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Seasonal changes in plasma thyroxine kinetics in coho salmon *Oncorhynchus kisutch* during smoltification

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Abstract

Growth-accelerated yearling coho salmon smolts, weighing approximately 200 g, were collected in spring and cannulated via the dorsal aorta; they were held individually in containers during the process. A cannula was connected outside the container with a syringe, and the fish received an intra-arterial injection of 13.3 ng/g body weight thyroxine (T_4). A group of growth-accelerated smolts weighing more than 190 g were used as control fish. Another group of normal body-sized fish was monitored smoltification parameters through the parr–smolt transformation to evaluate the validity of the growth-accelerated smolts. Although condition factor (CF) of the growth-accelerated smolts decreased from February to March, it did not change afterward until a significant increase in July. The plasma T_4 levels increased from February to a peak in late April and decreased thereafter. Gill Na^+, K^+–ATPase activity showed a peak in late June. According to the smolt parameters, the smoltification developed from March and desmoltfied in July. Peak levels of plasma T_4 1 min after the T_4 injection were lower during mid smolt stage than those at the beginning and end of smoltification. The T_4 metabolic clearance rate (MCR) increased rapidly and attained a peak in late March, and decreased thereafter when the plasma T_4 level was at the peak. The T_4 secretion rate exhibited also a peak in late March with a tendency to decrease afterward, similar to the MCR. These results indicate that the highest MCR of circulating T_4 appears in the early stage of smoltification when plasma T_4 level is still low, and MCR lowers when the fish reach the full smolt stage. In the full smolt stage, the increased circulating T_4 at the period of T_4 surge is the result of the lower T_4 metabolism.

Keywords: Coho salmon; Kinetics; Metabolic clearance rate; *Oncorhynchus kisutch*; Secretion rate; Smolt; Smoltification; T_4 surge; Thyroxine

1. Introduction

Many salmonids are anadromous and migrate down to the ocean after complex morphological, physiological, and behavioral changes. These changes are termed as smoltification, parr–smolt transformation, or smolting (Hoar, 1988; Boeuf, 1993; Iwata, 1995). Many studies have been conducted on the hormonal control of smoltification in salmonids with regard to morphological changes, osmoregulation, growth, etc. (Bern and Nishioka, 1993). Thyroid hormones, prolactin, growth hormone (GH), insulin, corticosteroids, and gonadal steroids are thought to play a role in smoltification (Boeuf, 1993). The thyroid is probably the most well studied endocrine system with regard to smoltification, primarily by examination of morphology and circulating blood levels (Fontaine, 1975; Miwa and Inui, 1983, 1985). Studies have revealed that a surge occurs in blood thyroxine (T_4) at the end of smoltification in fresh water just before the highest level of gill Na^+, K^+–ATPase activity in both Pacific and Atlantic salmon (Hoar, 1988;

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Boeuf, 1993). Correlations were found between plasma T_4 level and growth, seawater adaptability, and lunar phase (Grau et al., 1981; Farbridge and Leatherland, 1987; Bern and Nishioka, 1993). T_4 treatment, however, does not show a consistent effect on seawater adaptability of chum salmon fry (Iwata et al., 1987). Blood T_4 levels can also be modified by changes in freshwater quality, water flow, rearing conditions, and rainfall (Nishioka et al., 1985; Yamauchi et al., 1985; Youngson et al., 1986; Boeuf and Gaignon, 1989; Fujioka et al., 1990; Hoffnagle and Fivizzani, 1990).

Iwata et al. (2003) have reported that hatchery-released chum salmon (*Oncorhynchus keta*) fry showed a surge in blood T_4 during the process of downstream migration from hatchery to river mouth. The T_4 levels decreased when the fry reached the estuary. The T_4 peak was also detected in the fry 2 h after the release, and following this, the high T_4 level was maintained during downstream migration. In chum salmon fry, the T_4 surges were also induced by environmental stimuli such as rainfall, turbid water, and cold water. These comprehensive results suggest a possibility that salmon juveniles require the T_4 surge in the migratory season in order to be motivated for searching behavior, school formation, departure from a stream habitat, maintaining downstream movement, and other behaviors related to seaward migration. There is a distinct increase in the circulating level of T_4; however, the dynamics of circulating T_4 and the role of the T_4 surge during smoltification remain unclear.

Dissatisfaction with the inability to induce complete development of smolt characteristics in parr using exogenous thyroid hormones has shifted attention to peripheral T_4 events. Eales (1985) has demonstrated a model of the peripheral metabolism of thyroid hormones. In this model, the plasma T_4 levels alone cannot be good indicators of hormone involvement in the regulation of developmental processes. Further, according to this model, the tissue level regulation of T_4 uptake, deiodination, and receptor abundance ultimately determine the degree of hormone activity. To date, minimal research has been done on potentially important peripheral events in relation to salmonid development. If any of morphological, physiological, or behavioral characteristics of smoltification involves thyroid hormones in those processes, dynamics of peripheral T_4 should be explained.

Specker et al. (1984) proposed that the target organs for T_4 were initially slow tissues, possibly muscle; and then, after the T_4 peak, the predominant targets are fast tissues, possibly liver. The plasma T_4 exhibited a more rapid turnover at the beginning than at the end of smoltification without relation to the plasma T_4 levels. Specker et al. (1992) also examined T_4 concentrations in brain, liver, and muscle tissue at three weeks before and after the peak of plasma T_4 level. The T_4 content in the brain and muscle before the T_4 peak was higher than after the peak. Plasma triiodothyronine (T_3) concentrations remained unchanged in March and April, but they decreased in May. These results raised the possibility that hormone utilization may vary in ways that do not bear an obvious relationship with the plasma patterns of T_3 and T_4. To consider the function of T_4 at the peak of smoltification and the T_4 surge for the onset of downstream migration, it is necessary to clarify the dynamics of plasma T_4 throughout the smoltification processes and the process in the onset of downstream migratory behaviors. Therefore, this study attempted to reveal in detail the changes in T_4 metabolic clearance rate (MCR) and secretion rate (SR) in the smoltification process and particularly during the plasma T_4 surge phenomenon.

2. Materials and methods

2.1. Fish maintenance

Juveniles of coho salmon *Oncorhynchus kisutch* were donated by the Daimaru Kaiei Corporation (Tono, Iwate). The fish were transferred to the Kitasato University in June 2004 (0+ parr; 8.8 ± 0.28 g), and reared in 2000-L running freshwater indoor-tanks. The fish were maintained under natural photoperiod and at natural water temperature, except in summer when water coolers were installed to maintain temperature less than 15 °C. The water temperature was 15 °C in summer 2004 and decreased to 3.9 °C in February, and then it increased to 15 °C in July. Normal body-sized coho salmon were fed 2% of body mass of salmon chow. The fish grew from 24.9 ± 2.7 g in December to 59.9 ± 8.2 g in May; in the middle of each month, they were used to monitor the smolt parameters. To accelerate growth, the fish were fed same chow twice a day (at 1000 and 1600) until satiation, and most of the fish attained a weight of more than 200 g at the beginning of 1+ in age. The fish that weighed more than 150 g were used for the cannulation experiment. The experiments were carried out twice a month from late February to June in the cannulation experiments and to July to monitor the smolt parameters of the growth-accelerated coho salmon. The growth-accelerated coho juveniles smoltified in fall of 0+ in age (Iwata and Clarke, 1987) with silvery body color and black pigmentation at the fin margins, these characteristics were maintained throughout winter and spring.

2.2. Sampling of normal body-sized coho salmon juveniles

Between mid-December and mid-July, 10 fish were sampled at monthly intervals except for February. Fish were anesthetized in 0.04% 2-phenoxyethanol. Smolt stages were evaluated into four stages according to our standards: immature parr (stage 1), partially silvered fish with clear parr marks (stage 2), silvered fish with obscure parr marks (stage 3), fully silvered fish with no