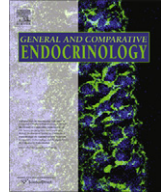




Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

Environmental endocrinology of salmon smoltification

Björn Thrandur Björnsson^a, Sigurd O. Stefansson^b, Stephen D. McCormick^{c,*}^a Fish Endocrinology Laboratory, Department of Zoology/Zoophysiology, University of Gothenburg, Box 463, SE-40530 Göteborg, Sweden^b Department of Biology, University of Bergen, Bergen High Technology Centre, N-5020 Bergen, Norway^c USGS, Conte Anadromous Fish Research Center, One Migratory Way, P.O. Box 796, Turners Falls, MA 01376, USA

ARTICLE INFO

Article history:

Received 4 June 2010

Accepted 7 July 2010

Available online 11 July 2010

Keywords:

Salmon
Trout
Parr
Smolt
Post-smolt
Smoltification
Cortisol
Thyroid hormones
Growth hormone
Insulin-like-growth factor I
Prolactin
Environmental cues

ABSTRACT

Smolting is a hormone-driven developmental process that is adaptive for downstream migration and ocean survival and growth in anadromous salmonids. Smolting includes increased salinity tolerance, increased metabolism, downstream migratory and schooling behavior, silvering and darkened fin margins, and olfactory imprinting. These changes are promoted by growth hormone, insulin-like growth factor I, cortisol, thyroid hormones, whereas prolactin is inhibitory. Photoperiod and temperature are critical environmental cues for smolt development, and their relative importance will be critical in determining responses to future climate change. Most of our knowledge of the environmental control and endocrine mediation of smolting is based on laboratory and hatchery studies, yet there is emerging information on fish in the wild that indicates substantial differences. Such differences may arise from differences in environmental stimuli in artificial rearing environments, and may be critical to ocean survival and population sustainability. Endocrine disruptors, acidification and other contaminants can perturb smolt development, resulting in poor survival after seawater entry.

Published by Elsevier Inc.

1. Introduction

All salmonids begin their lifecycle in freshwater (FW), and the anadromous forms move into seawater (SW) as juveniles, for longer or shorter periods. For a few salmon species, in particular pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*), the larval fry become SW tolerant soon after hatching, allowing them to enter the ocean at an early life-stage. However, other anadromous salmonids, including Atlantic salmon (*Salmo salar*), coho salmon (*O. kisutch*), chinook salmon (*O. tshawytscha*), masu salmon (*O. masu*), amago salmon (*O. rhodurus*), steelhead trout (*O. mykiss*), brown trout (*S. trutta*) and Arctic charr (*Salvelinus alpinus*) do not develop strong SW tolerance until at a significantly later juvenile stage, most often the fish has reached 10–15 cm in body length (McCormick and Saunders, 1987). At this stage, environmental cues/zeitgebers, primarily photoperiod and temperature (Björnsson and Bradley, 2007), initiate the smoltification process, preparing the fish for downstream migration and transition to the marine life-stage.

Smoltification, or parr–smolt transformation, is the biological mechanism which allows the anadromous salmonids to make

use of both the FW and SW environments during their spectacular lifecycle (Hoar, 1976; Folmar and Dickhoff, 1980; Barron, 1986; McCormick and Saunders, 1987; Stefansson et al., 2008; McCormick, 2009). Smoltification is driven by the endocrine system and encompasses, in addition to the establishment of strong hypo-osmoregulatory capacity, a number of morphological, biochemical, physiological and behavioral changes, all of which improve fitness for the pelagic, marine life-stage. These changes include an elongation of the caudal peduncle, suggested to improve pelagic swimming performance (Winans and Nishioka, 1987), further aided by a change in hemoglobin isoforms, increasing the oxygen carrying-capacity of the blood (Fyhn et al., 1991). The change in color from the dark parr coloration, to a silvery body color of the smolt functions as cryptic coloration in open water (Hoar, 1988). There is also a major behavioral switch, from territorial behavior of parr needed to secure the food in rivers with low nutritional sources, to that of schooling behavior of smolts (McCormick et al., 1998), which may decrease predation risks during the river and early marine migration, and can also be an effective predator strategy for salmon in the open ocean.

Salmonid smoltification can be defined as a unique biological process, but in a broader perspective, it is of importance to recognize the number of parallel and/or similar processes which take place in different animal groups. One such important parallel is flatfish

* Corresponding author. Fax: +1 413 863 9810.

E-mail address: mccormick@umext.umass.edu (S.D. McCormick).

metamorphosis (Power et al., 2008), a dramatic larval–juvenile life-stage transition, which, as smoltification, includes a change in body shape, physiology and behavior, allowing a shift in adaptive landscape. However, while flatfish metamorphosis does include a major habitat change, as smoltification, this is a shift within the marine environment from the pelagic to the benthic niche. This does thus not necessitate the major functional reorganization of osmoregulatory tissues linked to the hypo- to hyperosmotic environmental change which takes place during smoltification. Such environmental transitions are, on the other hand, seen in other diadromous fish species such as eels, lampreys striped bass and shads, and even in a number of highly euryhaline fish species such as flounder, killifish, tilapia and others (McDowall, 1988). Even amphibian metamorphosis has most of the same elements as salmon smoltification, with changes in body shape, behavior, respiration and osmoregulation, allowing a shift from aquatic to terrestrial environments (Brown and Cai, 2007).

Over the last few decades, research into the biology of smoltification has generated a huge, published body of data (see Björnsson and Bradley, 2007), as well as a being the focus of a long series of international conferences (Iwata, 2007). There is thus substantial information on how environmental factors impact on the endocrine regulation of smolt development which has been summarized in previous reviews (Björnsson, 1997; Dickhoff et al., 1990; McCormick et al., 1998; Stefansson et al., 2008).

Most of these data are, however, derived from hatchery-raised fish being studied in hatchery or laboratory environments, often with rough simulation of environmental conditions. Although these studies have been of major importance in elucidating key features of the physiological smoltification process and its endocrine control, there are indications that such data may still not accurately depict the processes which take place in wild fish in nature.

The main focus of the present review on “the environmental endocrinology of smoltification” is therefore to examine in greater detail the information available on environmental and endocrine control of smolting, with emphasis on wild salmonids. We will review the available studies on salmon in their natural environment, and through make inferences through comparisons with laboratory studies. Through an understanding of the environmental factors controlling smolt development we hope to allow prediction of impacts of climate change, endocrine disrupting compounds and other anthropogenic impacts on salmon. We will also point out important gaps in our knowledge and potentially fruitful areas for future investigations.

2. Hormones and environmental cues

Smolt development involves the interaction of several endocrine systems, including stimulation by the GH-IGF-I system, cortisol and thyroid hormones, and inhibition by prolactin (Barron, 1986; Björnsson, 1997; McCormick, 2009). GH and cortisol are both significantly elevated during smoltification and induce the major changes in osmoregulatory capacity by stimulating the development of branchial, SW-type chloride cells as well as changing intestinal osmoregulatory function. This allows the fish to compensate for osmotic water losses in the marine environment through drinking of SW, with subsequent extrusion of monovalent ions by the gills and divalent ions by kidneys. Thyroid hormones are also elevated during the smoltification process, and there is evidence for their role in both morphological (silvering) and behavioral (downstream migration) changes, although their precise mechanism of action in promoting downstream migration is still unclear (Ojima and Iwata, 2007). Prolactin increases early in smolt development and decreases at the peak of smolting (Young et al., 1989), and recent data indicate that prolactin is inhibitory to the

actions of GH and smolt development itself (Nilsen et al., unpublished results). In addition, changes in other hormones such as insulin (Plisetskaya et al., 1988; Mayer et al., 1994) and sex steroids (Nagahama et al., 1982; Patiño and Schreck, 1986; Sower et al., 1992; Yamada et al., 1993) have been observed during salmon smoltification, but much less research has been carried out, leaving their roles even more speculative.

Although the whole smoltification may take months to complete, rapid changes in physiology and/or behavior can occur within this time-frame. Thus, establishing well-defined endocrine profiles requires a substantial series of sampling points from a well-defined population of fish. Obtaining this from wild fish populations remains a major challenge, especially as the smoltification period encompasses a migratory phase. The most complete endocrine profiles have therefore been established on captive fish. The best documented species is the Atlantic salmon, for which comprehensive smoltification profiles have been established in a series of studies; for GH (Prunet et al., 1989; Stefansson et al., 1991; Björnsson et al., 1995; McCormick et al., 1995, 2000, 2002; Agustsson et al., 2001; Handeland et al., 2003), IGF-I (Agustsson et al., 2001; McCormick et al., 2000, 2002), cortisol (McCormick et al., 2000, 2002), thyroid hormones (Prunet et al., 1989; McCormick et al., 1995, 2000, 2002) and prolactin (Prunet et al., 1989). Comprehensive endocrine profiles exist also for coho salmon (Sweeting et al., 1985; Björnsson et al., 1989; Young et al., 1989; Sower et al., 1992; Shrimpton et al., 1994a) and to lesser extent for other species.

Both the developmental timing and environmental cues controlling smolt development differ among species and even among populations of the same species (McCormick, 1994). Adding complexity, the various aspects of smolting process are likely to be under the control of different environmental cues. Thus, physiological changes appear to precede the switch to migratory behavior, and it has been suggested that changes in behavior require environmental (e.g., photoperiod) and endocrine ‘priming’ factors that may be similar to those that control physiological development, followed by ‘releasing’ factors (e.g., water temperature or flow) that initiate behaviors (McCormick et al., 1998).

Photoperiod is the most important determinant of the timing of smolt development in Atlantic and coho salmon (McCormick, 1994). Temperature is less important than photoperiod in regulating physiological smolt development, but still has substantial impact (McCormick et al., 2000, 2002). The relative importance of photoperiod and temperature is critical especially in relation to predicted increases in temperature due to climate change. Temperature is likely to control ecological conditions that determine smolt survival during downstream migration and early ocean entry (an “ecological smolt window”). If smolt migration is primarily cued by temperature, then the fish may respond appropriately. However, if photoperiod or water flow is the major cue for migration timing then smolts may have only a limited capacity to shift to earlier migration which would be appropriate for earlier springs caused by climate change (McCormick et al., 1998). Another important factor will be the relative response of freshwater and ocean conditions to climate change; if rivers change more rapidly than coastal environments, then their may be a mismatch between the migratory timing that would promote maximum survival in the two environments.

In at least some species of anadromous salmonids, temperature regulates the length of time during which the smolts are capable of good survival after ocean entry, with elevated temperatures narrowing this “physiological smolt window”. “Desmoltification” is a process including the loss of some, but not all, smolt characters, and takes place if the fish do not reach seawater before the “physiological smolt window” closes. The best documented characteristic of desmoltification is the loss of hypo-osmoregulatory ability (Zaug and McLain, 1976; McCormick et al., 1997), but the involve-

ment of the endocrine system in the loss of smolt characteristics has not been elucidated in detail. In Atlantic salmon smolts, there is a strong correlation between high GH levels in FW and improved hypo-osmoregulatory ability after reaching seawater (Björnsson et al., 1998). Although data on plasma GH levels of FW smolts following peak of smoltification are somewhat ambiguous, both for coho salmon (Young et al., 1989) and Atlantic salmon (Agustsson et al., 2001), both pituitary GH mRNA and *in vitro* pituitary GH secretion rate decreases (Agustsson et al., 2001), indicating a role of GH in desmoltification.

3. Comparisons between hatchery and natural environment

Billions of salmon smolts are raised each year in hatcheries to be aquacultured or released into the wild. This provides easy access to experimental animals and facilities where the smoltification process and its endocrine control can be studied. In contrast, only a few studies have attempted to elucidate the hormonal control of the smoltification process in wild fish in nature, or indeed, if this is affected by the hatchery environments. This is an important issue, as salmonids are still essentially non-domesticated species, being held and studied in man-made environments.

The *Salmo* and the *Salvelinus* species, together with *O. mykiss*, the rainbow/steelhead trout, are iteroparous. Thus, in commercial salmon aquaculture, selected fish can be kept at broodstock facilities for several spawning cycles, and/or used in large selective breeding programs. Most prominent of these is the Norwegian AquaGen selection program for Atlantic salmon (<http://www.aquagen.no/en/>), with the farmed salmon in Norway currently of the 9th AquaGen selection generation. For the above species, large-scale, net-pen cultures are the most common, with growth after smolting of Atlantic salmon occurring in SW, whereas in rainbow, brown, and brook trout as well as Arctic char growth through maturation usually takes place in FW. For both Atlantic salmon and some trout species, there are significant, hatchery-driven restoration and/or recreational fishing programmes in which juveniles, raised from wild-caught parents, are released into the wild, at the alevin, parr or smolt stage. In contrast to the iteroparous species, the Pacific *Oncorhynchus* species are semelparous, dying after spawning. For these species, the dominating aquaculture strategy is to obtain eggs and sperm from returning “wild” adults, and rear juveniles until release for restoration and/or commercial sea ranching.

Irrespective of whether directed rearing-selection programs are being used or not, hatchery rearing will unavoidably have phenotypic as well as genetic effects on the reared fish, likely including epigenetic effects. Thus, hatchery fish are influenced by the rearing environment, which is most often lacking in structural complexity, differences and/or lack of environmental cues, and a higher population density than found in nature. Hatchery practices of parental selection, together with hatchery-related differences in survival relative to wild condition, may have substantial impact on the genetic composition of the fish population (Crozier, 1998).

Artificial rearing environments with environmental cues which differ from those in the wild can result in important differences in smolt development and its endocrine control between captive and wild salmon. This is a significant issue in light of the huge numbers of hatchery-reared juvenile salmon released world wide annually. Hatchery-reared fish generally have lower return rates than fish in the wild (Jonsson et al., 2003), and altered environmental control of smolting may be an important contributing factor to these differences (McCormick et al., 1998). While it is often possible to simulate important environmental conditions/cues such as photoperiod and temperature, or keep them ambient, in the hatchery/laboratory, this is in most cases not practical, and numerous

more subtle environmental parameters are not as easy to emulate. These include the diurnal changes in light intensity, including dawn and dusk, as well as changing nocturnal light conditions due to the lunar cycle. Unless the fish have access to unfiltered, free-flowing river water, such possible environmental cues as diurnal and seasonal changes in temperature, flow rate and silting, as well as seasonal changes in prey items, are lost. Further differences between captive and wild conditions are related to the raceway/tank structures most always used in research. Irrespective of shape or size, these are usually devoid of the complex structural features normally present in the natural environment, including bottom structures such as gravel, rocks and vegetation, as well as banks and bank vegetation, all providing variation in water flow speeds and opportunities for cover and foraging. Such rearing environment impacts negatively on the cognitive development of the fish (Marchetti and Nevitt, 2003), and in combination with high stocking density, effectively abolishes the natural behavior pattern of salmonid juveniles such as establishment of social hierarchies and territoriality. This, in turn, may create conditions of elevated stress, especially notable as cortisol is one of the major smoltification-related hormones. The lack of predators in the captive environment, together with rhythmic, predictable feeding schedules with high-energy diet, further creates conditions different from the natural environment.

However, it should be emphasized that despite all the numerous differences in biotic and abiotic factors noted above, rendering most hatchery and laboratory environments at best an imperfect simulation of the natural conditions, the fact remains that salmonids do smoltify under these “artificial” conditions, and these hatchery-raised fish can successfully survive the SW phase of their lifecycle. This indicates that the smoltification process is a fundamentally robust process, which makes biological sense. If successful parr-smolt transformation was dependent on a large number of environmental signals and conditions, the geographic variation of salmon habitats, together with unpredictable variation in temperature, water flow, nutrient availability, and to some extent light conditions, would easily disrupt the seasonal smoltification process.

As noted earlier, there are, however, a number of indications that there are significant differences between wild and hatchery-reared smolts in number of physiological parameters as well as ultimate reproductive success. McCormick and Björnsson (1994) examined endocrine differences between migrating Atlantic salmon smolts and non-migrant parr that had been released as fry into tributaries of the Connecticut river 2 years earlier as part of a restoration program. Comparisons were also made with the same population of fish kept in the hatchery environment throughout smoltification. Plasma thyroxine (T_4), cortisol and growth hormone (GH) levels were all significantly (5- to 100-fold) elevated in the smolts compared with parr, underscoring the importance of these hormones in driving the smoltification process. In comparison between the river-released smolts, smolts raised and kept in the hatchery had reduced plasma GH and T_4 levels during the smoltification period, and larger increases in plasma cortisol. Wild brown trout smolts captured in two Swedish streams had higher plasma GH and gill Na^+,K^+ -ATPase (NKA) activity compared with hatchery-reared fish of the same stock released into the same stream (Sundell et al., 1998). Coho salmon smolts from the Quinsam River (British Columbia, Canada) were shown to have greater increases in plasma cortisol and the number of gill cortisol receptors in wild fish compared with the same stock maintained and sampled in the hatchery (Shrimpton et al., 1994b). This same stock of wild Quinsam River coho salmon (Canada) had higher gill NKA activity at the time of release, spent less time in the river and estuary, and had higher marine survival than hatchery-reared fish (Chittenden et al., 2008).

Substantial changes in physiological and endocrine status have been observed in hatchery smolts after release into the wild. Higher levels of salinity tolerance, gill NKA activity, plasma GH, IGF-I and T_4 were observed in hatchery-reared Atlantic salmon smolts that had been released into the wild and recaptured a month later during downstream migration compared to fish that remained in the hatchery (McCormick et al., 2003). These endocrine and physiological changes were similar to those seen in the same stock of smolts that had been reared in the wild from first feeding. Thus, many of the differences in hatchery and wild fish may be due to differences in environmental conditions between the two environments.

The environmental factors that are responsible for the stimulation of hormone activity after release of hatchery fish into the wild are unclear. Biotic factors such as food availability and predator-related foraging risks, social interactions such as territorial competition as well as schooling behavior and can affect physiology and endocrine control. Similarly, abiotic factors such as environmental structures, flow, temperature and water quality, could be of importance. Transfer of hatchery-reared Atlantic salmon to 5 and 11 °C temperature treatments characteristic of the hatchery and wild conditions, respectively, resulted in higher levels of plasma GH and IGF-I and lower plasma T_4 in the warmer temperature regime (McCormick et al., 2003). When hatchery-reared honmasu salmon (*O. rhodurus* × *O. masou*) parr were released into a river system and compared with wild parr and parr kept at the hatchery, GH levels were found to be lowest in the wild parr, higher in the hatchery parr and highest in the river-released hatchery parr for 3 months, after which GH levels decreased to become similar to those of the wild parr (Munakata et al., 2000). In interpreting the data, it must be noted that the study covered a period (June–November) of river-resident parr development (0+ age) and not the smoltification period. Starvation or restricted rations result in elevated GH levels within 5–10 days (Pierce et al., 2005) and fast-growing salmonids have lower GH levels than slow-growing conspecifics, a phenomenon related to higher GH-receptor densities and thus also higher GH turn-over rate in fast-growing fish. The elevated post-release GH levels of the honmasu salmon parr over a 3-month period are thus likely the result of a lower feed intake by the released parr than the wild parr during the first 2 months of post-release, seen as a lower stomach fullness (Munakata et al., 2000). While not a release into the natural environment, Zydlewski et al. (2003) transferred 1+ aged hatchery-raised steelhead trout from traditional concrete raceways to a “semi-natural” rearing pond which included some submerged structures. The transfer also resulted in a change in rearing density, but rations were kept similar between the raceway- and pond-reared fish over a 5-month period, from August to January. A striking physiological difference between pond- and raceway-reared fish was the significantly higher levels of plasma GH in pond-reared fish seen both in November and January. This was concomitant with higher growth rate of the pond-reared fish as well as a greater seawater tolerance, indicating a smoltification-related change in physiology and endocrinology.

4. Endocrinology of post-smolts during coastal and ocean migration

Following parr–smolt transformation and downstream migration, salmon move through estuarine and coastal environments before reaching the open ocean. They are considered post-smolts when they leave the estuary and enter full salinity seawater in the coastal zone. Studies from Norwegian and British waters suggest that Atlantic salmon post-smolts spend less than a month in the fjords and coastal waters before continuing their migration towards the richer feeding grounds in the ocean (Holm et al., 1982;

Dutil and Coutu, 1988; Hvidsten and Lund, 1988; Thorpe, 1994). During their early marine migration, the diet of Atlantic salmon post-smolts changes, and feeding conditions and early marine growth are suggested to be critical to the overall marine survival and year-class strength (Andreassen et al., 2001; Friedland et al., 2000, 2009; Rikardsen et al., 2004; Haugland et al., 2006; Peyronnet et al., 2007; McCarthy et al., 2008). The completion of parr–smolt transformation and downstream migration represents the culmination of a series of physiological and behavioral changes which are preparatory for seawater entry (Hoar, 1988; McCormick, 2009), 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 et al., 1989; McCormick, 1995, 2009; Nilsen et al., 2003, 2007, 2008; Stefansson et al., 2003, 2008, in press). These physiological changes 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 (Levings et al., 1994; Andreassen et al., 2001; Stefansson et al., 2003, in press).

A major challenge of salmon smolts during the estuarine and early marine phase is the acclimation to the high salinity of full-strength SW. Gill NKA activity is high in wild smolts during downstream migration (McCormick and Björnsson, 1994; Stefansson et al., 2003, in press), and remains high or increases further in post-smolts in SW. The NKA levels in wild post-smolts in SW, in the range 10–20 $\mu\text{mol ADP mg prot.}^{-1} \text{h}^{-1}$ (Stefansson et al., 2003, in press), are in line with laboratory studies (Nilsen et al., 2007; Stefansson et al., 2007), and likely represent long-term NKA activity of Atlantic salmon in SW. Concurrent with the changes in NKA activity, the relative expression of NKA α subunit isoforms changes. FW smolts show high expression of NKA $\alpha 1b$, and levels remain high in post-smolts in SW. In contrast, NKA $\alpha 1a$ mRNA levels decrease between smolts in FW and post-smolts in the fjord, with a further reduction to undetectable levels in Atlantic salmon post-smolts caught on the summer feeding grounds in the Norwegian Sea (Stefansson et al., in press). These changes agree with laboratory results (Nilsen et al., 2007) during smoltification and SW transfer of Atlantic salmon, and further illustrate the concept of NKA $\alpha 1a$ and $\alpha 1b$ as FW and SW isoforms, respectively (Richards et al., 2003; Nilsen et al., 2007; McCormick et al., 2009).

Once the smolts have left the estuary and entered the coastal zone their growth rate increases as they begin feeding on abundant marine prey (Levings et al., 1994; Andreassen et al., 2001; Stefansson et al., 2003, in press; Rikardsen et al., 2004). Atlantic salmon post-smolts may grow at a rate as high as 1 mm per day during their first spring and summer at sea (Stefansson et al., in press). This high growth estimate is supported by data on marine growth of larger Atlantic salmon post-smolts, found to grow by 0.45 mm a day (Jacobsen, 2000), as well as increased muscle RNA/DNA ratio during the coastal post-smolt migration (Stefansson et al., in press). Post-smolts appear to prioritize rapid growth and protein deposition during the feeding migration in spring and summer, and their energy intake during this period is high enough to allow deposition of energy as lipid and glycogen (Stefansson et al., 2003, in press). From low levels in smolts and early post-smolts, condition factor increases in oceanic fish, concurrent with an increase in lipid levels, hepato-somatic index and total energy content.

The physiological adaptations which take place during the early phase of salmon ocean migration, i.e., high hypo-osmoregulatory capacity, growth and energy metabolism, are all processes that are under control of the growth hormone–IGF-I system (Björnsson, 1997; Björnsson et al., 2002; Reinecke et al., 2005). Plasma GH levels of wild Atlantic salmon smolts were shown to be higher in smolts captured in the fjord compared to those captured in-river

(Stefansson et al., 2003, in press). Similarly, higher levels of plasma GH and IGF-I were observed in hatchery-released smolts in the estuarine zones in Maine (USA) compared to those during river migration (McCormick et al., unpublished results). These increases were followed by slight decreases in both hormones as fish moved several kilometers offshore, perhaps an indication that increased GH and IGF-I is important during initial exposure to seawater. In rapidly growing post-smolts caught off the Norwegian coast and in the Norwegian Sea in summer there were strong reductions in plasma GH levels and a concurrent increase in IGF-I levels. A decrease in the plasma GH/IGF-I ratio is in agreement with laboratory data on fast-growing Atlantic salmon (Stefansson et al., 1991; Nordgarden et al., 2006) and coho salmon post-smolts (Larsen et al., 2001; Beckman et al., 2004a). The findings of Stefansson et al. (in press) of a decrease in circulating GH levels and an increase in IGF-I are in line with the general vertebrate model for the relationship between GH and IGF-I (Wood et al., 2005). Concurrent with low circulating GH levels, an increase in GH production (judged by high pituitary mRNA levels) was observed in rapidly growing oceanic post-smolts, suggesting that GH is quickly removed from circulation by high GH-receptor (GH-R) activity in the liver (judged by increased hepatic GH-R mRNA levels), stimulating hepatic IGF-I production (judged by high hepatic IGF-I mRNA levels) and release of IGF-I into circulation. Comparing the increase in RNA/DNA ratio through post-smolt migration from the river to the high seas with a concurrent increase in IGF-I levels, our results further support IGF-I as a candidate endocrine indicator of growth in fish (Beckman et al., 2004b; Picha et al., 2008).

The findings of Stefansson et al. (in press) further suggest important roles of GH and IGF-I at the level of the brain and pituitary, both as regulators of cellular proliferation and differentiation, and as key elements in the feedback loops regulating production and release of GH and IGF-I. Brain GH and IGF-I receptor transcription was higher in post-smolts than in smolts in FW, suggesting a possible role of GH in the growth and differentiation of the brain in post-smolt salmon. Significant changes were also observed in pituitary IGF-I receptor mRNA levels, with higher transcription in post-smolts in the Norwegian Sea.

THs are involved in a wide range of physiological, developmental and behavioral processes in teleosts (Power et al., 2001; Dufour and Rousseau, 2007; McCormick, 2009). Salmonid smoltification is generally associated with an increase in circulating T_4 levels, while T_3 levels are regulated within a more narrow range (Dickhoff et al., 1985, 1997; Ebbesson et al., 2000, 2008; McCormick et al., 2007; Stefansson et al., 2007). Exposure of smolts to seawater causes a further increase in plasma T_4 levels (McCormick and Saunders, 1990; Young et al., 1995). In hatchery and wild Atlantic salmon smolts there is an increase in both plasma T_4 and T_3 levels in the estuarine and near coastal zone after entry into seawater compared to in-river levels (Stefansson et al., in press; McCormick et al., unpublished results). The high T_4 levels and the continued increase in circulating levels of the biologically more active form, T_3 , suggests a major activation of hepatic conversion of T_4 to T_3 in post-smolts in SW, probably related to the high metabolic activity and rapid growth and development of the post-smolts on the feeding grounds in the Norwegian Sea (Stefansson et al., in press).

5. Endocrine disruption of smolt development

As noted in Section 1, the parr-smolt transformation is a preparatory adaption for downstream migration and seawater entry. There is substantial natural mortality during this period with important consequences for adult return rates. The complexity of this developmental event and the variety of adaptations necessary for migration and success in an altered habitat appear to make smolts susceptible to a variety of external stressors. The anthropo-

genic factors affecting smolts and their consequences for marine survival have recently been reviewed (McCormick, 2009), and we will summarize the key features known to date.

As an endocrine driven developmental event, smolting may be susceptible to environmental contaminants that can act as endocrine disruptors (McCormick, 2009). It has been known for some time that sex steroids can have negative effects on salinity tolerance, behavior, and other aspects of smolt development (Ikuta et al., 1987). Fairchild et al. (1999) observed a positive relationship between the amount of aerial spraying for spruce budworm (which contained the surfactant nonylphenol, a known estrogen mimic) and reduced numbers of returning adults, and hypothesized that nonylphenol may have negatively impacted smolt development. Physiological studies indicate that nonylphenol could disrupt smolt development (Madsen et al., 1997), likely acting through reduced IGF-I plasma levels (McCormick et al., 2005). The levels of nonylphenol required for this inhibition, however, are relatively high and unlikely to affect smolts under environmentally relevant conditions (Lerner et al., 2007a). Further research indicated that exposure of yolk-sac larvae to environmentally relevant levels of nonylphenol can affect smolt development a full year after the exposure period, decreasing salinity tolerance and preference through effects on thyroid hormones, IGF-I and perhaps other endocrine pathways (Lerner et al., 2007b). The mechanism(s) of this potentially epigenetic effect of estrogenic compounds is unclear, but the results underscore the importance of developmental impacts of endocrine disrupting compounds.

The osmoregulatory development that allows smolts to have high seawater tolerance while still in freshwater, may make them more susceptible to external stressors, particularly those that affect ion regulation. The smolt stage of Atlantic salmon is particularly sensitive to acidification and associated increases in aluminum; moderate conditions can lead to direct mortality and less severe conditions result in loss of salinity tolerance and reduced adult return rates (Saunders et al., 1983; Kroglund et al., 2007). These effects on smolts are thought to be responsible for the extirpations of Atlantic salmon that have occurred in response to acid rain in Norway and eastern Nova Scotia (Parrish et al., 1998). Heavy metals also affect ion regulatory capacity in fish, though their impact on smolts has not been widely examined.

A number of persistent organic pollutants have been found to affect smolt development at levels well below those causing mortality. Atlantic salmon smolts exposed to $100 \mu\text{g l}^{-1}$ atrazine have compromised osmoregulatory ability in freshwater, reduced salinity tolerance and lower growth rate after initial seawater exposure (Waring and Moore, 2004; Nieves-Puigdollé et al., 2007). Exposure of coho salmon smolts to the wood preservative didecyl dimethylammonium chloride at 0.75 mg l^{-1} for 24 h resulted in increased plasma cortisol, reduced gill NKA activity and lower salinity tolerance (Johnston et al., 1998). Exposure of Atlantic salmon smolts to $10 \mu\text{g l}^{-1}$ polychlorinated biphenyls (Aroclor 1254) results in reduced gill NKA activity, loss of plasma ions in freshwater and lower behavioral preference for seawater (Lerner et al., 2007c). Pink salmon eggs exposed to polynuclear aromatic hydrocarbon (PAHs, $1\text{--}45 \mu\text{g l}^{-1}$) experienced a dose-dependent decrease of growth rate in sea cages 10 months after the exposure period (Heintz et al., 2000). PAH-exposure ($19 \mu\text{g l}^{-1}$) of pink salmon embryos that were subsequently released as downstream migrating fry resulted in reduced marine survival from 1.3% in controls to 0.8% in exposed fish in 1 year and from 2.0% to 1.7% in the next, underscoring the importance of environmental conditions in determining the impact of contaminants. Environmental contaminants may also interact to affect smolt development; exposure of Atlantic salmon smolts to a mixture of 4-nonylphenol and atrazine resulted in mortality and reduced salinity tolerance, whereas the compounds alone had no detectable effect (Moore et al., 2003).

In addition to effects on development of salinity tolerance, environmental contaminants may affect other aspects of smolt development. The olfactory system of salmonids is affected by a variety of anthropogenic factors, including low pH, carbofuran, cypermethrin and atrazine (McCormick et al., 2009). These factors may affect the ability of smolt to detect prey and predators, and adversely impact imprinting. Migratory behavior, salinity preference and swimming capacity may also be impacted by contaminants with negative effects on smolt survival (McCormick et al., 2009).

6. Conclusions and perspectives

To date, there have been only a few studies that have examined the endocrine and physiological changes that occur during smolt development in the wild. Under appropriate photoperiod and temperature conditions in the hatchery and laboratory, it appears that smolt development occurs in a pattern which is fundamentally similar to that which occurs in nature. It is also clear, however, that the timing and intensity of these changes can differ between hatchery and wild fish, and that these may have substantial implications for survival and the use of hatcheries as a mitigation tool. These differences may arise both from genetic differences, which appear capable of developing within just a few generations, and environmental differences that will be inherent in virtually all captive rearing. However, it may be possible to minimize these differences by determining the environmental factors that contribute to difference in hatchery and wild fish. This is a useful goal, but will require a much greater understanding of how environmental factors control smolt development than we currently possess.

Due to its ease of measure and its obvious importance, there has been a large focus on salinity tolerance and growth in seawater. This may be the most important metric for the salmon culture industry, but other changes involved in smolt development will be important for fish in the wild. Sustained swimming ability, imprinting and homing, prey and predator detection and a myriad of other changes will be important for ocean survival. These are more difficult to quantify, but will be important areas of research to accomplish a more complete understanding of the factors controlling smolt survival.

A classic approach in elucidating endocrine regulation of physiological processes involves *in vivo* hormonal treatments. This approach has been widely and successfully used in the laboratory to elucidate functional relationships, for example between GH and branchial NKA activity in salmonids (Björnsson, 1997). However, to apply this approach in field studies is challenging, with recapture as one of the main problems. Only a few endocrine treatment field studies have been carried out on salmonids, and only during the freshwater phase of the anadromous lifecycle (allowing experimental fish to migrate out to sea certainly augments the recapture problem). In a series of studies, long-term, slow-release GH implants have been used to examine different aspects of growth, foraging, predator risks and survival in semi-natural experimental streams (Johnsson et al., 1999, 2000) or in natural stream systems (Johnsson and Björnsson, 2001; Martin-Smith et al., 2004; Sundt-Hansen et al., 2009), both in resident brown trout parr (Johnsson et al., 1999, 2000; Sundt-Hansen et al., 2009) as well as in Atlantic salmon (Martin-Smith et al., 2004). These studies demonstrate that GH is effective in stimulating increased growth rate at the parr/resident freshwater stage. Even if these studies are only indirectly related to the endocrinology of smoltification, the approach is relevant in terms of future studies on the endocrinology of smoltification in the wild. Examination of the impacts of hormone manipulation on behavioral and physiological aspects of smolting and survival in the marine environment is a challenging but important area for future studies.

Continued development of telemetry and data-logging techniques will allow ever more sophisticated retrieval of physical data from wild, free-swimming fish. The novel use of magnetic field information in data loggers to establish geographic location of migration fish is a recent, important step forward. Development of tag technologies should allow the assessment of the physiological condition of wild fish. Heart rate monitors have already been used in wild fish (Lucas et al., 1991). Future break-through could include development of implantable sensors assessing intraperitoneal fluid or plasma ion concentration or osmolality, and even nutrient and hormone levels. Small and accurate glucose sensors have been developed for diabetics and can be potentially applied to fish. The integration of sophisticated geospatial positioning with physiological monitors would dramatically increase our understanding of the environmental physiology and endocrinology of fish.

Molecular methods have increasingly been used for the last several years to help elucidate molecular mechanisms and their regulation during the smoltification process. For field studies, molecular approaches can provide practical advantages in terms of the relative simplicity of collecting tissue samples, and a way to gain insights into the molecular activity of endocrine tissues. However, it is important not to lose sight of the fact that in endocrinology, it's the circulating hormone which stimulate target tissues, and gene expression or even hormonal content of endocrine tissues have to be interpreted with caution in terms of endocrine system activation. This is exemplified in a recent study on GH endocrinology in Atlantic salmon, where complex and shifting relationships were found between pituitary GH mRNA expression, pituitary GH content and plasma GH levels, with all parameters assessed in the same fish (Benedet et al., 2010). Recently, the "exploratory approach" of using microarrays to identify differential gene expression during salmon smoltification has been employed (Aubin-Horth et al., 2009; Seear et al., 2010). While this is also likely to be valuable approach in studying many physiological processes, the challenges in using this approach in endocrinological research are both that genes involved in hormone production are often only expressed in defined (endocrine) tissues, and the that receptor gene expression is often quite low. Further, as with all observational approaches, it is not the identification of differentially expressed genes themselves which is the key, but placing them in the correct functional endocrine pathways. This may require further development of rapid functional assays.

Laboratory studies have provided a solid foundation for the understanding of the environmental and endocrine control of smolting in anadromous salmonids. However, many of the challenges for salmon conservation and restoration affect smolts, and may specifically involve smolt development, migration and survival. To understand and predict responses to climate change, endocrine disruptors and other anthropogenic influences, it will be crucial to increase our understanding of the environmental endocrinology of smolt development of salmon in nature.

Acknowledgment

This paper has been partly supported by the University of Gothenburg Platform on Integrative Physiology (GRIP).

References

- Agustsson, T., Sundell, K., Sakamoto, T., Johansson, V., Ando, M., Björnsson, B.Th., 2001. Growth hormone endocrinology of Atlantic salmon: pituitary gene expression, hormone storage, secretion, and plasma levels during parr-smolt transformation. *J. Endocrinol.* 170, 227–234.
- Andreassen, P.M.R., Martinussen, M.B., Hvidsten, N.A., Stefansson, S.O., 2001. Feeding and prey-selection of wild Atlantic salmon post-smolts. *J. Fish Biol.* 58, 1667–1679.

- Aubin-Horth, N., Letcher, B.H., Hofman, H.A., 2009. Gene-expression signatures of Atlantic salmon's plastic life cycle. *Gen. Comp. Endocrinol.* 163, 278–284.
- Barron, M.G., 1986. Endocrine control of smoltification in anadromous salmonids. *J. Endocrinol.* 108, 313–319.
- Beckman, B.R., Shimizu, M., Gadberry, B.A., Cooper, K.A., 2004a. Response of the somatotrophic axis of juvenile coho salmon to alterations in plane of nutrition with an analysis of the relationships among growth rate and circulating IGF-I and 41 kDa IGFBP. *Gen. Comp. Endocrinol.* 135, 334–344.
- Beckman, B.R., Fairgrieve, W., Cooper, K.A., Mahnken, C.V.W., Beamish, R.J., 2004b. Evaluation of endocrine indices of growth in individual post-smolt coho salmon. *Trans. Am. Fish. Soc.* 133, 1057–1067.
- Benedet, S., Andersson, E., Mittelholzer, C., Taranger, G.L., Björnsson, B.Th., 2010. Pituitary and plasma growth hormone dynamics during sexual maturation of female Atlantic salmon. *Gen. Comp. Endocrinol.* 167, 77–85.
- Björnsson, B.Th., 1997. The biology of salmon growth hormone: from daylight to dominance. *Fish Physiol. Biochem.* 17, 9–24.
- Björnsson, B.Th., Bradley, T., 2007. Past successes, present misconceptions and future milestones in salmon smoltification research. *Aquaculture* 273, 384–391.
- Björnsson, B.Th., Young, G., Lin, R.J., Deftos, L.J., Bern, H.A., 1989. Smoltification and seawater adaptation of coho salmon, *Oncorhynchus kisutch*: plasma calcitonin levels, calcium regulation and osmoregulation. *Gen. Comp. Endocrinol.* 74, 346–354.
- Björnsson, B.Th., Stefansson, S.O., Hansen, T., 1995. Photoperiod regulation of plasma growth hormone levels during parr-smolt transformation of Atlantic salmon: implications for hypoosmoregulatory ability and growth. *Gen. Comp. Endocrinol.* 100, 73–82.
- Björnsson, B.Th., Stefansson, G.V., Berge, Å.I., Hansen, T., Stefansson, S.O., 1998. Circulating growth hormone levels in Atlantic salmon following seawater transfer: effects of photoperiod regime, salinity, duration of exposure and season. *Aquaculture* 168, 121–137.
- Björnsson, B.Th., Johansson, V., Benedet, S., Einarsdottir, I.E., Hildahl, J., Agustsson, T., Jonsson, E., 2002. Growth hormone endocrinology of salmonids: regulatory mechanisms and mode of action. *Fish Physiol. Biochem.* 27, 227–242.
- Brown, D.D., Cai, L., 2007. Amphibian metamorphosis. *Dev. Biol.* 306, 20–33.
- Chittenden, C.M., Sura, S., Butterworth, K.G., Cubitt, K.F., Plantalech Manel-La, L., Balfry, S., Økland, F., McKinley, R.S., 2008. Riverine, estuarine and marine migratory behaviour and physiology of wild and hatchery-reared coho salmon *Oncorhynchus kisutch* (Walbaum) smolts descending the Campbell River, BC. *Can. J. Fish. Biol.* 72, 614–628.
- Crozier, W.W., 1998. Genetic implications of hatchery rearing in Atlantic salmon—effects of rearing environment on genetic composition. *J. Fish Biol.* 52, 1014–1025.
- Dickhoff, W.W., Sullivan, C.V., Mahnken, C.V.W., 1985. Thyroid-hormones and gill ATPase during smoltification of Atlantic salmon (*Salmo salar*). *Aquaculture* 45, 376.
- Dickhoff, W.W., Brown, C.L., Sullivan, C.V., Bern, H.A., 1990. Fish and amphibian models for developmental endocrinology. *J. Exp. Zool.* 4 (Suppl.), 90–97.
- Dickhoff, W.W., Beckman, B.R., Larsen, D.A., Duan, C., Moriyama, S., 1997. The role of growth in endocrine regulation of salmon smoltification. *Fish Physiol. Biochem.* 17, 231–236.
- Dufour, S., Rousseau, K., 2007. Neuroendocrinology of fish metamorphosis and puberty: evolutionary and ecophysiological perspectives. *J. Mar. Sci. Technol.* (Taiwan) 15, 55–68.
- Dutil, J.D., Coutu, J.M., 1988. Early marine life of Atlantic salmon, *Salmo salar* post-smolts in the Northern Gulf of St. Lawrence. *Fish. Bull.* 86, 197–212.
- Ebbesson, L.O.E., Björnsson, B.Th., Stefansson, S.O., Ekström, P., 2000. Free plasma thyroxine levels in coho salmon, *Oncorhynchus kisutch*, during parr-smolt transformation: comparison with total thyroxine, triiodothyronine, and growth hormone levels. *Fish Physiol. Biochem.* 22, 45–50.
- Ebbesson, L.O.E., Björnsson, B.Th., Ekström, P., Stefansson, S.O., 2008. Daily endocrine profiles in parr and smolt Atlantic salmon. *Comp. Biochem. Physiol.* A 151, 698–704.
- Fairchild, W.L., Swansburg, E.O., Arsenaute, J.T., Brown, S.B., 1999. Does an association between pesticide use and subsequent declines in catch of Atlantic salmon (*Salmo salar*) represent a case of endocrine disruption? *Environ. Health Perspect.* 107, 349–357.
- Folmar, F.C., Dickhoff, W.W., 1980. The parr-smolt transformation (smoltification) and seawater adaptation in salmonids: a review of selected literature. *Aquaculture* 21, 1–37.
- Friedland, K.D., Hansen, L.P., Dunkley, D.A., MacLean, J.C., 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES J. Mar. Sci.* 57, 419–429.
- Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., O'Maoláidigh, N., McCarthy, J.L., 2009. The recruitment of Atlantic salmon in Europe. *ICES J. Mar. Sci.* 66, 289–304.
- Fyhn, E.E.H., Clarke, W.C., Whitler, R.E., 1991. Hemoglobins in smoltifying Chinook salmon, *Oncorhynchus tshawytscha*, subjected to photoperiod control. *Aquaculture* 95, 359–372.
- Handeland, S.O., Järvi, T., Fernö, A., Stefansson, S.O., 1996. Osmotic stress, antipredatory behaviour and mortality of Atlantic salmon (*Salmo salar* L.) post-smolts. *Can. J. Fish. Aquat. Sci.* 53, 2673–2680.
- Handeland, S.O., Berge, Å., Björnsson, B.Th., Stefansson, S.O., 1998. Effects of temperature and salinity on osmoregulation and growth of Atlantic salmon (*Salmo salar* L.) smolts in seawater. *Aquaculture* 168, 289–302.
- Handeland, S.O., Berge, Å., Björnsson, B.Th., Lie, Ø., Stefansson, S.O., 2000. Seawater adaptation by out-of-season Atlantic salmon (*Salmo salar* L.) smolts at different temperatures. *Aquaculture* 181, 377–396.
- Handeland, S.O., Porter, M., Björnsson, B.Th., Stefansson, S.O., 2003. Osmoregulation and growth in a wild and a selected strain of Atlantic salmon smolts on two photoperiod regimes. *Aquaculture* 222, 29–43.
- Haugland, M., Holst, J.C., Holm, M., Hansen, L.P., 2006. Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the northeast Atlantic. *ICES J. Mar. Sci.* 63, 1488–1500.
- Heintz, R.A., Rice, S.D., Wertheimer, A.C., Bradshaw, R.F., Thrower, F.P., Joyce, J.E., Short, J.W., 2000. Delayed effects on growth and marine survival of pink salmon *Oncorhynchus gorbuscha* after exposure to crude oil during embryonic development. *Mar. Ecol. Prog. Ser.* 208, 205–216.
- Hoar, W.S., 1976. Smolt transformation—evolution, behavior, and physiology. *J. Fish. Res. Board Can.* 33, 1233–1252.
- Hoar, W.S., 1988. The physiology of smolting salmonids. In: Hoar, W.S., Randall, D.J. (Eds.), *Fish Physiology*, vol. XIB. Academic Press, NY, pp. 275–343.
- Holm, M., Huse, I., Waatevik, E., Døving, K.B., Aure, J., 1982. Behaviour of Atlantic salmon smolts during seaward migration: I. Preliminary report on ultrasonic tracking in a Norwegian fjord system. *ICES CM* 1982/M:7, 10p.
- Hvidsten, N.A., Lund, R.A., 1988. Predation on hatchery-reared and wild smolts of the Atlantic salmon, *Salmo salar* L., in the estuary of River Orkla, Norway. *J. Fish Biol.* 33, 121–126.
- Ikuta, K., Aida, K., Okumoto, N., Hanyu, I., 1987. Effects of sex steroids on the smoltification of masu salmon, *Oncorhynchus masou*. *Gen. Comp. Endocrinol.* 65, 99–110.
- Iwata, M., 2007. Prologue and acknowledgements. *Aquaculture* 273, 183–184.
- Jacobsen, J.A., 2000. Aspects of the marine ecology of Atlantic salmon. (*Salmo salar* L.). Dr. scient. thesis, University of Bergen, Norway, ISBN 82-7744-072-3.
- Johnsson, J.I., Björnsson, B.Th., 2001. Growth-enhanced fish can be competitive in the wild. *Funct. Ecol.* 15, 654–659.
- Johnsson, J.I., Petersson, E., Jönsson, E., Järvi, T., Björnsson, B.Th., 1999. Growth hormone induced effects on mortality, energy status and growth: a field study on brown trout (*Salmo trutta*). *Funct. Ecol.* 13, 514–522.
- Johnsson, J.I., Jönsson, E., Petersson, E., Järvi, T., Björnsson, B.Th., 2000. Fitness-related effects of growth investment in brown trout under field and hatchery conditions. *J. Fish Biol.* 57, 326–336.
- Johnston, J.M., Seubert, B.D., Kennedy, C.J., 1998. Biochemical effects of didecylidimethylammonium chloride (DDAC) exposure and osmoregulatory stress on juvenile coho salmon, *Oncorhynchus kisutch*. *Arch. Environ. Contam. Toxicol.* 34, 275–279.
- Jonsson, N., Jonsson, B., Hansen, L.P., 2003. The marine survival and growth of wild and hatchery-reared Atlantic salmon. *J. Appl. Ecol.* 40, 900–911.
- Kroglund, F., Finstad, B., Stefansson, S.O., Nilsen, T.O., Kristensen, T., Rosseland, B.O., Teien, H.C., Salbu, B., 2007. Exposure to moderate acid water and aluminum reduces Atlantic salmon post-smolt survival. *Aquaculture* 273, 360–373.
- Larsen, D.A., Beckman, B.R., Dickhoff, W.W., 2001. The effect of low temperature and fasting during the winter on metabolic stores and endocrine physiology (Insulin, insulin-like growth factor-I and thyroxine) of coho salmon, *Oncorhynchus kisutch*. *Gen. Comp. Endocrinol.* 123, 308–323.
- Lerner, D.T., Björnsson, B.Th., McCormick, S.D., 2007a. Aqueous exposure to 4-nonylphenol and 17 β -estradiol increases stress sensitivity and disrupts ion regulatory ability of juvenile Atlantic salmon. *Environ. Toxicol. Chem.* 26, 1433–1440.
- Lerner, D.T., Björnsson, B.Th., McCormick, S.D., 2007b. Larval exposure to 4-nonylphenol and 17 β -estradiol affects physiological and behavioral development of seawater adaptation in Atlantic salmon smolts. *Environ. Sci. Technol.* 41, 4479–4485.
- Lerner, D.T., Björnsson, B.Th., McCormick, S.D., 2007c. Effects of aqueous exposure to polychlorinated biphenyls (Aroclor 1254) on physiology and behavior of smolt development of Atlantic salmon. *Aquat. Toxicol.* 81, 329–336.
- Levings, C.D., Hvidsten, N.A., Johnsen, B.O., 1994. Feeding of Atlantic salmon, *Salmo salar* post-smolts in a fjord in central Norway. *Can. J. Zool.* 72, 834–839.
- Lucas, M.C., Priede, I.G., Armstrong, J.D., Gindy, A.N.Z., Devera, L., 1991. Direct measurements of metabolism, activity and feeding behaviour of pike, *Esox lucius* L., in the wild, by the use of heart rate telemetry. *J. Fish Biol.* 39, 325–345.
- Madsen, S.S., Mathiesen, A.B., Korsgaard, B., 1997. Effects of 17 beta-estradiol and 4-nonylphenol on smoltification and vitellogenesis in Atlantic salmon (*Salmo salar*). *Fish Physiol. Biochem.* 17, 303–312.
- Marchetti, M.P., Nevitt, G.A., 2003. Effects of hatchery rearing on brain structures of rainbow trout, *Oncorhynchus mykiss*. *Environ. Biol. Fish.* 66, 9–14.
- Martin-Smith, K.M., Armstrong, J.D., Johnsson, J.I., Björnsson, B.Th., 2004. Growth hormone increases growth and dominance of wild juvenile Atlantic salmon without affecting space use. *J. Fish Biol.* 65 (Suppl. A), 156–172.
- Mayer, I., Borg, B., Plietskaya, E.M., 1994. Plasma-levels of insulin and liver-glycogen contents in one-year and 2-year old Atlantic salmon (*Salmo salar* L.) during the period of parr-smolt transformation. *Fish Physiol. Biochem.* 13, 191–197.
- McCarthy, J.L., Friedland, K.D., Hansen, L.P., 2008. Monthly indices of the post-smolt growth of Atlantic salmon from the Drammen River, Norway. *J. Fish Biol.* 72, 1572–1588.
- McCormick, S.D., 1994. Ontogeny and evolution of salinity tolerance in anadromous salmonids: hormones and heterochrony. *Estuaries* 17, 26–33.
- McCormick, S.D., 1995. Hormonal control of gill Na⁺,K⁺-ATPase and chloride cell function. In: Wood, C.M., Shuttleworth, T.J. (Eds.), *Cellular and Molecular Approaches to Fish Ionic Regulation*. Academic Press, San Diego, pp. 285–315.
- McCormick, S.D., 2009. Evolution of the hormonal control of animal performance: insights from the seaward migration of salmon. *Integr. Comp. Biol.* 49, 408–422.

- McCormick, S.D., Björnsson, B.Th., 1994. Physiological and hormonal differences among Atlantic salmon parr and smolts reared in the wild, and hatchery smolts. *Aquaculture* 121, 235–244.
- McCormick, S.D., Saunders, R.L., 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. *Am. Fish. Soc. Symp.* 1, 211–229.
- McCormick, S.D., Saunders, R.L., 1990. Influence of ration level and salinity on circulating levels of thyroid hormones in Atlantic salmon (*Salmo salar*). *Gen. Comp. Endocrinol.* 78, 224–230.
- McCormick, S.D., Moyes, C.D., Ballantyne, J.S., 1989. Influence of salinity on the energetics of gill and kidney of Atlantic salmon (*Salmo salar*). *Fish. Physiol. Biochem.* 6, 243–254.
- McCormick, S.D., Björnsson, B.Th., Sheridan, M., Eilertson, C., Carey, J.B., O'Dea, M., 1995. Increased daylength stimulates plasma growth hormone and gill Na^+ , K^+ -ATPase in Atlantic salmon (*Salmo salar*). *J. Comp. Physiol. B* 165, 245–254.
- McCormick, S.D., Shrimpton, J.M., Zydlewski, J.D., 1997. Temperature effects on osmoregulatory physiology of juvenile anadromous fish. In: Wood, C.M., McDonald, D.G. (Eds.), *Global Warming: Implications for Freshwater and Marine Fish*. Cambridge University Press, Cambridge.
- McCormick, S.D., Hansen, L.P., Quinn, T.P., Saunders, R.L., 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 55 (Suppl. 1), 77–92.
- McCormick, S.D., Moriyama, S., Björnsson, B.Th., 2000. Low temperature limits the photoperiod control of smolting in Atlantic salmon through endocrine mechanisms. *Am. J. Physiol.* 278, R1352–R1361.
- McCormick, S.D., Shrimpton, J.M., Moriyama, S., Björnsson, B.Th., 2002. Effects of an advanced temperature cycle on smolt development and endocrinology indicate that temperature is not a zeitgeber for smolting in Atlantic salmon. *J. Exp. Biol.* 205, 3553–3560.
- McCormick, S.D., O'Dea, M.F., Moeckel, A.M., Björnsson, B.Th., 2003. Endocrine and physiological changes in Atlantic salmon smolts following hatchery release. *Aquaculture* 222, 45–57.
- McCormick, S.D., O'Dea, M.F., Moeckel, A.M., Lerner, D.T., Björnsson, B.Th., 2005. Endocrine disruption of parr-smolt transformation and seawater tolerance of Atlantic salmon by 4-nonylphenol and 17 β -estradiol. *Gen. Comp. Endocr.* 142, 280–288.
- McCormick, S.D., Shrimpton, J.M., Moriyama, S., Björnsson, B.Th., 2007. Differential hormonal responses of Atlantic salmon parr and smolt to increased daylength: a possible developmental basis for smolting. *Aquaculture* 273, 337–344.
- McCormick, S.D., Lerner, D.T., Monette, M.Y., Nieves-Puigdoller, K., Kelly, J.T., Björnsson, B.Th., 2009. Taking it with you when you go: how perturbations to the freshwater environment, including temperature, dams, and contaminants, affect marine survival of salmon. *Am. Fish. Soc. Symp.* 69, 195–214.
- McDowall, R.M., 1988. Life history deviation and landlocking. In: *Diadromy in Fishes Migrations Between Freshwater and Marine Environments*. Chapman & Hall, London, pp. 71–185.
- Moore, A., Scott, A.P., Lower, N., Katsiadaki, I., Greenwood, L., 2003. The effect of 4-nonylphenol and atrazine on Atlantic salmon (*Salmo salar* L.) smolts. *Aquaculture* 222, 253–263.
- Munakata, A., Björnsson, B.Th., Jönsson, E., Amano, M., Ikuta, K., Kitamura, S., Kurokawa, T., Aida, K., 2000. Post-released adaptation process of the hatchery-reared masu salmon fry in a river. *J. Fish Biol.* 56, 163–172.
- Nagahama, Y., Adachi, S., Tashiro, F., Grau, E.G., 1982. Some endocrine factors affecting the development of seawater tolerance during parr-smolt transformation of the amago salmon (*Oncorhynchus rhodurus*). *Aquaculture* 28, 81–91.
- Nieves-Puigdoller, K., Björnsson, B.Th., McCormick, S.D., 2007. Effects of hexazinone and atrazine on the physiology and endocrinology of smolt development in Atlantic salmon. *Aquat. Toxicol.* 84, 27–37.
- Nilsen, T.O., Ebbesson, L.O.E., Stefansson, S.O., 2003. Smolting in anadromous and landlocked strains of Atlantic salmon (*Salmo salar*). *Aquaculture* 222, 71–82.
- Nilsen, T.O., Ebbesson, L.O.E., Madsen, S.S., McCormick, S.D., Andersson, E., Björnsson, B.Th., Prunet, P., Stefansson, S.O., 2007. Differential expression of gill Na^+ , K^+ -ATPase α - and β -subunits Na^+ , K^+ , 2Cl^- -cotransporter and CFTR anion channel in juvenile anadromous and landlocked Atlantic salmon *Salmo salar*. *J. Exp. Biol.* 210, 2885–2896.
- Nilsen, T.O., Ebbesson, L.O.E., Kailerich, P., Björnsson, B.Th., Madsen, S.S., McCormick, S.D., Stefansson, S.O., 2008. Endocrine systems in juvenile anadromous and landlocked Atlantic salmon (*Salmo salar*): seasonal development and seawater acclimation. *Gen. Comp. Endocrinol.* 155, 762–772.
- Nordgarden, U., Fjellidal, P.G., Hansen, T., Björnsson, B.Th., Wargelius, A., 2006. Growth hormone and insulin-like growth factor-I act together and independently when regulating growth in vertebral and muscle tissue of Atlantic salmon postsmolts. *Gen. Comp. Endocrinol.* 149, 253–260.
- Ojima, D., Iwata, M., 2007. The relationship between thyroxine surge and onset of downstream migration in chum salmon *Oncorhynchus keta* fry. *Aquaculture* 273, 185–193.
- Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D., Reeves, G.H., 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Can. J. Fish. Aquat. Sci.* 55 (Suppl. 1), 281–287.
- Patiño, R., Schreck, C.B., 1986. Sexual dimorphism of plasma sex steroid levels in juvenile coho salmon, *Oncorhynchus kisutch*, during smoltification. *Gen. Comp. Endocrinol.* 61, 127–133.
- Peyronnet, A., Friedland, K.D., Maoiléidigh, N.O., Manning, M., Poole, W.R., 2007. Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar* L. *J. Fish Biol.* 71, 684–700.
- Picha, M.E., Turano, M.J., Beckman, B.R., Borski, R.J., 2008. Endocrine biomarkers of growth and applications to aquaculture: a minireview of growth hormone, insulin-like growth factor (IGF)-I, and IGF-binding proteins as potential growth indicators in fish. *N. Am. J. Aquacult.* 70, 196–211.
- Pierce, A.L., Shimizu, M., Beckman, B.R., Baker, D.M., Dickhoff, W.W., 2005. Time course of the GH/IGF axis response to fasting and increased ration in chinook salmon (*Oncorhynchus tshawytscha*). *Gen. Comp. Endocrinol.* 140, 192–202.
- Plisetskaya, E.M., Swanson, P., Bernard, M.G., Dickhoff, W.W., 1988. Insulin in coho salmon (*Oncorhynchus kisutch*) during the parr to smolt transformation. *Aquaculture* 72, 151–164.
- Power, D.M., Llewellyn, L., Faustino, M., Nowell, M.A., Björnsson, B.Th., Einarsdottir, I.E., Canario, A.V.M., Sweeney, G.E., 2001. Thyroid hormones in growth and development of fish. *Comp. Biochem. Physiol. C* 130, 447–459.
- Power, D.M., Einarsdottir, I.E., Pittman, K., Sweeney, G.E., Hildahl, J., Campinho, M.A., Silva, N., Sæle, Ø., Galay-Burgos, M., Smáradóttir, H., Björnsson, B.Th., 2008. The molecular and endocrine basis of flatfish metamorphosis. *Rev. Fish. Sci.* 16 (S1), 93–109.
- Prunet, P., Boeuf, G., Bolton, J.P., Young, G., 1989. Smoltification and seawater adaptation in Atlantic salmon (*Salmo Salar*). Plasma prolactin, growth hormone, and thyroid hormones. *Gen. Comp. Endocrinol.* 74, 355–364.
- Reinecke, M., Björnsson, B.Th., Dickhoff, W.W., McCormick, S.D., Navarro, I., Power, D.M., Gutierrez, J., 2005. Growth hormone and insulin-like growth factors in fish: where we are and where to go. *Gen. Comp. Endocrinol.* 142, 20–24.
- Richards, J.G., Sample, J.W., Bystriansky, J.S., Schulte, P.M., 2003. Na^+ / K^+ -ATPase α -isoform switching in gills of rainbow trout (*Oncorhynchus mykiss*) during salinity transfer. *J. Exp. Biol.* 206, 4475–4486.
- Rikardsen, A.H., Haugland, M., Bjørn, P.A., Finstad, B., Knudsen, R., Dempson, J.B., Holst, J.C., Hvidsten, N.A., Holm, M., 2004. Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. *J. Fish Biol.* 64, 1655–1679.
- Saunders, R.L., Henderson, E.B., Harmon, P.R., Johnston, C.E., Eales, J.G., 1983. Effects of low environmental pH on smolting of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 40 (8), 1203–1211.
- Seear, P.J., Carmichael, S.N., Talbot, R., Taggart, J.B., Bron, J.E., Sweeney, G.E., 2010. Differential gene expression during smoltification of Atlantic salmon (*Salmo salar* L.): a first large-scale microarray study. *Mar. Biotechnol.* 12, 126–140.
- Shrimpton, J.M., Bernier, N., Randall, D.J., 1994a. Changes in cortisol dynamics in wild and hatchery-reared juvenile coho salmon (*Oncorhynchus kisutch*) during smoltification. *Can. J. Fish. Aquat. Sci.* 51, 2179–2187.
- Shrimpton, J.M., Bernier, N.J., Iwama, G.K., Randall, D.J., 1994b. Differences in measurements of smolt development between wild and hatchery-reared juvenile coho salmon (*Oncorhynchus kisutch*) before and after saltwater exposure. *Can. J. Fish. Aquat. Sci.* 51, 2170–2178.
- Sower, A.S., Karlson, K.H., Fawcett, R.S., 1992. Changes in plasma thyroxine, estradiol-17 β , and 17 α ,20 β -dihydroxy-4-pregnen-3-one during smoltification of coho salmon. *Gen. Comp. Endocrinol.* 85, 278–285.
- Stefansson, S.O., Björnsson, B.Th., Hansen, T., Haux, C., Taranger, G.L., Saunders, R.L., 1991. Growth, parr-smolt transformation and changes in growth hormone of Atlantic salmon (*Salmo salar*) reared under different photoperiods. *Can. J. Fish. Aquat. Sci.* 48, 2100–2108.
- Stefansson, S.O., Björnsson, B.Th., Sundell, K., Nyhammer, G., McCormick, S.D., 2003. Physiological characteristics of wild Atlantic salmon post-smolts during estuarine and coastal migration. *J. Fish Biol.* 63, 942–955.
- Stefansson, S.O., Nilsen, T.O., Ebbesson, L.O.E., Wargelius, A., Madsen, S.S., Björnsson, B.Th., McCormick, S.D., 2007. Molecular mechanisms of continuous light inhibition of Atlantic salmon parr-smolt transformation. *Aquaculture* 273, 235–245.
- Stefansson, S.O., Björnsson, B.Th., Ebbesson, L.O.E., McCormick, S.D., 2008. Smoltification. In: Finn, R.N., Kapoor, B.G. (Eds.), *Fish Larval Physiology*. Science Publishers, Enfield, pp. 639–681.
- Stefansson, S.O., Haugland, M., Björnsson, B.Th., McCormick, S.D., Holm, M., Ebbesson, L.O.E., Holst, J.C., Nilsen, T.O., in press. Growth, osmoregulation and endocrine changes in wild Atlantic salmon smolts and post-smolts during marine migration. *Aquaculture*.
- Sundell, K., Dellefors, C., Björnsson, B.Th., 1998. Wild and hatchery-reared brown trout, *Salmo trutta*, differ in smolt related characteristics during parr-smolt transformation. *Aquaculture* 167, 53–65.
- Sundt-Hansen, L., Neregård, L., Einum, S., Höjesjö, J., Björnsson, B.Th., Hindar, K., Økland, F., Johnsson, J.L., 2009. Growth enhancement increases movement activity of brown trout in the wild. *Funct. Ecol.* 23, 551–558.
- Sweeting, R.M., Wagner, G.F., McKeown, B.A., 1985. Changes in plasma glucose, amino acid nitrogen and growth hormone during smoltification and seawater adaptation in coho salmon, *Oncorhynchus kisutch*. *Aquaculture* 45, 185–197.
- Thorpe, J.E., 1994. Salmonid fishes and the estuarine environment. *Estuaries* 17, 76–93.
- Waring, C.P., Moore, A., 2004. The effect of atrazine on Atlantic salmon (*Salmo Salar*) smolts in fresh water and after sea water transfer. *Aquat. Toxicol.* 66, 93–104.
- Winans, G.A., Nishioka, R.S., 1987. A multivariate description of change in body shape of coho salmon (*Oncorhynchus kisutch*) during smoltification. *Aquaculture* 66, 235–245.
- Wood, A.W., Duan, C.M., Bern, H.A., 2005. Insulin-like growth factor signaling in fish. *Int. Rev. Cytol.* 243, 215–285.
- Yamada, H., Ohta, H., Yamauchi, K., 1993. Serum thyroxine, estradiol-17 β , and testosterone profiles during the parr-smolt transformation of masu salmon, *Oncorhynchus masou*. *Fish. Physiol. Biochem.* 12, 1–9.

- Young, G., Björnsson, B.Th., Lin, R.J., Bolton, J.P., Prunet, P., Bern, H.A., 1989. Smoltification and seawater adaptation in coho salmon, *Oncorhynchus kisutch*: plasma prolactin, growth hormone, thyroid hormones and cortisol. *Gen. Comp. Endocrinol.* 74, 335–345.
- Young, G., McCormick, S.D., Björnsson, B.Th., Bern, H.A., 1995. Circulating growth hormone, cortisol and thyroxine levels after 24 hour seawater challenge of yearling coho salmon at different developmental stages. *Aquaculture* 136, 371–384.
- Zaugg, W.S., McLain, L.R., 1976. Influence of water temperature on gill sodium, potassium-stimulated ATPase activity in juvenile coho salmon (*Oncorhynchus kisutch*). *Comp. Biochem. Physiol.* 54A, 419–421.
- Zydlewski, G.B., Foott, S., Nichols, K., Hamelberg, S., Zydlewski, J.D., Björnsson, B.Th., 2003. Enhanced smolt characteristics of steelhead trout exposed to alternative hatchery conditions during the final months of rearing. *Aquaculture* 222, 101–117.