

Correlations Between Homing, Migration, and Reproduction of Chum Salmon

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The onset of gonadal maturation which is regulated by the endocrinological functions is considered to play leading roles in making salmon migrate a long distance from the ocean to their natal streams for spawning. Both cytological profiles of salmon gonadotropin-releasing hormone (sGnRH) neurons and serum gonadal steroid hormone profiles are investigated in chum salmon (*Oncorhynchus keta*) during the homing migration. Cytophysiological differences were observed between sGnRH neurons in the olfactory nerve and those in the preoptic area before and after upstream migration; the former could possibly be involved in the olfactory functions, and the latter would appear to be involved in gonadal maturation. Changes in serum steroid hormone levels were measured during the homing migration from the North Pacific Ocean to the spawning grounds, and the results revealed good correlations between estradiol-17 β and vitellogenesis, 11-ketotestosterone and spermatogenesis, and 17 α ,20 β -dihydroxy-4-pregnen-3-one and final gonadal maturation in both sexes, but the roles of testosterone in gonadal development in both sexes were still obscure. These findings are discussed in relation to homing migration and gonadal maturation of chum salmon.



INTRODUCTION

Salmon have the ability to migrate thousands of kilometers from the ocean to their natal streams for spawning after a few years of feeding migration (Smith 1985). Although the shift from feeding migration to homing migration has been thought to coincide with the onset of gonadal maturation (Ueda and Yamauchi 1995), the mechanisms controlling this shift are still unknown. Since the gonadal maturation is mainly regulated by the hypothalamo-pituitary-gonadal axis (Fink 1988), it is highly important to investigate endocrinological changes of various hormone profiles in salmon during homing migration.

Anadromous chum salmon (*Oncorhynchus keta*) migrating from the North Pacific Ocean to natal streams in Japan are a good model for studying the correlations between homing migration and reproduction, because mature chum salmon of both sexes return to the natal area with high accuracy. The present paper reviews the endocrinological functions of chum salmon during the homing migration with special reference to cytophysiological profiles of salmon type gonadotropin-releasing hormone

(sGnRH) as well as serum gonadal steroid hormone profiles.

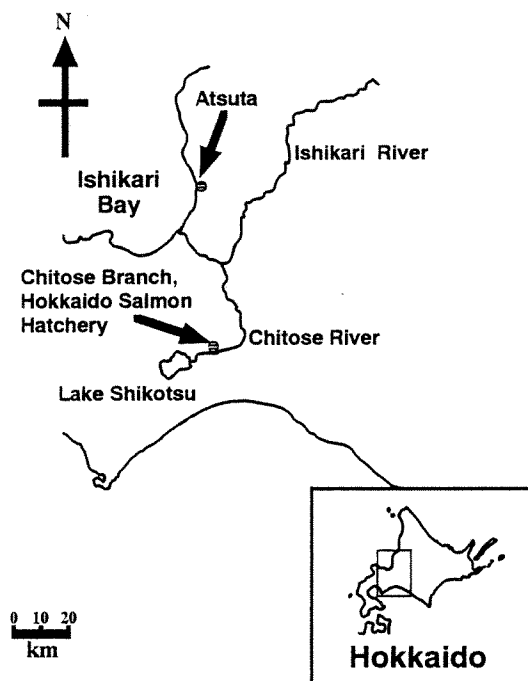
MATERIALS AND METHODS

Salmon Gonadotropin-Releasing Hormone (sGnRH)

Ten male and ten female four year old adult chum salmon were captured at two locations during their homing migration. Fish at an early phase of the homing migration were captured in the coastal sea near the maternal river, Atsuta, Hokkaido, Japan on October, 1992, and those at the time of spawning on the spawning ground itself in the maternal river were obtained just after the completion of upstream migration at the Chitose Branch, Hokkaido Salmon Hatchery on October, 1992 (Fig. 1). Fish were deeply anesthetized, and the forebrain (olfactory nerve, olfactory bulb, telencephalon, and preoptic area) were isolated.

The procedures of immunocytochemistry using the antiserum to sGnRH (Okuzawa et al. 1990) and in situ hybridization using the oligonucleotide for pro-sGnRH mRNA probe (Suzuki et al. 1992) were described previously (Kudo et al. 1996).

Fig. 1 Map of the coastal sea and the Ishikari and Chitose Rivers showing the sampling areas for chum salmon.



Serum steroid Hormones

Fourteen male and female adult chum salmon of age 3 to 5 years were caught at 14 sampling points from 41.30°N-156.30°E to 45.32°N-173.31°E in the north Pacific Ocean in May and June, 1982. Thirty male and twenty-three female were captured in the coastal sea near the maternal river, Atsuta and at the Chitose Branch, Hokkaido Salmon Hatchery on October, 1982.

Serum levels of various steroid hormones (estradiol-17b, testosterone, 11-ketotestosterone, and 17α,20β-dihydroxy-4-pregnen-3-one) were measured by radioimmunoassay methods specific to each steroid (Kagawa et al. 1982; Ueda et al. 1991a; Ueda et al. 1985; Young et al. 1983).

Statistics

Significance of differences were determined by use of Student's test or Student-Newman-Keuls' multiple range test.

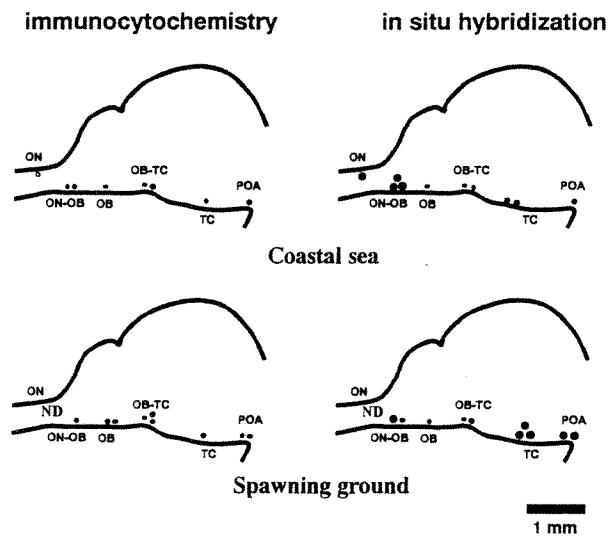
RESULTS

Salmon Gonadotropin-Releasing Hormone (sGnRH)

Cytophysiological changes of sGnRH producing neurons in chum salmon were examined during

homing migration by immunocytochemistry with a specific antiserum to sGnRH and *in situ* hybridization with an oligonucleotide encoding the sGnRH precursor. In the forebrain (olfactory nerve, ON; olfactory bulb, OB; telencephalon, TC; preoptic area, POA), sGnRH immunoreactive neurons and neurons showing signals for pro-sGnRH mRNA were compared between fish in the coastal sea and those on the spawning ground. Neurons in the ON and between the ON and OB (ON-OB) exhibited strong sGnRH immunoreactivity and strong hybridization signals in fish in the coastal sea, whereas these activities and signals disappeared or decreased in animals on the spawning ground. In contrast, neurons in the TC and POA showed sGnRH immunoreactivity and hybridization signals of sGnRH during homing migration, and the hybridization signals of sGnRH in the TC and POA were stronger in fish on the spawning ground than those in the coastal sea (Fig. 2).

Fig. 2 Distribution of neurons showing sGnRH immunoreactivity and hybridization signals for pro-sGnRH mRNA in the forebrain of chum salmon during homing migration. Small and large circles indicate weak and strong hybridization signals, respectively. ND, non-detectable.

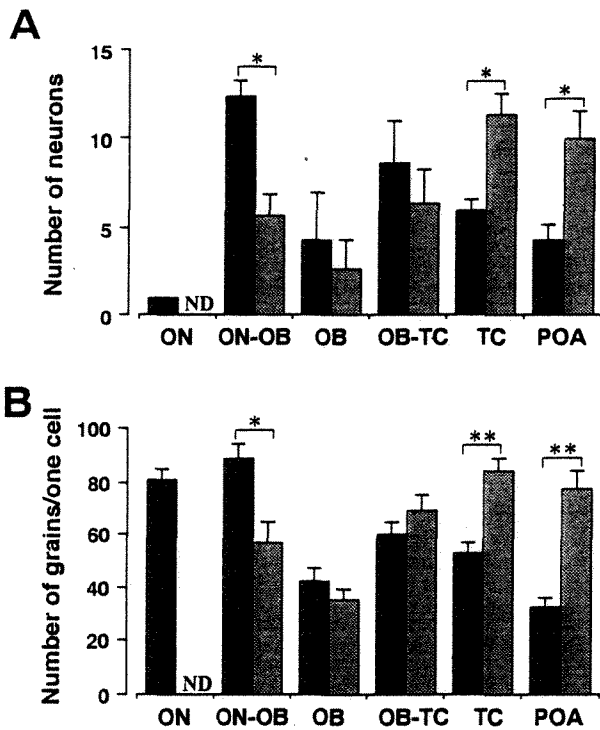


Both the number of neurons and the intensity of signals for pro-sGnRH mRNA between the ON-OB were significantly greater in fish in the coastal sea than those on the spawning ground. However, neurons showing signals for pro-sGnRH mRNA in the TC and POA increased significantly in number and in intensity in fish on the spawning ground (Fig. 3).

Serum Steroid Hormones

Changes in serum steroid hormones were measured during spawning migration from the North Pacific Ocean to the spawning ground of chum

Fig. 3 Changes in the number of neurons showing signals for pro-sGnRH mRNA (A) and the intensity of pro-sGnRH mRNA levels in sGnRH neurons (B) in chum salmon from the coastal sea (darker stippled bars) and from the spawning ground (Lighter stippled bars). Vertical bars represent the mean + SE. Significant differences at 5% (*) and 0.1% (**) levels are indicated.



salmon (Ueda et al. 1984a; 1991a; 1991b). In females, serum estradiol-17β (E₂) levels increased sharply during seawater migration, but were followed by a sharp drop during upstream migration. Serum 17α,20β-dihydroxy-4-pregnen-3-one (DHP) levels were very low collected from the North Pacific Ocean to the river at the pre-spawning period, and increased dramatically at the spawning ground (Fig. 4).

In males, serum 11-ketotestosterone (11KT) and testosterone (T) levels increased sharply and gradually from the North Pacific Ocean to the coastal sea and to the river at the pre-spawning period, respectively. Levels of both androgens in serum decreased at the spawning period when serum DHP level rapidly increased (Fig. 5).

DISCUSSION

Salmonid homing migration is considered to be closely related with the gonadal maturation which is regulated by the endocrinological functions, mainly by the hypothalamo-pituitary-gonadal axis. Briefly, GnRH controls gonadotropin (GtH) release from the pituitary gland, GtHs induce steroidogenesis in the gonads, and steroid hormones stimulate gameto-

Fig. 4 Changes in serum estradiol-17β (E₂) and 17α,20β-dihydroxy-4-pregnen-3-one (DHP) levels during the spawning migration of female chum salmon. The vertical bars represent the means ± SE.

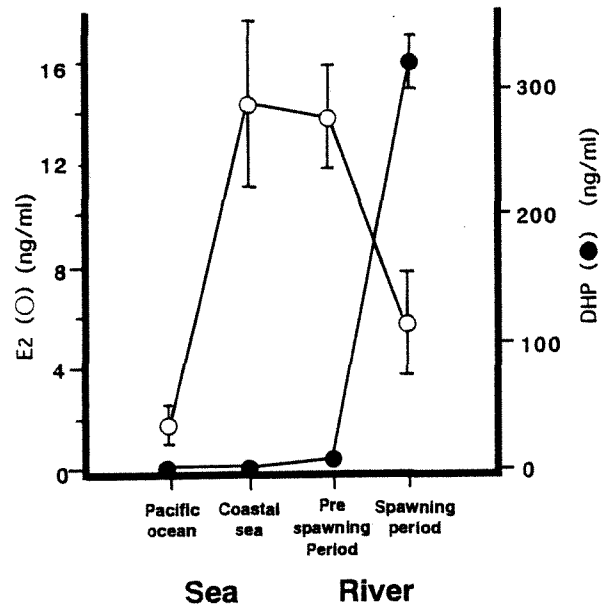
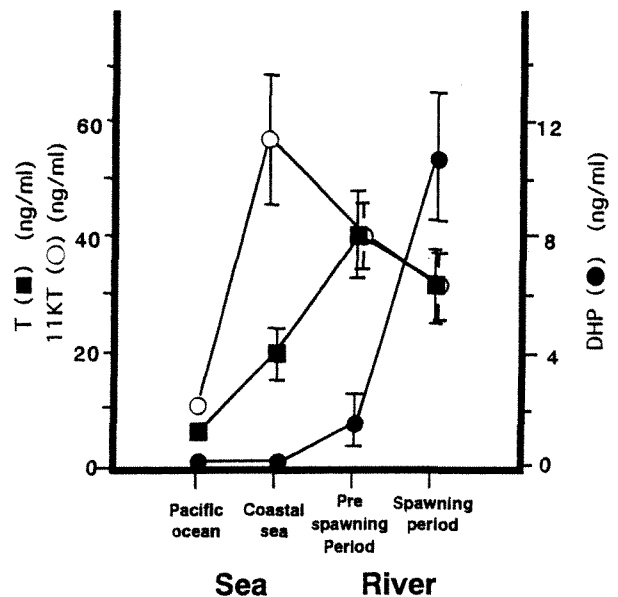


Fig. 5 Changes in serum testosterone (T), 11-ketotestosterone (11-KT) and 17α,20β-dihydroxy-4-pregnen-3-one (DHP) levels during the spawning migration of male chum salmon. The vertical bars represent the means ± SE.



genesis and final gameto-maturation. The present review focuses on the homing migration of chum salmon in connection with cytophysiological profiles of sGnRH producing neurons as well as serum steroid hormone profiles.

sGnRH neurons in the ON showed distinct cytophysiological changes; both immunoreactivity of sGnRH and strong hybridization signals for pro-sGnRH mRNA were observed in fish at the early phase of the upstream migration, but were rare in fish at the time of the spawning period. These somata were still observed by counterstaining with cresyl violet, but the sGnRH immunoreactivity was lacking and the hybridization signals were hardly detectable, suggesting that the ON neurons had stopped production of sGnRH on the spawning ground. Both the number of somata and the intensity of the signals of sGnRH neurons in the ON-OB also decreased during upstream migration. On the contrary, sGnRH neurons in the TC and POA showed a different cytophysiological pattern from those in the olfactory system. sGnRH-immunoreactive neurons were more abundant in the TC and POA in fish on the spawning ground, and the signals for pro-sGnRH mRNA were stronger than those in fish in the coastal sea. These findings suggest that sGnRH neurons in the ON and ON-OB have different pattern of sGnRH production from those in the TC and POA in the chum salmon during the homing migration.

Involvement of sGnRH in olfactory functions of masu salmon (*O. masou*) was also examined by means of immunocytochemical technique. sGnRH immunoreactive bipolar neuron, which might be related to the terminal nerve, is located in dorsal portion of the olfactory nerve in masu salmon as in chum salmon. Immunoelectron microscopy reveals the presence of sGnRH immunoreactive electron-dense granule-like structure of 50 nm in fibers of the olfactory nerve close to both the olfactory epithelium and to the olfactory bulb (Kudo et al. 1994). These findings suggest that sGnRH in the olfactory system might participate in neurotransmission and/or neuromodulation, and might have important roles in olfactory recognitions since the coastal sea stage is the most important time for discriminations of the natal stream odorants. In contrast, sGnRH in the TC and POA is considered to be participated in gonadal maturation, mainly in the stimulation of gonadotropin(s) release from the pituitary gonadotrophs.

It is now widely accepted that the functional roles of gonadal steroid hormones in salmonid gametogenesis are E_2 in vitellogenesis, 11KT in spermatogenesis, and DHP in final gameto-

maturation (Nagahama 1994). The shifts from E_2 to DHP in females and 11KT to DHP during homing migration as the predominant steroid in serum are also found in other salmonid species (Ueda and Yamauchi 1995). Although the roles of T in gamatogenesis have not been clarified yet, high serum levels of T are detected in many salmonid fishes of both sexes during the spawning period (Lou et al. 1986; Fitzpatrick et al. 1986; Mayer et al. 1992), and T was considered to be a substrate for E_2 and 11KT biosyntheses (Kagawa et al. 1982; Ueda et al. 1984b). During spawning migration of salmonids, serum T levels maintained high and declined after spawning (Truscott et al. 1986; Slater et al. 1994). The peak of plasma T levels in land-locked sockeye salmon of both sexes was observed at the time when they gathered at the mouth of natal stream in Lake Chuzenji (Ikuta 1996).

Recently, homing behavior of lacustrine sockeye salmon (*O. nerka*) in Lake Shikotsu has been studied in connection with changes in serum gonadal steroid hormone (Unpublished data). In males, the shortening of homing duration coincided with the increase of serum T and 11KT levels, and the reduction of homing percentage is associated with the decrease of serum T levels and the increase of serum DHP levels. In females, the shortening of homing duration corresponds with the elevation of serum T and DHP levels, and the drop of serum E_2 levels. Moreover, GnRH analog (GnRHa) implantation is highly efficient in shortening of homing duration, especially in females. The GnRHa treatment causes dramatical increase of serum DHP levels in both sexes on average, but early returned GnRHa-treated males show higher serum T levels and lower serum DHP levels than late returned ones. These results indicate that homing behaviors of lacustrine sockeye salmon are sexually different, and these differences may be reflected by changes in serum steroid hormone levels, particularly of T.

CONCLUSION

The present paper reviews several previous findings on the relations between homing migration and reproduction in chum salmon. Each salmonid species should have different strategies of homing migration using different sensory abilities which could be directly affected by hormone states. Further behavioral and molecular biological analyses using other salmonid species will help to clarify the mechanisms of homing migration and gonadal maturation as well as to evaluate the status of salmonid stocks.

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