Aquaculture 362–363 (2012) 127–136

Contents lists available at ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aqua-online

Growth, osmoregulation and endocrine changes in wild Atlantic salmon smolts and post-smolts during marine migration

Sigurd O. Stefansson [a,*], Monika Haugland [a,d], Björn Thrandur Björnsson [b], Stephen D. McCormick [c], Marianne Holm [d], Lars O.E. Ebbesson [a], Jens Chr. Holst [d], Tom O. Nilsen [a]

[a] Department of Biology, University of Bergen, Bergen High Technology Centre, N-5020 Bergen, Norway
[b] Fish Endocrinology Laboratory, Department of Zoology/Zoophysiology, University of Gothenburg, Box 463, SE-40530 Göteborg, Sweden
[c] USGS, Conte Anadromous Fish Research Center, One Migratory Way, PO Box 796, Turners Falls, MA 01376, USA
[d] Institute of Marine Research, P.O. Box 1870 Nordnes, 5817 Bergen, Norway

ARTICLE INFO

Article history:
Received 2 November 2009
Received in revised form 27 April 2011
Accepted 1 July 2011
Available online 13 July 2011

Keywords:
Energetics
Growth hormone
IGF-I
Thyroid hormones
Na^+,K^+-ATPase
IGF-I receptor

ABSTRACT

We have examined physiological parameters associated with seawater adaptability, growth and energetics, as well as major endocrine regulators of these processes in wild migrating Atlantic salmon smolts and post-smolts from the river through the fjord, coastal areas and the open ocean. Muscle RNA/DNA ratio suggests that growth rate increases soon after entry into seawater and continues to increase after the post-smolts reach the offshore banks and the feeding grounds in the Norwegian Sea. Post-smolts prioritize rapid growth and protein deposition in spring and summer, and their energy intake during this period is so high that deposition of energy is possible in addition to muscle growth. An increase in thyroxine (T_4) and triiodothyronine (T_3) levels was observed, suggesting a major activation of hepatic conversion of T_4 to T_3 in post-smolts in seawater, probably related to the high metabolic activity and rapid growth and development of the post-smolts. Decreased plasma growth hormone (GH) levels were observed from the river through the fjord, with levels around 2 ng ml^{-1} in rapidly growing post-smolts, concurrent with an increase in circulating insulin-like growth factor I (IGF-I). An increase in pituitary GH expression levels and hepatic GH receptor (GH-R) and local IGF-I mRNA levels suggest a physiological basis for the changes in circulating GH and IGF-I levels. Receptor expression in brain and pituitary suggests that both hormones are actively involved in the growth and differentiation of these tissues during the critical early marine phase. Gill Na^+,K^+-ATPase (NKA) activity increased to post-smolt levels above 20 μmol ADP mg $prot.^{-1}$ h^{-1}, probably representing long-term NKA activity levels of Atlantic salmon in seawater. Concurrent with the changes in NKA activity the expression of the NKA α1b isoform remained high in post-smolts, while the expression of the NKA α1a decreased from smolts to post-smolts. Both cystic fibrosis transmembrane conductance regulator (CFTR) I and II showed a reduction in mRNA levels from smolts to post-smolts, and remained stable at low expression levels in seawater.

1. Introduction

Following parr–smolt transformation and downstream migration, many stocks of Atlantic salmon (*Salmo salar* L.), including most Norwegian stocks, begin their oceanic migration in large fjord systems and archipelagos before reaching the open ocean. Although our knowledge about the ecology of wild Atlantic salmon post-smolts is limited, previous studies from Norwegian and British waters have suggested that these life stages spend less than a month in the fjords and coastal waters (Dutil and Coutu, 1988; Holm et al., 1982; Hvidsten and Lund, 1988; Thorpe, 1994) before continuing their migration towards the richer feeding grounds in the ocean. During their marine migration, the diet of Atlantic salmon post-smolts changes, and feeding conditions and early marine growth have been postulated to be critical to the overall marine survival and year-class strength of Atlantic salmon (Andreassen et al., 2001; Friedland et al., 2000, 2009; Haugland et al., 2006; McCarthy et al., 2008; Peyronnet et al., 2007; Rikardsen et al., 2004). In the northeast Atlantic, post-smolts are generally found in close relation with the North Atlantic Current (Holm et al., 2000, 2004; Holst et al., 2000; Shelton et al., 1997). In autumn and winter, salmon are present north of the Faroe Islands, feeding mainly on small mesopelagic fish and crustaceans, (Jacobsen and Hansen, 2001) in areas where Atlantic and Arctic water masses meet (Jákupsstovu, 1988).

The completion of parr–smolt transformation and downstream migration represents the culmination of a series of physiological and behavioral changes which are pre-adaptive for seawater entry (Hoar, 1988), with further adaptations taking place in response to seawater (see e.g. Björnsson, 1997; Björnsson et al., 1998; Handeland et al., 1996, 1998, 2000; McCormick, 1995, 2009; McCormick et al., 1989;

* Corresponding author. Tel.: +47 55584470; fax: +47 55584450.
E-mail address: Sigurd.stefansson@bio.uib.no (S.O. Stefansson).

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doi:10.1016/j.aquaculture.2011.07.002

Nilsen et al., 2003, 2007, 2008; Stefansson et al., 2003, 2008). These physiological responses represent a critical part of the adaptive process to ocean conditions and studies have suggested that they confer substantial selective advantages during the critical early marine phase of anadromous salmonids (Andreassen et al., 2001; Levings et al., 1994; Stefansson et al., 2003). Despite the proposed critical role of rapid physiological adaptations for survival and growth, information on the physiological and endocrine changes in wild salmonids during their early marine phase is very limited.

We hypothesize that significant physiological adjustments are made during this period, concurrent with changes in behavior and feeding. Specifically, our hypothesis is that muscle growth (protein synthesis and deposition) is prioritized from the beginning of the oceanic migration in Atlantic salmon post-smolts, concurrent with significant osmoregulatory adjustments, in terms of adaptive changes in the Na^+,K^+-ATPase (NKA) system, the Na^+,K^+,$2Cl^-$ co-transporter (NKCC) and the cystic fibrosis transmembrane conductance regulator (CFTR) in the gills. Further, we propose that these changes are regulated by the key components of the endocrine system; hence we describe changes in the GH–IGF-I system and the thyroid hormones. The objective of this study was, therefore, to examine several important physiological parameters associated with seawater adaptability, growth and energetics, as well as major endocrine regulators of these processes in wild Atlantic salmon smolts and post-smolts during their migration from the river through the fjord, coastal areas and into the open ocean.

2. Materials and methods

2.1. Study area and fish material

The fish used in this study were sampled in 2002 at the following locations; the Vosso River in western Norway, the Trondheimsfjord in central Norway, two offshore banks (the Halten bank and the Sklinna bank off the Norwegian coast) and the major summer feeding area (the Norwegian Sea, Fig. 1, Jákupsstovu, 1988). Smolts from the Vosso River were captured in fresh water (FW) by use of a fish wheel (smolt screw, Meehan, 1961) located near the estuary at Bolstad. The fish wheel rotates with the river current, lifting the smolts gently into a flow-through cage where they are kept until sampling. Post-smolts were captured with a modified surface trawl (Haugland et al., 2006; Holst and McDonald, 2000; Valdemarsen and Misund, 1995) in the fjord and offshore banks during surveys carried out in May and early June 2002 (Table 1). The summer feeding area in the Norwegian Sea was sampled in late June 2002. Briefly, the trawl was fitted with extra flotation on the headline to sample the upper 14 m and was hauled at 3–5 knots. The cod end of the trawl was modified with a live fish capture device, the FISH-LIFT (Holst and McDonald, 2000), which is essentially a floating aquarium. Tow duration ranged from 30 min to 1 h. Our own video observations during trawling have demonstrated that post-smolts are able to sustain the trawling speed, maintaining position inside the trawl and FISH-LIFT for extended periods of time, suggesting that capture stress is not a major concern. Water temperature was 5.9 °C in the river on 11 May 2002. Average temperatures (0–5 m depth) in the marine zones ranged from 10.0 °C in the fjord, 11.5 °C offshore and 11.7 °C in the Norwegian Sea (Table 1). For further details on trawling and sampling see Haugland et al. (2006).

2.2. Sampling

Smolts were gently dip-netted from the fish wheel and kept in a container with flow through fresh water. On board the research vessel, post-smolts were sorted from the rest of the fish in the FISH-LIFT, and kept in a container with flow-through seawater (SW). Within minutes after capture and sorting, smolts and post-smolts

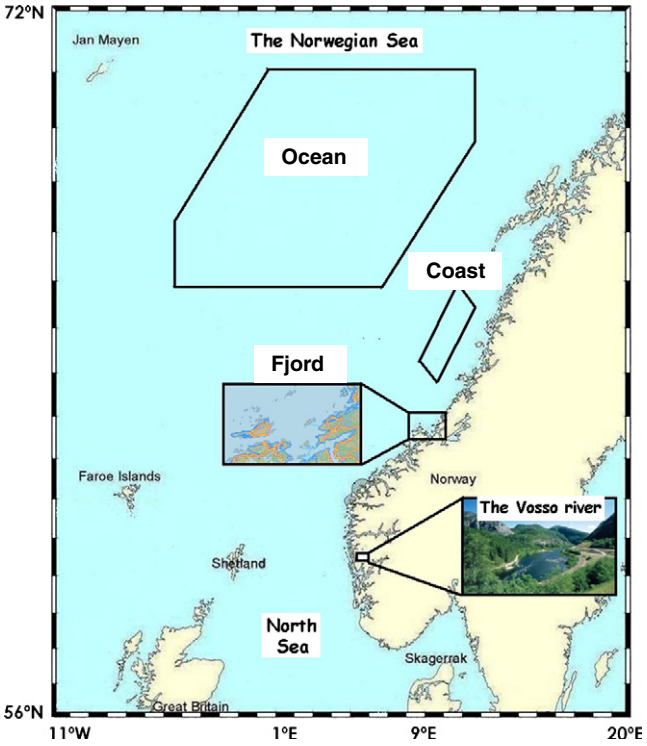

Fig. 1. Map of the study area with reference to sampling areas. Atlantic salmon smolts were sampled from the Vosso River, while post-smolts were sampled from the outer Trondheimsfjord/Frohavet (Fjord), the Halten bank and Sklinna bank (Coast) and the Norwegian Sea (Ocean).

were quickly dip-netted, anesthetized directly in 100 mg l^{-1} buffered tricaine methanesulphonate (MS222; Sigma, St. Louis, MO, USA) and blood was collected from the caudal vessels using 1 ml heparinised syringes. Plasma was separated by centrifugation, frozen on dry ice and stored at −80 °C for subsequent hormone analysis. All fish were weighed (wet weight) and measured (fork length) and the condition factor (CF) was calculated (CF = body weight × 100 × fork length^{-3}). Tissues for determination of mRNA levels and protein abundance were quickly dissected out and frozen directly on dry ice. For Na^+,K^+-ATPase (NKA) activity analysis, the second gill arch on the left side was dissected out, immersed in SEI buffer (250 mM sucrose, 10 mM Na_2-EDTA, 50 mM imidazole at pH 7.3), frozen on dry ice and stored at −80 °C until analysis. The fish were then opened by an incision along the mid-ventral line, their liver weight determined and their stomach contents removed. Post-smolts caught in the Norwegian Sea had a high forage ratio and high proportion of 0-group herring (for further details on analysis of stomach contents see Haugland et al., 2006). Hepatosomatic index was calculated as HSI = liver weight × 100 × body weight^{-1}.

2.3. Analysis

2.3.1. Energetics and muscle moisture

Moisture content was determined as the difference between wet and dry weight (after drying the carcass to a stable dry weight at 70 °C). The carcasses were then homogenized and lipid, protein and energy content of the homogenate were determined. Total protein was determined in a Leco FP-528, utilizing the principle of combustion of a sample and analysis of N_2 gas (Leco, St. Joseph, Michigan, USA). Energy content was analyzed in an IKA C 2000 combustion calorimeter (IKA GmbH, Staufen, Germany). Lipid contents were determined gravimetrically following ethyl acetate/isopropanol extraction, filtration and evaporation of solvent.