with the finding that hatchery juveniles released away from their rearing site tend to return to the point of their release (Donaldson and Allen, 1957; Solazzi et al., 1991). However, the closer these sites are to each other, the higher percentage of adult fish that return to their rearing site, because olfactory signals from this site may be detected by returning fish (Johnson et al., 1990).

In addition to thyroid hormones, other hormones are involved in imprinting formation in juveniles. As it is stated above, the processes of imprinting are directly associated with smoltification, so the hormones regulating smoltification such as insulin, growth hormone, cortisol, and other stress hormones directly or indirectly influence the process of imprinting (Dickhoff and Sullivan, 1987; McCormic et al., 1998; McCormic, 2009). In hatchery environments, the intensity of many hormonal and physiological processes is reduced in reared juveniles (Bjørnsson et al., 2011), which disrupts imprinting, weaken homing of returning adults and enhance straying.

NATURE OF OLFACTORY SIGNALS

To date, there is an opinion that not only the unique chemical composition of water at natal sites and along routes of downstream migration but specific substances secreted by juveniles of particular populations in their habitats, i.e., pheromones, act as olfactory signals imprinted by juveniles and are detected by adults that return for spawning (Keefer and Caudill, 2014). A pheromone hypothesis of homing was proposed by Nordeng (1977), who suggested that salmon of the species *Salmo* and *Salvelinus* returning to spawn detect the odor of pheromones released by juveniles of their populations. However, this hypothesis did not explain the homing of the species and populations of salmon, in which juveniles have already performed seaward migrations before the adult return. At present, the pheromone hypothesis is a complementary part of the general theory of olfactory imprinting and homing (Keefer and Caudill, 2014).

Electrophysiological experiments were conducted to record the response of the olfactory bulb in the fish brain in order to identify the chemical substances creating the odor of the natal river (Hara et al., 1965; Groot et al., 1986). The olfactory organs of salmon responded to such dissolved chemicals as amino acids, bile salts, steroids, nucleotides, and prostaglandins. Salmon olfaction was the most sensitive to amino acids (Yamamoto et al., 2010; Ueda, 2011). The response to artificial stream water with dissolved free amino acids closely resembled the response to natural stream water. The composition of dissolved free amino acids in the natal river water is proposed to be natal stream odors for fish (Ueda, 2012). The specific composition of dissolved free amino acids in the stream water is mainly associated with complex biological processes in the ecosystem of the stream. The composition and concentration of dissolved free amino acids in a watercourse are determined by the influence both of internal and external factors such as soil, vegetation, geological structure, and the activity of different microbes (Thomas, 1997). The role of microbial communities turned out to be especially important: they form the so-called biofilms, which are the main source of dissolved free amino acids in stream water, as was demonstrated by special studies (Ishizawa et al., 2010).

OLFACTORY CHEMORECEPTION AND THE GENES ASSOCIATED WITH IT

Aquatic chemical cues are received by fish through nares and nasal cavities, each of which contain an olfactory organ, the olfactory rosette (Johnstone et al., 2012). Like other vertebrates, the olfactory epithelium of the fish olfactory rosette contains numerous sensory neurons, each of which expresses one olfactory receptor (OR). The OR is a special protein structure in the neuron membrane. Olfactory receptors belong to the superfamily of G-protein-coupled receptors, which have seven alfa-helix transmembrane (extending across the neuron cell membrane) regions or domains. In fish, they are coded by 100–200 genes, which is five to ten times smaller than that of mammalian species (Alioto and Ngai, 2005). Sensory neurons have thin projections, axons or olfactory tracts, that transmit primary sensory information to the glomerular layer of the olfactory bulb in the brain. There are three types of sensory neurons that discriminate odors in the olfactory rosette: ciliated, microvillous, and crypt cells. ORs are localized in the membranes of cilia and microvilli. The olfactory chemoreception is realized by odorant binding to the OR and transmission of the signal (which is transduced into the electric signal via a cascade of biochemical reactions) into the olfactory bulb in the brain, where the information is memorized (Nevitt and Dittman, 1999). In the opinion of these authors, the olfactory imprinting suggests information preservation not only in the brain but in neurons of the nasal epithelium as well; the latter is considered "peripheral memory."

There are four types of olfactory receptors in fish: the main ORs (MORs), which are expressed in ciliated olfactory receptor cells; vomeronasal ORs (VORs) of two types (V1R and V2R, which are expressed in microvillous olfactory receptor cells (Hino et al., 2009); and trace amino-associated receptors (TAARs), for which very little data are available (Hussain et al., 2009). MORs, V1Rs, and V2Rs are coded by the *mor* gene families; the V1R-like genes are called *ora* and the V2R-like genes are named *olf.* Several studies used biochemical and genomic techniques to identify and characterize the genes of olfactory receptors and some related proteins (Wickens et al., 2001; Dukes et al., 2006; Morinishi et al., 2007; Johnstone et al., 2012).

Thus, Johnstone et al. (2012) identified the genes of olfactory receptors in the Atlantic salmon *Salmo salar* and studied their genomic organization. As a rule, each receptor type is coded by gene families that include both functional genes and pseudogenes. In addition to the group of *ora* genes, 48 *mor* genes were identified in *S. salar*, 24 of which appeared to be pseudogenes. Earlier, Duke et al. (2006) identified 16 *mor* genes and 10 *olf* genes in the same salmon species. In another study, Johnstone et al. (2011) demonstrated significantly higher expression of seven *olf* genes in juvenile anadromous *S. salar* than in adults, which suggests their potential role in imprinting; such expression was not found in the nonanadromous population. The regulation of these genes in the anadromous population is probably linked to physiological processes of smoltification and environmental cues, but it is still unknown how such regulation occurs in nonanadromous populations.

In the olfactory system of the sockeye salmon *O. nerka*, N24 specific protein was identified in sensory neurons and olfactory bulb cells (Shimizu et al., 1993). It has been established that this protein is homologous to glutathione S-transferase enzyme and the transcryptome analysis showed that N24 mRNA is expressed in the olfactory epithelium (Kudo et al., 1999). The functional role of N24 protein during homing is still unclear, but it is suggested that the protein participates in neuromodulation in the olfactory bulb. Hino et al (2007) identified the salmon olfactory imprinting–related gene (*soig*) in the olfactory system of sockeye salmon at the smoltification stage. The expression level of *soig* mRNA in sockeye salmon was higher at the larval stage than at the embryonic stage. The expression of *soig* mRNA in the olfactory epithelium of the chum salmon *O. keta* was higher during homing migration to estuaries and the approach to spawning areas. The exact function of this gene is still unclear, but it is suggested that it may be related to olfaction and cell proliferation in the olfactory system during smoltification and at the final stage of homing (Hino et al., 2009).

ROLE OF THE OLFACTORY SYSTEM AND HORMONES IN ADULT HOMING

Different hormones are involved in the homing migration of adult salmon. The transition from marine to freshwater habitats causes reorganization of the physiological state of the organism associated with the processes of osmo- and ionoregulation, sexual maturation, feeding termination, and the development of secondary sexual traits. During this period the olfactory sensitivity is enhanced. All of these processes are hormone-regulated. The stress hormones, cortisol and other glucocorticoids, play a role in olfactory stimulation, recognition, and recall of the imprinted memory of odors in fish migrating to spawn (Carruth et al., 2002). During this period the enhancement of the olfactory sensitivity is also related to the reproductive hormone gonadotropin (Fitzpatrick et al., 1986) and the guanylyl-cyclase enzyme (Dittman et al., 1997). Gonadotropin regulates gonadal maturation; at the same time, it is increased in the olfactory bulb and other brain regions associated with olfaction during homing migration (Hasler and Scholtz, 1983; Ueda, 2011). Guanylyl-cyclase is a chemoreceptor, and its level in the olfactory system increases during salmon maturation and prior to spawning. A correlation between sexual maturation and recognition of imprinted odors was experimentally demonstrated by a comparison of the response to the natal river odors in immature and mature fish (Hasler and Scholtz, 1983; Dittman et al., 1996).

The reproductive homing migration of salmon requires an exact interaction between the perception of externally-arising olfactory signals for navigation to spawning grounds and the regulation of sexual maturation. This question has been elucidated in the course of recent studies on the basis of modern biochemical and molecular genetic methods (Ueda, 2012; Palstra et al., 2015). The sexual maturation of fish is regulated by interaction among the brain, pituitary, and gonads, or the so-called brain–pituitary–gonadal axis. The gonadotropin-releasing hormone regulates the synthesis of pituitary gonadotropins: follicule-stimulating hormone and luteinizing hormone and their secretion from the brain establishes a physical and functional connection between the brain and the pituitary. Gonadotropins induce the synthesis of steroid hormones in gonads, and steroid hormones stimulate gametogenesis and the final maturation (Ueda, 2012). Palstra et al. (2015) studied the hypothesized functional link between olfactory sensing of the spawning ground and final sexual maturation using the genomic technique. The presence and expression levels of olfactory genes in the olfactory rosette were assessed in chum salmon that migrated from the coastal sea upstream the river to the spawning ground at the coastal stage and at the prespawning area. Simultaneously, the process of sexual maturation along the brain—pituitary–gonadal axis was assessed. Sexual maturation was determined by plasma steroid levels, by gene expression levels of pituitary gonadotropin and gonadotropin-releasing hormone in the brain. Progression towards final maturation in fish at the prespawning area was characterized by certain concentrations of steroid hormones in blood plasma and increased gene expression of luteinizing hormone and gonadotropin-releasing hormone in the brain. Comparison of the transcriptomes of olfactory rosettes in fish at the coastal and prespawning stages revealed the expression of 75 known and 27 unknown olfactory genes, 13 of which had increased expression prior to spawning and were *mor* genes. The genes of potential signal molecules, ependymin and olfactomedines, were expressed in the olfactory rosettes, which may be receptors and modulators of signal pathways. The authors suggest that olfactory signals cannot be directly connected to maturation by gonadotropin-releasing hormone; intermediate messengers such as ependymin and olfactomedines are required. Previously conducted studies on chum salmon by the authors of the same research groups revealed a functional link between the olfactory sensitivity and sexual maturation induced by the gonadotropin-releasing hormone. The level of this hormone in the prosencephalon and the testosterone level in blood plasma showed coincident peaks in both sexes at the prespawning ground, which confirmed the critical role of the gonadotropin-releasing hormone in homing of returning adult fish (Ueda et al., 2011, 2012).

Nevertheless, at this stage, interactions among homing migration, physiology of maturation, and olfactory sensitivity are not certainly clear, with regard to the diversity of modes of prespawning migratory behavior (Keefer and Caudill, 2014). This concerns the populations of some salmon species that migrate to large rivers at great distances and then stay there for weeks or even months until complete maturation, e.g. the steelhead salmon (High et al., 2006).

MECHANISMS OF STRAYING AND EFFECT OF DIFFERENT FACTORS ON ITS RATES

There are no data on the genetic predisposition for straying at the individual level, though the possibility of its presence cannot be excluded. Different mechanisms of homing disruption and straying are considered below according to Keefer and Caudill (2014).

Incomplete juvenile imprinting plays a role in an increase of adult straying. It may be associated with individual features, e.g., insufficient hormone surges and lower olfactory activity (McCormick et al., 2003), reduced brain development (Marchetti and Nevitt, 2003), and species and population features, e.g., short freshwater residence times (Quinn, 1993; Thorpe, 1994), and spawning in small rivers with unstable water regimes. It was demonstrated by a comparison of ocean-type Chinook salmon migrating to the ocean in the year of its birth and river-type Chinook salmon spending up to two years in the river and straying at sufficiently lower rates (Westley et al., 2013) (Table 1). Chum salmon that migrate to small rivers for spawning have higher rates of straying than chum salmon spawning in large rivers, e.g. the Yukon River (Olsen et al., 2008). Incomplete imprinting is also associated with pollution of the aquatic environment (Arkoosh et al., 2011). In hatchery conditions the rates of many hormonal and physiological processes are reduced (Bjørnsson et al., 2011), which disrupts the process of imprinting and reduces the homing of returning adults and enhances their straying.

Interrupted imprinting in juveniles also promotes an increase in adult straying rates and is, as a rule, associated with human interference, i.e., with features of artificial reproduction, especially with juvenile transfer between hatcheries or to a release site remote from the hatchery. In this case, the sequential imprinting is interrupted.

Straying can be caused by *damage to sensory systems in adult fish*, primarily to the olfactory system, and fish may lose the correct orientation. Such disruptions are usually caused by the effect of different ambient chemical contaminants (Klaprat et al., 1992). If adult fish do not reach the natal spawning ground in time, they spawn in another available spawning ground.

A number of studies have demonstrated that straying rates are higher in fish that mature at an older age due to more durable sea migration than in fish that mature at younger stages because of memory impairment. This is observed in Atlantic salmon (Johnsson et al., 2003), Chinook salmon (Quinn et al., 1991), and coho salmon (Labelle, 1992), though the opposite pattern is described in other studies on coho salmon (Hard and Heard, 1999; Candy and Beacham, 2000). However, it is possible that memory may be impaired during long-term sea migration or that the complex of olfactory signals may change slightly during freshwater migration.

The *density-dependent behavior* of salmon also affects straying rates, though its effect is ambiguous. There is some evidence that homing is enhanced in years of high population abundance, probably due to the increase in the intensity of social and chemical signals (Quinn and Fresh, 1984; Altukhov and Salmenkova, 1994). On the other hand, cases of straying in large chum salmon populations from large Alaskan rivers and the formation of breeding aggregations in nearby small rivers are reported (Lin et al., 2011). It is known that chum salmon occurs in the rivers of the Arctic coast in years of its high abundance in the rivers of the northeastern Far East. However, such straying is temporary and is not completed with effective reproduction in the new site, due to the absence of conditions for juvenile survival. Another kind of temporary straying is related to the behavior of salmon when fish enters a nonnatal river or tributary during spawning migration, as if testing the environment, and then leave it and continue migration to the natal river (Keefer and Caudill, 2014). Before entering the natal river for spawning, Atlantic salmon can spend up to three months in lower reaches of the other river and return to the sea (Potter and Russel, 1994). A very low density of spawners may promote higher straying in order to find a breeding partner (Thorpe, 1994).

Straying depends on the *age structure of the species and population*. Thorpe (1994) reports that a complex multiage structure, as in Chinook salmon, sockeye salmon, steelhead, and Atlantic salmon, is, as a rule, associated with precise homing, i.e., the risk of unsuccessful reproduction in one year is distributed over several years and several age cohorts. On the contrary, the simple age structure of pink salmon is associated with less precise homing and higher straying, as spawners must seek an alternative spawning ground when environmental conditions in the natal site turn out to be unfavorable for them.

In addition, juvenile chum salmon and pink salmon as compared to other salmon species are characterized by a shorter freshwater period that is less diverse in environmental conditions. Therefore, divergent selection throughout the range should be weaker, and interpopulation divergence should be weaker expressed, which, to a lesser extent, counteracts the reproductive success of the spawning of alien specimens with native ones (Hendry et al., 2004).

Straying is not occasional on the spatial scale and happens more frequently to nearby rivers with similar physical and chemical conditions. For example, it was found that more than 95% of Chinook salmon strays occurred within 30 km of the natal river system or the release site at a hatchery (Quinn and Fresh, 1984; Quinn et al., 1991). This is confirmed by other studies too (Keefer and Caudill, 2014). *Straying, as a rule, is* *negatively correlated with geographic distance* from the studied population (Hendry et al., 2004). However, the correlation between straying and geographic distance is not always observed, for example, in Chinook salmon from the basin of the large Columbia River (Quinn, 2005).

Artificial reproduction affects the straying rates. Salmon reared at a hatchery, especially from eggs or juveniles transported from another river and released from the hatchery site, have higher rates of straying compared to nontransported or wild salmon (Labelle, 1992; Quinn, 1993; Hansen and Johnsson, 1994; Johnsson et al., 2003). Straying, as a rule, increases with the distance the fish were transported (Reisenbichler, 1988; Quinn et al., 1989). As was mentioned above, under conditions of artificial reproduction, the intensity of hormonal and physiological processes in reared salmon is low (Bjørnsson et al., 2011), which disrupts imprinting formation and enhances the straying of adult fish.

Hendry et al. (2004) paid attention to the pink salmon population in the Little Susitna River in Alaska with unique mitochondrial DNA that was described by Churikov and Gharrett (2002). They suggested that *straying depends on the evolutionary age of the population*: straying must be higher in evolutionarily young populations and minimal in evolutionarily old populations. Such a population has probably been preserved after long isolation in a glacial refugium, i.e., it is more ancient, a relict with respect to the six other studied populations in Alaska.

As stated above, the straying of salmon is no incidental phenomenon but a natural behavioral trait of salmon that is manifested, to some extent, depending on the inherent features of the species and populations and the environmental conditions. Historical dispersion, the colonization of new areas, and the formation of spawning ranges of salmon species occurred due to straying (Thorpe, 1994; Hendry et al., 2004). In the modern age, there is evidence of recolonization of those areas in which earlier salmon populations disappeared because of natural disaster or under anthropogenic effect (Pess, 2009). In sites with restored favorable environmental conditions and eliminated obstacles to salmon migration, i.e., constructed fish waterpasses and eliminated river barriers, straying became the basis for self-sustaining populations in a short period. Thus, recolonization and the formation of pink salmon populations in the upper reaches of the Fraser River after the rockslide at Hell's Gate, which hindered downstream migration, have lasted over 20 years (Pess, 2009; Pess et al., 2012). Due to straying from nearby streams, pink, coho, and sockey salmon and Dolly Varden trout have colonized recently deglaciated streams in the Glacier Bay in Alaska within the last 20–150 years (Milner and Bailey, 1989). However, such distribution does not always result in the formation of self-sustaining populations. Thus, it is obvious that the correspondence between evolutionary adaptations of the species population and geographical, hydrological, and ecological characteristics of colonized areas is important and necessary for colonization success (Altukhov et al., Pess, 2009).

The overwhelming majority of introductions of anadromous salmon outside their natural range did not result in the formation of new populations (Withler, 1982; Crawford and Muir, 2008), but such introductions were successful in some cases and accompanied by colonization of adjacent areas due to straying from the original self-sustaining populations. This is shown by the following few examples: the formation of self-sustaining populations of Chinook salmon in rivers of New Zealand after the successful introduction of Chinnok salmon into one of them from the rivers of North America (McDowall, 1994); the distribution of pink salmon in the Great Lakes after the accidental introduction of a batch of juveniles into Lake Superior (Kwain and Lawrie, 1981); the dispersal of pink salmon in rivers of the basins of the White and Barents seas and penetration (probably temporary) into some Norwegian rivers and more remote areas after its long-term multistage introduction to northern European Russia from rivers of Sakhalin and Magadan oblast (Bakshtansky, 1980; Alekseev and Kulachkova, 2000). It is evident that the loss of the usual cues after the migration of anadromous salmon outside their natural ranges significantly enhances straying, especially at the beginning of colonization of new habitats by alien species. The functioning of internal mechanisms of homing and straying in these cases is unknown, but all of these facts indicate high flexibility of this behavioral system.

Diverse anthropogenic effects on salmon populations (artificial reproduction, various transplantations between hatcheries or aimed at stocking rivers within the range, environmental contamination) may increase the straying rates of hatchery-reared or "alien fish" into natural populations. The large-scale straying of domesticated salmon from large hatcheries and fish farms to surrounding natural populations poses a special threat (Flemming et al., 2000; McGinnity et al., 2003; Brenner et al., 2012). As a result of their genetic interaction, i.e., hybridization and introgression, interpopulation genetic diversity, adaptability, productivity, and the stability of recipient population may decrease and ecological interaction may result in the competition for spawning grounds and displacement of small natural populations (Waples, 1991; Altukhov and Salmenkova, 1994; Utter, 1998; Chilcote et al., 2011; etc.).

CONCLUSIONS

Homing and its complementary straying (deviation from exact homing) are fundamental behavioral characteristics of salmon. The homing ability was the basis for the formation of numerous reproductively isolated, locally adapted populations and for large-scale artificial reproduction of salmon. Straying allows salmon to avoid unfavorable changes in the environment, colonize new habitats and recolonize former ones after the extinction of local populations. Since estimates of straying vary between species and populations within the species and depend on many external, including anthropogenic factors, their comparisons are not always correct. The orientation mechanisms in homing during the sea period include orientation to the Sun's position, currents, and the Earth's magnetic field, but they are still unclear; they have been more completely studied in the freshwater period. Olfaction plays a crucial role in the homing mechanism, allowing imprinting on the chemical features (odor) of natal streams in juveniles. Imprinting mainly occurs during the smoltification period, at earlier stages of development, and during downstream migration. When returning to the natal rivers, adult fish orient by recognizing odors imprinted in their memories. The olfactory system of salmon perceives diverse substances in the river water of biological and nonbiological origins, including pheromones excreted by juveniles, but it is the most sensitive to the complex of dissolved amino acids produced by microbial communities in particular rivers. Imprinting is preceded by the secretion of thyroid hormones of the thyroid gland, which enhances olfaction and stimulates the development of receptor neurons. Hormone surges occur during individual development and are caused by different environmental changes over a long-term period before, during, and after smoltification; the corresponding olfactory cues are sequentially fixed in olfactory structures of fish, thus forming sequential imprinting. Olfactory chemoreception is the basis of sequential imprinting; it is provided by a system of sensory neurons with olfactory receptors coded by 100–200 genes in salmon. In experimental studies the groups of genes of olfactory receptors in salmon have been identified, and their differential expression has been demonstrated at different stages of juvenile development.

The homing of adult fish is directly linked to sexual maturation, and this link is realized through the hormonal system, which is driven by gonadotropin-releasing hormone released by the brain. The secretion of gonadotropin regulates gonad maturation during spawning migration and simultaneously enhances olfactory sensitivity via an increase of activity in some olfactory receptor genes.

The straying rates in salmon depend on a variety of factors: incomplete or disrupted imprinting as a result of some species, population, ecological, or individual features; environmental contamination; artificial reproduction; and different transplantations of eggs or juveniles. Straying rates depend also on density-dependent salmon behavior, the age structure of the species or population, the distance from the site of spawning or release, and the evolutionary age of the population. The estimated straying of artificially produced, domesticated salmon into natural populations can reach high values and pose a serious threat to the adaptability, productivity, stability, and survival of recipient populations.

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