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Growth Hormone and Thyroid Hormones during Atlantic Salmon, *Salmo salar* L., Smolting, and After Transfer to Seawater

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ABSTRACT

Boeuf, G., Le Bail, P.Y. and Prunet, P., 1989. Growth hormones and thyroid hormone during Atlantic salmon, *Salmo salar* L., smolting, and after transfer to seawater. *Aquaculture*, 82: 257–268.

Gill (Na^+-K^+)-ATPase activity of juvenile salmon, *Salmo salar* L., increased "classically" from February to the end of April in experiments in two different years, and its level before transfer to seawater was correlated directly with seawater performance (survival, plasma osmotic pressure and plasma chloride levels). A thyroxine (T4) surge occurred 2–3 weeks before the peak of gill enzyme levels. After the T4 peak the fish were clearly euryhaline, but T4 levels were not correlated with seawater adaptability. They remained able to adapt rapidly to seawater for at least 1 month after the surge. Two significant increases of tri-iodothyronine (T3) occurred while the fish were in freshwater: transfer to seawater either decreased T3 and T4 or had no effect. In freshwater, plasma growth hormone (GH) levels rose sharply concomitant with the T3 peak, 2 weeks before peak gill ATPase activity. After transfer to seawater GH increased significantly, remaining high for 7–10 days, and returning to base levels after 14 days. GH appeared to play a major role in smolting and seawater adaptation.

INTRODUCTION

The physiological, biochemical and endocrinological changes occurring at smolting have been reviewed frequently (Fontaine, 1975; Hoar, 1976; Folmar and Dickhoff, 1980; Wedemeyer et al., 1980; Boeuf, 1987). Zaugg and McLain (1970, 1972) first described the seasonal spring increase in gill (Na^+-K^+)-ATPase activity in coho salmon, *Oncorhynchus kisutch*, and other Pacific salmon prior to downstream migration. Saunders and Henderson (1978) and Boeuf et al. (1985) found similar patterns in Atlantic salmon, *Salmo salar* L., and Boeuf and Harache (1982, 1984) established such activity levels as predictors of readiness for seawater transfer.

Thyroxine (T4) surges have been recorded at smolting in Pacific (Dickhoff

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et al., 1978; Grau et al., 1981) and in Atlantic salmon (Lindahl et al., 1983; Youngson and Simpson, 1984; Boeuf and Prunet, 1985; Virtanen and Soivio, 1985), and may be used as an indicator of smolting status (Folmar and Dickhoff, 1981; Boeuf, 1987).

Growth hormone (GH) influences growth (Donaldson et al., 1979), smolting and seawater adaptation (Komourdjian et al., 1976; Clarke et al., 1977; Nagahama et al., 1977; Hirano et al., 1987), increasing during smolting in coho (Sweeting et al., 1985).

The present paper reports on changes in Atlantic salmon plasma thyroid hormones and GH levels, and their possible roles in osmoregulation and seawater adaptation: (1) during smolting, defined by gill ATP-ase activity as an indicator of seawater adaptability; and (2) after transfer to seawater (before, during and after smolting).

MATERIAL AND METHODS

Cultured Norwegian salmon were reared in river water (pH 6.5–7) at the Le Conquet hatchery, Brittany. From September preceding the smolting year (1984 and 1986) upper modal group fish (Thorpe, 1977; Boeuf et al., 1985) at 100 fish/m^2 were fed dry pellets (SS1 IFREMER) by automatic feeder, in 2×2 m Ewos tanks, under natural photoperiod (48°N) and temperature (Fig. 1). They were transferred to similar rearing conditions at the Centre Oceanologique de Bretagne at least 2 weeks before seawater transfer. On that day the freshwater supply was closed, the seawater supply opened, and the fish were in full seawater (34.4–35.6‰) within 1 h. The food was then changed to SS6 IFREMER pellets (Gaignon, 1987). Four transfers were made in 1984–85, and three in 1987 (Table 1).

Gill and plasma sampling from 10–25 fish (10 in seawater experiments) began in September 1984 and February 1987, respectively. Blood was sampled from the posterior aorta by heparinised syringe, between 09.00 and 11.00 h, and plasma was stored at −28°C. Gill filaments from the same fishes, rinsed with 0.25 *M* sucrose (pH 7.4) were stored immediately in liquid nitrogen. Gill

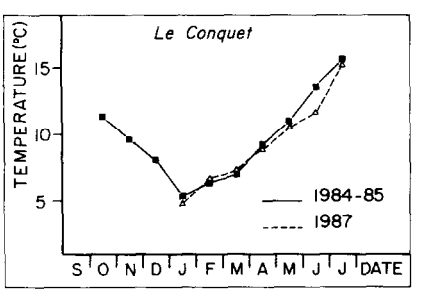

Fig. 1. Temperature regimes in the hatchery of Le Conquet.

TABLE 1

Experimental conditions at the beginning of the seven seawater transfers of Atlantic salmon performed in 1984–85 and in 1987

	Date						
	25.11.84 I	7.01.85 II	25.03.85 III	22.04.85 IV	23.03.87 1	20.04.87 2	18.05.87 3
Freshwater temperature (°C) (control fish)	11.4	6.1	9.5	9.5	9.9	11.2	11.3
Seawater temperature (°C)	13.8	9.8	9	11	10.2	11.0	12.5
Average fork length (mm)	116.9±1.6	121.6±0.4	160.9±4.6	162.2±4.2	136.6±2.0	158.2±1.9	172.7±4.9
Gill (Na^+-K^+)-ATPase activity level (μm Pi mg Prot.$^{-1}$ h^{-1})	6.5±0.4	4.5±0.5	14.8±1.1	25.2±1.0	10.4±1.2	21.5±1.6	18.5±0.7

(Na^+-K^+)-ATPase and Mg^{2+}-ATPase were measured by the method of Lasserre et al. (1978). Plasma tri-iodothyronine (T3) and T4 concentrations were determined by radioimmunoassay (Chopra, 1978; modified by McKenzie et al., 1978; Boeuf and Prunet, 1985). The intra-assay coefficient of variation was 3–7%, and all samples of the same experiment were measured in the same assay. Plasma GH levels were determined by radioimmunoassay (Le Bail et al., in prep.).

One-way analyses of variance and the SNK multiple range test were used to assess the significance of differences in the data. In the transfer experiments Student's *t*-test was used to assess differences between fish in fresh- and seawater.

RESULTS

Experiment 1: 1984–85

Freshwater (Fig. 2). (Na^+-K^+)-ATPase activity rose gradually from January to peak at a significantly high level ($P<0.01$) on 22 April, declining slowly thereafter. Plasma T3 increased from low levels before February to peak in mid-March at 11.2±1.0 ng/ml ($P<0.05$). This peak preceded that of T4, which, after a slight rise in November–December, surged sharply to 29.5±0.5 ng/ml on 14 April.

Seawater (Figs. 3–5). After seawater transfers I (25 October) and II (7 Janu-

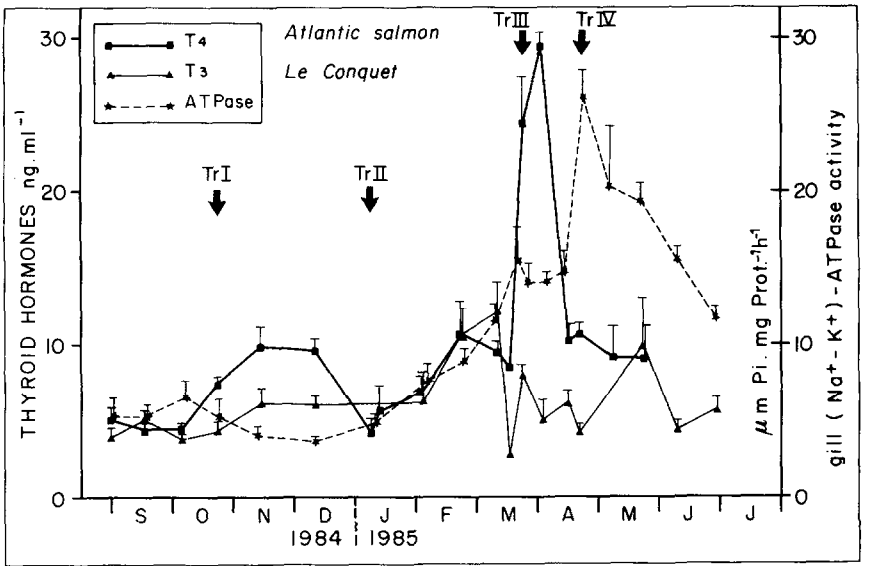

Fig. 2. Gill (Na^+-K^+)-ATPase activity and thyroid hormone changes during smolting in Atlantic salmon in freshwater. Date of each seawater transfer is indicated (Tr). Each point represents the mean ± standard error of 10 to 25 fish.

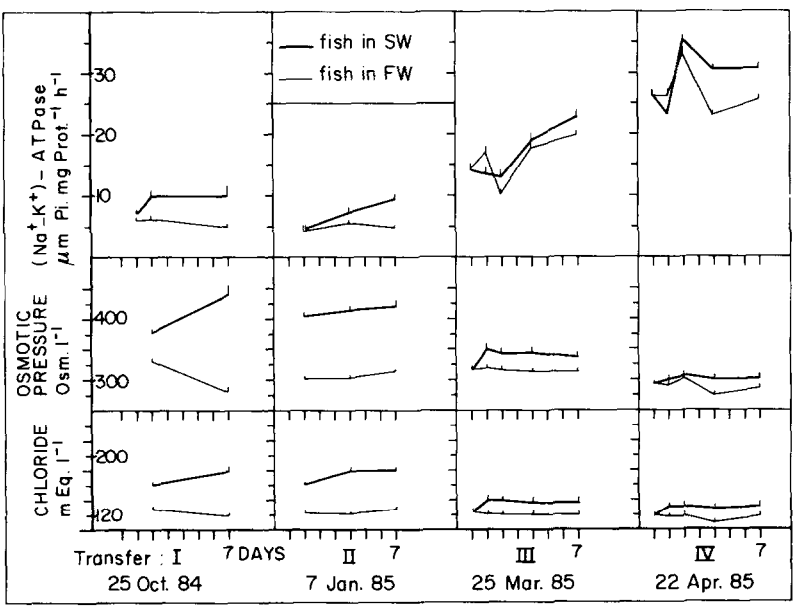

Fig. 3. Changes in osmotic parameters after four direct transfers to seawater in the Atlantic salmon (I, 25 October 1984; II, 7 January 1985; III, 25 March 1985; IV, 22 April 1985). Each point represents the mean ± the standard error of 10 fish.

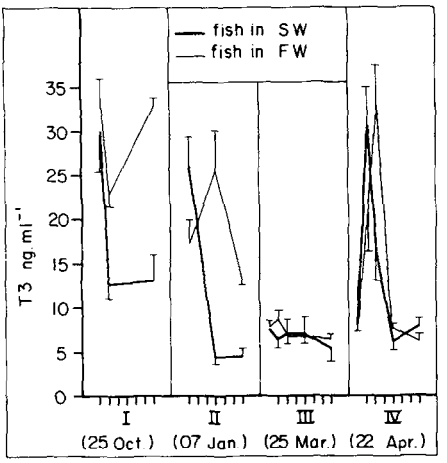

Fig. 4. Blood plasma tri-iodothyronine changes (legend as in Fig. 3).

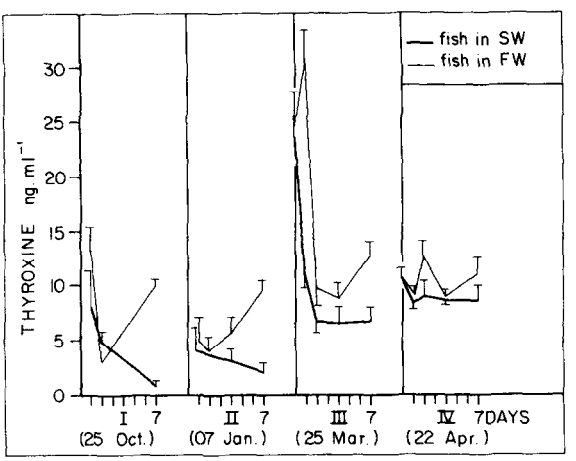

Fig. 5. Blood plasma thyroxine changes (legends as in Fig. 3).

ary) osmotic imbalance was high, plasma osmotic pressure (>400 mOsm/l) and chloride levels increasing rapidly. Gill ATPase activity increased slowly and stayed at low levels over 1 week (10 μm Pi mg Prot.$^{-1}$ h^{-1}). After transfers III (25 March) and IV (22 April) osmotic balance was restored rapidly, and ultimate changes in plasma osmotic pressure and chloride levels were less in April than in March. After transfer III, gill ATPase levels continued to rise, as in freshwater fish at this time. After transfer IV levels rose in seawater but decreased slightly in freshwater, although both levels were higher than in March.

T3 levels were unaffected by seawater transfer in March and April, but decreased sharply ($P<0.01$) from high freshwater values in October and Janu-

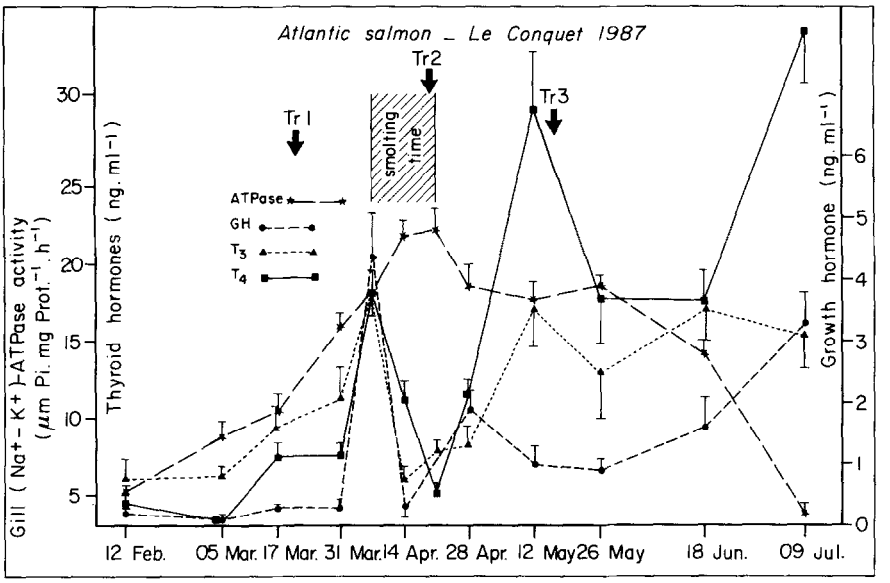

Fig. 6. Gill (Na^+-K^+)-ATPase activity, thyroid hormones and growth hormone (GH) changes during smolting in Atlantic salmon in freshwater. Each point represents the mean ± the standard error ($n = 10$ to 25 fish).

ary. T4 levels were unaffected by transfer in April, decreased rapidly in March, and less rapidly in October and January.

Mortalities after 7 days in seawater were 45%, 25%, 6% and 2% respectively, compared to 0 in freshwater.

Experiment 2: 1987

Freshwater (Fig. 6). Gill ATP-ase activity rose from mid-February to peak ($P < 0.01$) in late April, then declined gradually. T3 levels peaked on 7 April ($P < 0.01$) and again 4 weeks later, remaining high thereafter. T4 levels also peaked on 7 April and again on 12 May and 7 July (all $P < 0.01$). GH levels were low until March, peaked on 7 April, and then fell to levels significantly higher ($P < 0.01$) than before the peak.

Seawater (Fig. 7). On seawater transfer (23 March, 20 April and 18 May) plasma osmotic pressure increased <10% after 14 days, and chloride levels increased only slightly (after 48 h, $P < 0.01$) (Table 2). Disequilibrium was less than in transfers I and II of 1984–85, but greater than in transfer IV. These small increases were compatible with good adaptation (Boeuf et al., 1982).

Plasma GH increased significantly on transfer ($P < 0.001$), and still further

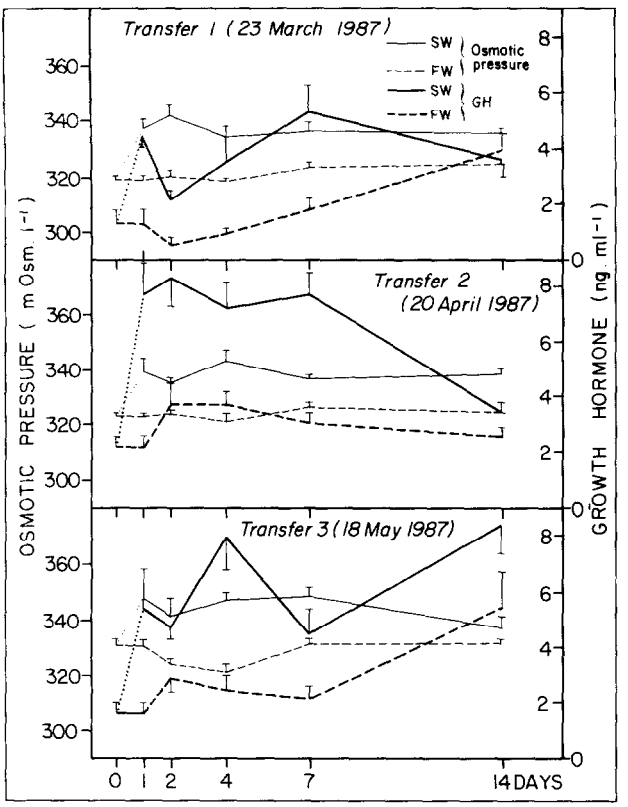

Fig. 7. Plasma growth hormone (GH) and osmotic pressure changes after three direct transfers from freshwater to seawater in the Atlantic salmon. Each point represents the mean ± the standard error ($n=10$).

TABLE 2

Plasma chloride levels in (meq l^{-1}) after transfers of Atlantic salmon ($n=10$) to seawater in 1987: mean ± standard error

	Tr 1	Tr 2	Tr 3
FW fish at 24 h	124.8±2.1	123.6±1.3	129.2±0.6
SW fish at 24 h	138.1±2.1	132.7±2.5	141.6±1.4
FW fish at 48 h	129.7±0.8	126.7±0.4	129.9±0.5
SW fish at 48 h	144.3±2.5	139.7±1.2	142.3±1.2
FW fish at 4 days	126.3±0.6	126.1±0.3	124.5±3.6
SW fish at 4 days	140.6±1.5	143.5±1.8	145.6±1.5
FW fish at 7 days	128.8±0.6	127.7±0.8	131.0±0.6
SW fish at 7 days	142.1±1.4	137.6±1.0	148.2±1.4
FW fish at 14 days	130.4±1.1	1270.±0.5	134.2±1.0
SW fish at 14 days	142.7±1.2	140.8±1.1	146.6±1.4

after 7 days ($P<0.01$). After 14 days the differences between fish in fresh- and seawater disappeared. Mortality after transfer was $<3\%$ at each date.

DISCUSSION

Milne and Leatherland (1980) concluded that if thyroid hormones were indirectly affected by ambient salinity, they could not play a direct role in ionic and osmotic regulation in rainbow trout, *S. gairdneri*, and coho salmon. By contrast, thyroid activity is indispensable for proper osmoregulation and survival in seawater in *Fundulus heteroclitus* (Knoeppel et al., 1982). Folmar and Dickhoff (1981) found that T4 levels just prior to seawater entry influenced seawater survival over 6 months in coho, but concluded that they had no osmoregulatory role there. Pereira and Adelman (1985) concluded likewise for chinook salmon, *Oncorhynchus tshawytscha*. The present results show no correlation between T3 or T4 levels and seawater adaptability in Atlantic salmon, but do agree with those of Dickhoff et al. (1982), Nagahama et al. (1982) and Grau et al. (1985) in *Oncorhynchus* spp., that osmotic capacities are high after the T4 surge. The transitory high level of T4 (and possibly T3) may determine the time of acquiring euryhalinity, followed by a long period of seawater tolerance. However, as in previous studies, high levels of gill (Na^+-K^+)-ATPase were more directly related to osmoregulatory capacity in seawater, and were good predictors of high seawater adaptability. If thyroid hormones are not implicated in seawater adaptation at smolting, this may account for apparently contradictory observations made by different authors at this time.

Thyroid hormone levels did not change or decreased on transfer to seawater. In Pacific salmon, T4 decreased on transfer (Grau et al., 1980; Dickhoff et al., 1982; Specker and Schreck, 1984), and so did T3 (Dickhoff et al., 1982). Boeuf (1987) found a small decrease of both in rainbow trout, but Milne and Leatherland (1980) found no difference. In eels, *Anguilla anguilla*, Leloup and De Luze (1985) showed an increase in T3, but no change in T4. In freshwater, the T4 surge occurred before peak gill ATPase activity (c.f. Boeuf and Prunet, 1985; Virtanen and Soivio, 1985). Other peaks also occurred after smolting. Such changes in plasma T3 and T4 levels were not dependent on differences of binding capacities of transport proteins during smolting (Boeuf et al., 1989).

The smolting and post-smolt periods should be separated, and the significance of thyroid hormone fluctuations after migration should be considered separately, especially if smolts are constrained to remain in freshwater. The results herein do not substantiate the observations of Grau et al. (1981) on the relationships between the T4 surge and the new moon phase of the lunar cycle in coho salmon. The observations of Boeuf and Prunet (1985) may have been coincidental.

T3 levels increased each year. Such changes were not reported by Lin et al.

(1988). In 1983 (Boeuf and Prunet, 1985) and in 1985, T3 increased before and after the T4 surge, but in 1987 both hormones peaked at the same time, and plasma T3 remained high (>15 ng/ml) after smolting. It is known that nuclear receptors have a higher affinity for T3 than T4 (Darling et al., 1982; Bres and Eales, 1986), and recently Leloup et al. (1986) found T3 receptors in the gills of brown trout, *S. trutta*. Knowing that T3 induces $(Na^+\text{-}K^+)$-ATPase synthesis in mammals (Bernal and De Groot, 1980), it may be responsible for activating the gill enzyme in salmon. However, different treatments with T3 did not increase ATPase levels in salmonids (Saunders et al., 1985; Omeljaniuk and Eales, 1986; Boeuf, unpublished, 1988).

T4 may also indicate the triggering of migratory behaviour (Fontaine et al., 1952; Godin et al., 1974; Fontaine, 1975; Youngson et al., 1986). Close relationships have been found recently between euryhalinity and growth during smolting, under thyroid hormone action (Boeuf and Gaignon, 1989; Boeuf and Le Bail, in prep.).

Few studies have been made on GH in salmonids (Sweeting et al., 1985; Young et al., 1989; Prunet et al., 1989). In Atlantic salmon, increased GH levels occurred coincident with T3 increases at smolting (Prunet et al., 1989). The first GH peak, but not the second, was confirmed using a totally different radioimmunoassay (Le Bail et al., in prep.). However, plasma levels of GH remained high after smolting. In the present study GH and T3 levels peaked together, indicating a possible influence of GH on the T4–T3 conversion (De Luze and Leloup, 1984; Eales, 1985). Hence the first GH surge may be involved in seawater adaptation in Atlantic salmon smolting.

Plasma GH levels rose significantly within 24 h and were sustained for 7–10 days after experience of seawater. After 14 days, seawater and freshwater levels were identical. Bolton et al. (1986) found a transient (24 h) increase after seawater transfer of rainbow trout. Two avenues of research are suggested by the present results: (1) as GH levels change more than do T3 and T4 after seawater transfer in Atlantic salmon, is GH involved in smolting and in seawater osmoregulation?; and (2) as high levels of GH have been associated with stunting in coho after seawater transfer (Bolton et al., 1987), do Atlantic salmon resume growth in seawater when GH levels decrease?

Further studies are also needed to clarify the interrelationships of GH, T3 and T4 during smolting and seawater adaptation.

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