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GROWTH HORMONE AND THYROID HORMONE LEVELS DURING SMOLTING IN DIFFERENT POPULATIONS OF ATLANTIC SALMON

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The physiological, biochemical, and endocrinological changes occurring at smolting are numerous and have been reviewed frequently (Fontaine, 1975; Boeuf, 1987; Hoar, 1988). Among hormones involved in the parr-smolt transformation (cortisol, PRL, adrenaline, ...) thyroid and growth hormones seem to play a major role: thyroxine (T_4) blood plasma surges have been recorded at smolting in Pacific species (Grau *et al.*, 1981; Dickhoff *et al.*, 1982) and in Atlantic salmon (Lindahl *et al.*, 1983; Boeuf and Prunet, 1985). Tri-iodothyronine (T_3) peaks can also occur in this last fish (Boeuf *et al.*, 1989; Prunet *et al.*, 1989). Growth hormone (GH) is known to increase sharply before the end of smoltification (Sweeting *et al.*, 1985; Boeuf *et al.*, 1989; Prunet *et al.*, 1989; Young *et al.*, 1989). Evidence for a direct and specific role of thyroid hormones (TH) in seawater adaptability is not yet forthcoming (Boeuf, 1987); with the recent development of specific radioimmunoassay for salmonid growth hormones, (Bolton *et al.*, 1986; P. Le Bail, J. Carragher, J. Sumpter, unpublished), we can now investigate their biological roles. We propose here to review rapidly the possible actions and the inter-relationships between TH and GH during smolting taking also in account, in field endocrinology, the origin of the salmon broodstock.

THYROID HORMONES

From the first studies published in the fifties and reviewed by Fontaine in 1975 we know of the involvement of TH in smolting processes. Studies have shown, in both Pacific and Atlantic species, the occurrence of T_4 surge(s) some weeks to some days before the best seawater adaptability time as indicated by the highest level of gill microsome (Na^+K^+)-ATPase activity in freshwater fish at the end of the parr-smolt transformation (Folmar and Dickhoff, 1978, 1981; Dickhoff *et al.*, 1982; Sullivan *et al.*, 1983; Boeuf and Prunet, 1985; Virtanen and Soivio, 1985; Boeuf *et al.*, 1989). The work of Grau *et al.* (1981) demonstrated

relationships between T_4 peaks and the lunar cycle in coho and chinook salmon. Such phenomena have subsequently been found in other Pacific species (Yamauchi *et al.*, 1984), but not in species of the genus *Salmo* (Lin *et al.*, 1985; Boeuf, 1987; Boeuf *et al.*, 1989). In the studies where levels were measured, very often no changes were observed during the smolting cycle in Pacific species; however, Dickhoff *et al.* (1982) encountered two increases, the first in February-March and the second, later. These occur regularly in Atlantic salmon (Boeuf and Prunet, 1985; Boeuf *et al.*, 1989). If they are reared in the same conditions (but in different tanks) numerous batches of fish of the same population exhibit T_3 and T_4 peaks exactly at the same time (Boeuf and Gagnon, 1989). These high TH peaks encountered during smolting are not due to changes in properties of plasma TH binding proteins; a high seasonal correlation appears between free and total hormones (Boeuf *et al.*, 1989b). Thyroxine probably exerts a tissue-specific role at these elevated levels.

After transfer to seawater the T_4 level is unaffected or can decrease (Folmar and Dickhoff, 1981; Dickhoff *et al.*, 1982; Boeuf, 1987; Boeuf *et al.*, 1989b) while T_3 can also decrease (Dickhoff *et al.*, 1982; Boeuf *et al.*, 1989a). Milne and Leatherland (1980) concluded that, if TH could be indirectly affected by the salinity, they did not play a major role in seawater adaptation. Folmar and Dickhoff (1981) found that T_4 just prior to seawater entry influenced survival over six months in coho salmon, but estimated that it had no osmoregulatory role there. Pereira and Adelman (1985) concluded likewise for chinook salmon. More recent results in Atlantic salmon (Boeuf, 1987; Boeuf *et al.*, 1989a,b) showed no correlation between T_3 or T_4 levels and seawater adaptability but do agree with previous studies (Dickhoff *et al.*, 1982; Nagahama *et al.*, 1982; Grau *et al.*, 1985) that osmotic capacities are high after the T_4 surge. The transitory high T_4 level (and possibly T_3) may determine the beginning of acquiring euryhalinity, followed by a long period of seawater tolerance; it is after the drop of T_4 , at the highest gill ATPase activity level, that the smolt reaches its maximum capacities of seawater adaptability. Despite this lack of evidence of direct implication of TH in salmonid osmoregulation at the end of the parr-smolt transformation, these hormones play a major role in metabolism, growth, stimulation of silvering, environment memorization, and imprinting, initiation of seawater tolerance, and triggering of migratory behaviour (see the reviews of Boeuf, 1987; Hoar, 1988). To examine this last aspect, we reared in the same hatchery (G. Boeuf, J. Gagnon, P. Le Bail, unpublished data), under the same conditions, three populations of Atlantic salmon originating in short (Namsen in Norway and Elorn in Brittany, <100 km) rivers and in a very long stream (Loire-Allier in France, >900 km). The fish of the two first brookstocks responded "classically" presenting T_3 and T_4 peaks, the latter having occurred 2-3 weeks before the highest gill enzyme activity level (third week of April). Salmon of the long stream exhibited T_4 increase one month earlier (beginning of March). It seems that, even when reared in the same conditions, the fish are able to "pre-determine" migration time so that long distance migrants experience these hormonal changes earlier, but both groups finish smoltification in fresh water and are fully preadapted when they reach the ocean.

GROWTH HORMONE

Few studies have been published on GH during salmonid smoltification (Sweeting *et al.*, 1985; Boeuf *et al.*, 1989; Prunet *et al.*, 1989; Young *et al.*, 1989a). In Atlantic salmon GH peak occurs coincident with T₃ increase at smolting (Boeuf *et al.*, 1989a; Prunet *et al.*, 1989). After the surge, 2-3 weeks before the maximum gill ATPase, the GH blood plasma level remains rather high. After transfer to high salinity seawater GH rises sharply within 24 hours, is sustained for 7-10 days and then decreases to levels identical with freshwater fish after two weeks, these changes occurring slightly before, during, and after the best time to contact seawater (Boeuf *et al.*, 1989a).

GH changes more than TH after freshwater-sea water transfer: is this hormone more directly involved in osmoregulation? GH injections or implants can stimulate gill ATPase activity (Richman and Zaugg, 1987; Boeuf *et al.*, in prep.) and improve seawater adaptability (Komourdjian *et al.*, 1976) better than TH (Miwa and Inui, 1983; Saunders *et al.*, 1985; Omeljaniuk and Eales, 1985; Boeuf, unpublished data). The synergistic effect T₃-GH seems very efficient (Miwa and Inui, 1985). GH is also known as being very active on the peripheral mechanism of T₄ deiodination (De Luze and Leloup, 1984), fundamental in TH action and metabolism (Eales, 1985).

In the experiment presented earlier comparing different Atlantic salmon broodstocks in relationship to the length of the original river, GH levels increased much earlier in Loire-Allier salmon than in short river fishes (G. Boeuf, J. Gaignon, P. Le Bail, unpublished data). In addition to the clear GH involvements in growth and osmoregulation in seawater, this molecule also perhaps plays a role in migration.

From all these data, it's clear that thyroid hormones and growth hormone play a major role during salmonid parr-smolt transformation. Smolting salmonids develop in freshwater most of the systems they will need later in sea water. The effective transfer into salt water (or the active migration) would act only as a final stimulus to achieve these processes. GH and TH appear to allow these transformations not only in terms of growth but also in several changes occurring during smoltification.

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