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Epilogue: Past successes, present misconceptions and future milestones in salmon smoltification research

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Abstract

Although the parr–smolt transformation of salmonids has been investigated for some fifty years, an array of specific aspects of the process remains unclear. At the 7th International Workshop on Salmon Smoltification convened in Tono, Japan, there was a consensus for the need for a review of the most pertinent findings on smoltification over the years and a discussion of what the future holds. We present here a three-part summary based to a large extent on the presentations and lively discussions which took place at the Workshop. The first part outlines some of the impressive successes this research has fostered. The second part deals with some current misconceptions, often based on over-interpretation of data and/or the lack of data. Finally, a discussion of future targets and aims and their applications is presented.

Keywords: Review; Parr; Smolt; Transformation

1. Introduction

Through the smoltification process, juvenile salmon parr transform into smolts, a physiological state which continues to defy definition. Following downstream migration and seawater entry, the smolts emerge as marine, predatory fish and later complete their adult lifecycle by an anadromous migration to spawn (and often to die) in their natal river (Hoar, 1976). Since the early eighties, scientists have gathered every four years to discuss the latest data on smoltification research in a series of workshops. Illustrating the wide international interest in the topic, these workshops have so far been held in the USA, Scotland, Norway, Canada, Finland and Ireland and in July 2005, Dr. Munehico Iwata hosted some 32 scientists in the rural town of Tono in Japan to continue this discussion at the 7th International Workshop on Salmon Smoltification (Fig. 1).

A total of 30 papers were presented covering migration/behavior (5 papers), ion transport (6), genetics (3), environment (3), nutrition (2), endocrinology (8) and impacts of pollution (3). After some 30 years of international research on the topic a degree of retrospection/introspection seems appropriate. In particular, what are the practical applications of this work, does it remain relevant and is there a pressing need to continue this research? The relevance and ubiquitous nature of smoltification research is readily apparent by simple internet searches. "Googling" the term "smoltification" generates approximately 68,300 hits and a BIOSIS (Biological Abstracts) search using the search term "smolt*" generates a list of 1502 papers (May 5, 2005 at 15:00 GMT). The fact that 126 of these papers were published in 2004 or later, clearly demonstrates that the research interest continues unabated. The progression of smoltification physiology

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Fig. 1.

research from basic morphology (e.g., silvering and condition factor) to molecular based approaches is obvious from the 37,909 gene product sequences submitted to GenBank that are classified as smoltification-associated. One likely reason for the continued relevance is that in smoltification research, there is an unusually small separation between "question-driven", fundamental, biological research and "problem-driven", aquaculture-related, applied research. This often allows seemingly basic data to be applied in the field within a relatively short time. Terms such as "strategic research" and "translational research" are now employed to avoid the somewhat obsolete separation of research into "basic" or "applied".

To explain not only to the scientific community, but in particular to granting agencies, program directors and legislators, the continuing need for research efforts in this area, we present here a three-part summary based to a large extent on the presentations and lively discussions which took place at the 7th Smolt Workshop. The first part outlines some of the impressive successes this research has fostered. The second part deals with some current misconceptions, often based on over-interpretation of data and/or the lack of data. Finally, a discussion of future targets and aims and their applications is presented.

2. Past successes

Basic research into parr–smolt transformation, includes studies which have probed the numerous biochemical, morphological, physiological and behavioral changes which take place during this developmental process, as well as the endocrine regulation of these processes and the underlying entrainment by environmental cues such as photoperiod, lunar phases, temperature, salinity, turbidity and flow rate (Hoar, 1988). Added dimensions are brought in with studies on genetics and ecology. At the time advances in our fundamental knowledge of the smoltification process are made, the impact on aquaculture production or other applied aspects of salmon biology is seldom clear. However, in retrospect it is all the more apparent how basic research has led to key advances in improving productivity and sustainability of a major industry, as well as advances in natural resource management. Several prominent examples come to mind.

2.1. Bimodality and threshold size

Early work on hatchery-reared populations of Atlantic (*Salmo salar*) and coho (*Oncorhynchus kisutch*) salmon revealed a bimodal size distribution (lower and upper growth modes) during the late parr stage due to different growth trajectories of individuals (Kristinsson et al., 1985). Fish in the upper size mode typically undergo smoltification the following spring at 1+ age, whereas lower mode individuals require an additional year before smolting at 2+ years (Thorpe, 1977; Thorpe and Morgan, 1978; Thorpe et al., 1980; Saunders et al., 1982; Thorpe et al., 1982). This phenomenon is linked to the existence of a threshold size for smoltification in these species, first hypothesized by Elson (1957) and confirmed in later work (Wedemeyer et al., 1980; Mahnken et al., 1982). These discoveries have been instrumental in understanding growth dynamics during the parr stage and facilitating prediction of smoltification well in advance of the process. This knowledge is the basis for several successful aquaculture management practices including grading and retaining parr in the upper mode which results in production of robust and functional 1+ year smolts exhibiting limited mortalities and stunting upon transfer to seawater.

2.2. Photoperiod as the zeitgeber

Photoperiod has long been known to be of crucial importance for the smoltification process (Saunders and Henderson, 1970), and may be defined as a *zeitgeber* for the process (Duston and Saunders, 1990; Björnsson et al., 1995). Manipulation of photoperiod, involving a long-day "summer" photoperiod interrupted with a "winter" period of short daylength has been employed successfully to produce out-of-season smolts (Björnsson et al., 2000; Handeland and Stefansson, 2001) allowing transfer or release of fish to the marine environment beyond the relatively short window of opportunity in the spring. More recently, the knowledge of threshold size and the importance of photoperiod have been combined in an aquaculture practice, where underyearling Atlantic salmon are grown at an accelerated rate to reach a threshold size in July after which a short-day photoperiod is used to induce smoltification of 0+ age fish in the autumn. The markedly reduced length of the freshwater phase and time to attain harvest size is a major new innovation in the intensive culture of Atlantic salmon, with some 30–40% of smolts produced in Norway out-of-season or at 0+ age (S. Stefansson, pers. com.).

2.3. Smolt indicators

Study of the physiology of parr–smolt transformation has revealed an array of physiological and endocrine pathways requisite for survival and growth in seawater. A direct benefit of this has been the development of indicators of smolt quality or readiness. Increased activity of branchial Na^+, K^+-ATPase accompanies hypoosmoregulatory ability and is currently a universally applied indicator of readiness of smolts for release or transfer to seawater netpens (Zaugg and Wagner, 1973; Langhorne and Simpson, 1986; McCormick et al., 1989). An *in vivo* measure derived from this is the seawater challenge test (Clarke, 1982) in which plasma ion levels are measured 24–72 h post-transfer to seawater or hypersaline conditions as an indicator of hypoosmoregulatory ability. Use of these markers helps avoid the problem of high mortality and/or growth suppression (stunting), which occurs when juvenile coho (Bern, 1978) and Atlantic salmon (Björnsson et al., 1988) are transferred to seawater prematurely. The enhanced survival of smolts in commercial aquaculture translates directly into increased economic gain to the producer. Intensive investigation of smolt physiology also has provided tools and indicators to measure overall smolt quality and the negative effects of various husbandry procedures (e.g., night security lights, constant elevated temperatures) on development (Patino et al., 1986; Handeland et al., 2003).

2.4. Environmental factors

Research has revealed the deleterious effects of environmental degradation on the smoltification process and ultimately returns of wild salmon. Perhaps the most striking example of this is acidification of streams and rivers and aluminum toxicity. In acidic waters, low molecular mass cationic Al-species (Al(i)) increase and accumulate on the epithelial cells of the gill causing ionoregulatory and respiratory failures in parr and smolt as well as mortality (Kroglund and Staurnes, 1999; Teien et al., 2005). Smolts appear to be particularly sensitive to acidic water (Kroglund and Staurnes, 1999). Addition of lime to the Bjerkreme and Mandal Rivers in southern Norway markedly increased fry density from 10 fish to 60 fish per 100 m^2 (NASCO, 2005). Even more notable is the increase in returning adults captured by angling from 5 MT prior to liming in the 1980s to some 40 MT in 2003. In southern Norway an extensive project is underway with 22 rivers receiving treatment with lime intermittently to increase pH. The efforts are projected to increase annual angling river catches by some 75–100 MT (NASCO, 2005).

3. Present misconceptions

At any given time in history, in any field of the natural sciences, both experts and laymen have had misconceptions about the state of the art. As new hypotheses are tested, rejected or accepted, new knowledge emerges and past misconceptions disappear. However, preconceived ideas, incorrect interpretation of data and insufficient testing of hypotheses may, at any given time, lead us astray. In the field of fish physiology, data from other vertebrate classes, especially mammals, are often accepted to hold true for fish even in the absence of evidence. With some 29,000 species in this highly diversified class of vertebrates, including 189 species of salmonids (www.fishbase.org), data from one or two species are often used inappropriately to draw generalized conclusions. Speculative interpretations of a single study are often referred to and reiterated without critical evaluation of the underlying data, creating dogmas which can pass unchallenged for all too long. Incorrect understanding of the smoltification process may not only lead scientists astray in developing new hypotheses and experimental designs, but of equal consequence, it can lead to incorrect practices by the aquaculture industry and those working on other aspects of natural resource management of salmonids. In the following section several potential misconceptions regarding smoltification are highlighted, including some long-held dogmas.

3.1. There is an underlying endogenous rhythm for parr–smolt transformation

Statements to this effect are widely repeated throughout the literature, often as a general statement in an introduction to smoltification in research papers. In reality, there is only a single study carried out by Eriksson and Lundquist in 1982, in which a serious attempt has been made to examine whether or not endogenous circannual rhythms influence spring smoltification of Atlantic salmon. The investigation was limited in scope, working with 2+ age parr over a period of 10 months, and as a result was somewhat inconclusive. Thus, almost 25 years after Eriksson and Lundquist first addressed the question of whether salmon smoltification is governed by an endogenous rhythm, it still remains largely unanswered. Although the question of whether or not salmon maintained in the laboratory can smoltify twice was raised a few years ago, and subsequently verified (Shrimpton et al., 2000), in the natural life cycle of anadromous coho and Atlantic salmon, smoltification is a once-in-a-lifetime event.

3.2. Laboratory studies accurately reflect the status, condition and behavior of wild fish

Salmon are readily reared in the laboratory and if maintained under appropriate environmental conditions will undergo smoltification. However, numerous studies have demonstrated that parr reared under standardized laboratory conditions or in hatcheries do not necessarily reflect the changes observed in wild smolts. Oftentimes the time frame or degree of change is shifted (Zaugg, 1982; Mizuno et al., 2000; Handeland et al., 2003). Indeed, marked changes have been observed in several smolt indicators only after fish are released to the wild (Zaugg and Wagner, 1973; McCormick et al., 2003).

3.3. Releases of hatchery-raised smolts will strengthen wild populations

The differences in laboratory/hatchery-reared fish and wild fish mentioned above raise the question of whether these fish contribute significantly to wild runs. This issue continues to be hotly debated, with introduction of pathogens by hatchery fish (Butler, 2002) and a potential dilution in the gene pool by interbreeding of wild and hatchery-reared fish cited as putative deleterious effects (Heggberget et al., 1993; McGinnity et al., 1997; Youngson et al., 2001). The ability of hatchery-reared fish to avoid predators and compete for resources also has been questioned (Brown and Laland, 2002; Brown et al., 2003).

3.4. Bigger is better

Although there is some merit to this old adage in that larger smolts appear better able to elude predators (Salminen and Kuikka, 1995), the use of high rearing temperatures over extended periods to enhance growth can deleteriously impact the smoltification process, e.g., inhibit an increase in Na^+,K^+-ATPase (Zaugg and Wagner, 1973; Ewing et al., 1979; Handeland et al., 2000).

3.5. A thyroxine surge initiates smoltification and downstream migration

A surge or peak in thyroid hormones associated with parr–smolt transformation has been well documented in a variety of species (Hoar, 1988). Although originally believed to be a critical factor regulating the timing of smoltification, more recent evidence suggests that T_3 and T_4 have a passive role in the process, perhaps by stimulating metabolic rate and acting synergistically with other hormones (Hoar, 1988). Although exogenous thyroid hormones are efficacious in inducing metamorphosis of anuran amphibians (Helbing et al., 1996), in anadromous salmonids oral or waterborne administration of thyroid hormones stimulates silvering and fin margination, but does not induce smoltification or hypoosmoregulatory ability (Refstie, 1982; Sullivan et al., 1987; McCormick 2001). Research by Ojima and Iwata (2007-this volume) presented at the workshop suggests that while thyroid hormones do play a pivotal role in preparation for downstream migration, multiple factors are involved in actual initiation of movement. Oral administration of exogenous T_4 (1 mg/kg diet) significantly increased circulating concentrations of T_3 and T_4, but did not stimulate downstream movement of chum salmon (*O. keta*) fry.

4. Future milestones

In 2003 some 1.82 million MT of salmonids were produced globally with an estimated value of US$5.6 billion (FAO, 2004). Since 1991 some 5–6 billion Pacific salmon juveniles have been released annually to the Pacific Ocean to supplement wild stocks (Beamish et al., 1997). For Atlantic salmon, a major strategy for stock conservation has been to eliminate ocean catches, which decreased to about 2000 MT in 2004. At the same time, ocean ranching of Atlantic salmon has all but ceased (ICES, 2005). Thus, while massive ocean releases of Atlantic salmon are not carried out, various local, regional and national release programs are ongoing, in order to restore and/or strengthen river populations. As an example, 2.5 M smolts are currently released annually in Sweden, to compensate for losses caused by hydroelectric power plants (Swedish Fisheries Board, unpublished statistics). Continued research on parr–smolt transformation is essential to address a variety of pertinent issues to facilitate enhancement efforts and increase economic gain to commercial producers. A constellation of new techniques in physiology, molecular biology, tracking fish movement and stock identification will facilitate addressing lingering questions and new issues such as those described below.

4.1. Production of "wild" salmonids for supporting/sustaining natural populations

It has become all too clear that stocks of many species of Pacific salmon and wild Atlantic salmon throughout the range of the animal are imperiled. Efforts to supplement wild stocks with hatchery-reared fish have met with mixed success (Virtanen et al., 1991; McCormick et al., 2003). A more comprehensive understanding of the comparative physiology, endocrinology, genetic and behavioral components of parr–smolt transformation in wild and hatchery-reared fish would facilitate the rearing and release of smolts better able to survive in the wild and enhance wild stocks without dilution of the gene pool.

4.2. The effects of toxicants and pollutants on parr–smolt transformation

Restoration of river systems and a reduction in pollution have become a priority in most developed nations. However, low levels of pollutants from a variety of sources entering the freshwater rearing habitat of anadromous salmonids continue to be a constraint toward maintenance or restoration of native runs. Research to assess the effects of low levels of anthropogenic compounds and their interactions on parr survival and smoltification is critical to maintain healthy, sustainable populations. Although research into the effects of compounds other than aluminum is limited, several reports suggest that estradiol and 4-nonylphenol may disrupt specific aspects of the smoltification process (Madsen et al., 2004; McCormick et al., 2005).

4.3. Genomics and proteomics

Sequencing of the Atlantic salmon genome will provide researchers with new tools to search for genes involved in smoltification related processes such as growth, osmoregulation, migration and imprinting. Efforts led by the Genomics Research on Atlantic Salmon Project (web.uvic.ca/cbr/grasp/) and the Norwegian Salmon Genome Project (www.salmongenome.no) have resulted in isolation of some 80,000 expressed sequence tags from salmon providing the basis for a number of DNA microarrays (Davey et al., 2001; Rise et al., 2004) and construction of highly redundant bacterial artificial chromosome libraries that will facilitate gene discovery (Thorsen et al., 2005) and mapping of the genome (Ng et al., 2005). Functional identification of genes would provide the opportunity for in-depth study of the mechanisms and pathways involved, with the potential for modifying expression of target genes or using them as markers for traits of interest. Functional analyses of novel gene products related to smoltification have been limited to a few genes markedly upregulated by osmotic stress such as Shop21 and SGRP (Pan et al., 2002, 2004). Quantitative trait loci (QTL) have been identified for a number of characteristics of commercial importance in Atlantic salmon such as bodyweight (Reid et al., 2005) and disease resistance (Moen et al., 2004) but not for smoltification related traits as of yet. Identification of QTLs for desirable smolt characteristics would assist in acquisition of these traits (e.g., increased growth rates) via traditional breeding or genetic engineering (Fjalestad et al., 2003). Recently, interest in biomedical sciences has turned to the proteome (PROTEin complement to a genOME; www.expasy.org). The field of proteomics was developed to complement physical genomic research and enable qualitative and quantitative comparison of the constellation of cellular proteins under different conditions. This approach has been employed to discover an array of differentially expressed proteins in liver and kidney of salmon infected with different pathogens (Booy et al., 2005). While such methodologies have great utility for unraveling the mysteries of smoltification, efforts on this front have been limited largely to the use of standard and two-dimensional gel electrophoresis (Johanning and Bradley, 1989; Smith et al., 1999).

4.4. New welfare standards for ethical aquaculture practices

A greater awareness of the need for humane treatment of agricultural animals has stimulated much discussion and alteration of husbandry procedures. While efforts have primarily focused on terrestrial endotherms, consideration should be given to methods employed for husbandry and harvest of salmonids (Damsgaard et al., 2006). Germane to this report is how husbandry methods (e.g., rearing densities, water quality, constant light regimens) might impact the production and "well-being" of smolts.

4.5. Improving sustainability by changing nutritional sources

To meet protein requirements, fish meal comprises up to 50% of the total mass of diets for anadromous salmonids. Although, a greater percentage of world fish meal production is used for terrestrial domestic animal feeds, a reduction in the use of fish meal in carnivorous fish diets would conserve dwindling fishery resources and potentially increase profitability of commercial operations (Naylor et al., 2000). Increased utilization of plant proteins in salmonid diets will require additional research in a variety of areas including anti-nutrients, digestibility and utilization. Of particular relevance is the effect of such feeds on juvenile growth and parr–smolt transformation.

5. Conclusions

Our understanding of parr–smolt transformation continues to expand in many areas. Significant progress has been made in addressing several issues pertinent to commercial culture and mitigation/restoration of stocks of anadromous salmonids. However, an array of physiological and ecological problems (e.g., the effects of global warming) remain to be investigated if wild fish are to prosper and commercial culture is to become more economical. It will be of great interest to see which of these problems are answered by the 8th International Workshop on Salmon Smoltification to be held in Oregon, USA, in 2009.

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