

How salmon prepare for life in the ocean: An introduction to William Hoar's "The physiology of smolting salmonids"

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In this paper Steve McCormick discusses the impact of William (Bill) S. Hoar's chapter "The Physiology of Smolting Salmonids" in *Fish Physiology*, Volume XIB, published in 1988.

As part of their anadromous life cycle most anadromous salmon undergo a parr-smolt transformation that prepares juveniles for downstream migration and seawater entry. This preparation is critical for survival in a new environment and has fascinated biologists for decades, teaching us about life history strategies, migration, osmoregulation, imprinting and navigation. Understanding these changes also has important applications to salmon conservation, the use of hatcheries for restoring and supplementing populations of salmon and the salmon aquaculture industry.

In the introduction to his review Professor Hoar provides a comparative overview of anadromy and smolting. The "degree of anadromy" or how much a species relies on the marine environment (Rounsefell, 1958) differs among salmonids with the most recently evolved *Oncorhynchus* species showing the greatest marine tilt. Later in the review it becomes clear that the timing of the development of salinity tolerance differs among and within species and is related to the degree of anadromy: "There are many species of salmonid fishes, with smolting as variable as their morphology, physiology and behavior.", and provides us a warning that "The hazard of general comments is recognized." Thus, he provides a comparative perspective that is present throughout the manuscript and primes the reader to expect that there will be both commonalities and differences among species.

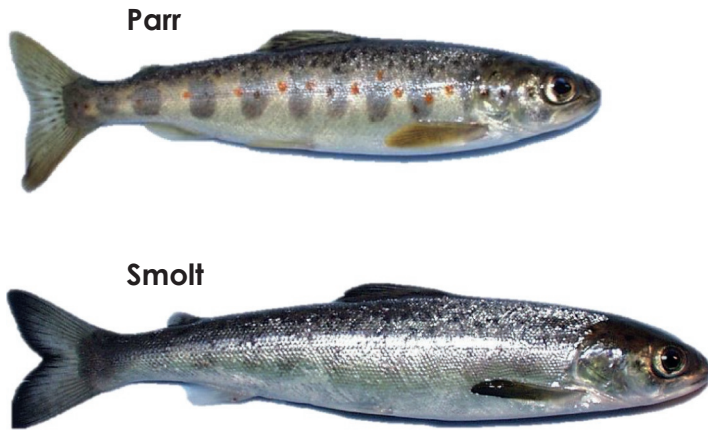


FIG. 1 Difference in morphology between Atlantic salmon parr and smolt. In smolts, note the loss of parr marks (vertical dark bands on the fishes flank), intense silvering and black fin margins. *Photo credit: Stephen D. McCormick.*

In the second and largest section of the paper (The Physiology of the Salmon Smolt) Hoar first describes the morphological differences in parr and smolt that can be seen in [Fig. 1](#). These differences in appearance were so large that for much of the 1700s the reigning wisdom was that these were two distinct species ([Flowerdew, 1871](#)). We now understand that the silvering, dark dorsal surface and fin margins characteristic of smolts “are adaptive to the survival of postsmolts in the marine habitat” through their facilitation of schooling behavior and predator avoidance in large rivers, estuaries, and the ocean. Size and growth are identified as critical to the decision to undergo smolting and the relative importance of the two appears to be species-specific. During smolting “metabolism and body composition are altered in many ways: the rate of oxygen consumption increases with heightened catabolism of carbohydrate, fat, and proteins.” These changes could be traced to specific alterations in metabolic pathways that were under hormonal control. New forms of hemoglobin appear that are likely to support a more constantly swimming lifestyle necessary in a pelagic environment.

Since parr have a very limited ability to tolerate seawater, the development of salinity tolerance is a critical and well-studied aspect of smolting. In one of the most synthetic and insightful parts of the paper, Hoar identifies nine “important points” from the many papers examining osmoregulation in smolts. All salmonid species can be gradually acclimated to seawater and returned to freshwater at any time during their life cycle. Within a species there appears to be a size-dependence of seawater tolerance which is independent of the size-dependent development of smolting. Only fish in the smolt stage can tolerate direct transfer to seawater, but this capacity is reversible, the timing of which is dependent on time, temperature, and species. The capacity for high growth in seawater that characterizes smolts appears to be closely tied to osmoregulatory

development. Changes in the major osmoregulatory organs (gill, gut, and kidney/urinary bladder) are described, emphasizing the preparatory nature of physiological changes and their connection to increased salinity tolerance.

Hormones have an important role in the parr-smolt transformation. Bill Hoar was the first to demonstrate that the thyroid is activated during smolting (Hoar, 1939), and it was thought that thyroid hormones may have a central, coordinating role in stimulating smolting, similar to what is seen in amphibian and flounder metamorphosis. But, by 1988, it was “now clear that thyroid hormones do not trigger the parr-smolt transformation.” Rather, Hoar recognized that “a number of endocrine systems are stimulated during smolting” (what Howard Bern termed a “pan-hyperendocrine process”) (Bern, 1978), and that different hormones are responsible for different aspects of smolt physiology. His fig. 3 summarizes increases in thyroxine, cortisol, insulin, and catecholamines, and he also discusses changes in growth hormone and prolactin (see Fig. 2 of this paper). Thyroid hormones stimulate some of the morphological and metabolic changes that occur during smolting and interact with other endocrine systems. Hoar correctly concluded that “growth hormone is the important factor in hydromineral regulation in the sea” though we now know that cortisol is also critical to the development of salinity tolerance and that the GH/IGF-I and interrenal axes have important interactions (McCormick, 2013).

Smolting and sexual maturation are both critical life history events for most salmon, with the former normally preceding the latter by 1 or 2 years. In some species and populations, however, there is an alternative strategy wherein maturation of males can precede smolting. Most of the work in this area has been done with Atlantic salmon, and Hoar reviews several concepts introduced by John Thorpe and colleagues (Thorpe, 1987). Prior maturation can influence subsequent growth rates which can in turn affect whether individual fish delay smolting. Sex steroids can interfere with smolt development and salinity tolerance, though in most cases fall maturation and spring smolt migration are sufficiently separated in time that this is not an issue.

With the possible exception of pink and chum salmon that smolt very early in development, the environment is a critical modulator of the timing of smolt development and downstream migration. Hoar provides evidence that photoperiod controls the timing of smolting (as it does for many other physiological processes in salmon), with some of the earliest work on Atlantic salmon coming from Richard (Dick) Saunders lab and in Pacific salmon from Craig Clarke's group. Temperature appears to control the rate at which fish respond to increased daylength, but also affects how quickly smolts lose their salinity tolerance and migratory tendency. The potential role of lunar rhythms in thyroid hormones and downstream migration is also summarized.

In his last section of the paper, Hoar tackles some of the “Practical Problems” relating to smolt physiology. Commercial salmon aquaculture (primarily Atlantic salmon) was in a strong growth phase in 1988 and continues to expand today. Then as now commercial operations usually produce smolts in freshwater hatcheries and then transfer fish to ocean net pens. Provincial, state, federal, tribal, and private

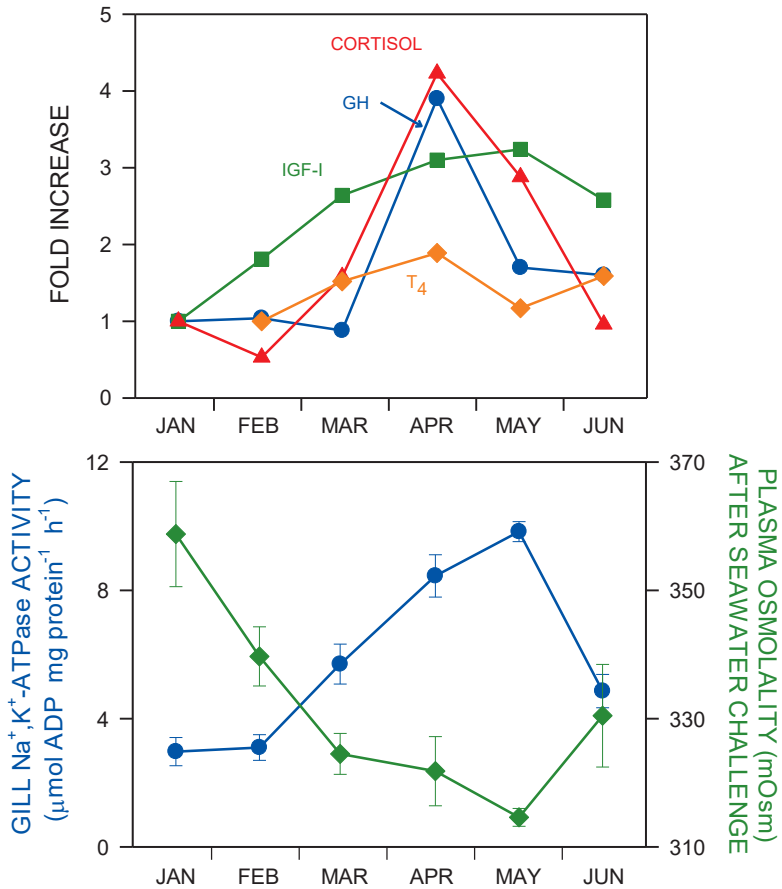


FIG. 2 Plasma hormone levels (upper panel), gill Na⁺, K⁺-ATPase activity and plasma osmolality 24h after exposure to seawater (lower panel) in juvenile Atlantic salmon during the parr-smolt transformation. Note that most endocrine changes peak in April, preceding the peaks in gill Na⁺, K⁺-ATPase activity and osmoregulatory capacity in May. *Abbreviations:* GH=growth hormone, IGF-I=insulin-like growth factor I, T₄=thyroxine. Increase in hormone levels were expressed by setting the mean value of the January sample (February in the case of thyroxine) to 1 and expressing all subsequent changes relative to that value. *Modified with permission from McCormick, S.D., Lerner, D.T., Monette, M.Y., Nieves-Puigdollér, K., Kelly, J.T., Björnsson, B.T., 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.*

hatcheries release juvenile salmon as fry, parr or smolts to conserve or restore damaged populations or to mitigate the impacts of dams and habitat loss. Hoar recognized that both commercial and restoration/mitigation hatcheries needed smolts that could survive transfer to and grow well in SW, but that fish released into the wild must also have the attributes of wild smolts to survive; the capacity for imprinting, navigation, high levels of swimming performance (for predator avoidance and prey capture) and immunocompetence among others. Commercial salmon hatcheries had highly variable success in rearing high quality smolts, with

poor survival and growth after SW transfer a rampant problem. While the return rates of wild smolts vary by species, river system, and year, the return rates from restoration/mitigation hatcheries were almost always lower (often up to 10-fold lower) than their wild counterparts. Hoar identified two areas that would be the focus of advances in commercial and mitigation/restoration culture of salmon. The first was minimizing the juvenile freshwater phase, which was particularly important to save costs in commercial culture. The second was successful transfer to the marine environment, which could be achieved by producing high quality smolts with knowledge of the optimal time for transfer to SW. Hoar advocated that basic and applied research into the nutritional, physiological, and genetic control of growth and smolt development could be used to achieve these goals.

In the intervening years the use of improved food formulations, optimal growth temperatures, exposure to continuous light and other innovations have reduced the rearing time of smolts to 8 months or less. Photoperiod manipulation of the timing of smolt development (by moving from continuous light to 12h of light for at least 6 weeks and back to continuous light) allows for the nearly year-round production of smolts. Yet the problem of poor survival and growth after transfer to SW persists, perhaps because these artificial conditions have unintended consequences for smolt quality. And while more natural rearing conditions such as normal photoperiod and temperature cycles, more complex habitats and predator conditioning at restoration/mitigation hatcheries have been shown to improve return rates, they still lag behind those of wild fish.

We have learned a tremendous amount about smolting in the intervening 35 years since this review was published. Our knowledge of smolt biology has also helped us address the many aspects of conserving wild species (McCormick et al., 2009). For example, smolts are particularly sensitive to acid rain, which can rob them of their salinity tolerance, such that survival in the marine environment is compromised (Thorstad et al., 2013). Knowledge of the effects that sex steroids have on smolt development was critical to understanding the negative impact of nonylphenol (an estrogenic mimic used in pesticide sprays) on salmon populations (Fairchild et al., 1999). Knowledge of the behavior of smolts has allowed for the development of downstream passage for smolts around dams. The advent of molecular approaches such as qPCR, RNA seq, and whole genome sequencing has allowed us to identify the gill ion transporters that are involved in the development of salinity tolerance. Similarly, our increased capacity to measure the abundance of hormones, binding proteins and receptors at both the transcriptional and protein levels has led to a more accurate and nuanced view of the endocrine regulation of the physiological changes that occur during smolting.

But much remains to be learned. The molecular and cellular pathways of gill ionocyte development, critical for development of salinity tolerance, have yet to be elucidated. Knowledge of smolt-related changes in the kidney and intestine lag behind our understanding of changes in the gill. The complexity of endocrine changes during smolting that include tissue-specific changes in receptors, binding proteins, and interaction among hormones are still active areas of research. Even more challenging has been how these hormones control the many aspects of smolt development; while salinity tolerance and

metabolic changes are highly tractable, changes in behavior, imprinting, navigation, and immunocompetence are more difficult to address. And what of the return migration of adult salmon to freshwater? Is there a “reverse smolting” where the physiologies necessary for freshwater entry and upstream migration occur in advance of riverine entry, or are they simply induced by exposure to freshwater? While there is some evidence for the former (Flores et al., 2012), much remains to be done.

Why has this review been so widely read and cited? It came at a time of intense interest in understanding the basic biology of smolting and applying that knowledge to commercial and restoration aquaculture. By 1988 there had already been two International Smolt Workshops (1981 in La Jolla California USA and 1984 in Stirling, Scotland), and these continue to be held every 4–5 years. Sufficient research on most salmonid species had been conducted by the mid-1980s to result in a large, complex and sometimes contradictory literature. Some of these apparent contradictions dissolved when placed in the context of evolution shaping important differences in timing, which were second nature to Hoar’s understanding of smolting. Bill Hoar showed us that a great deal could be learned from using reductionist approaches inherent in physiology, but we should expect to be challenged (and fascinated) by the diversity and complexity of salmon life history.

This was a comprehensive, exhaustive review, one that was full of robust conclusions that have stood the test of time. Bill Hoar had a compelling writing style that managed to be highly accessible and authoritative. Basic and practical aspects were addressed that were important and useful to the developing aquaculture industry and conservation hatcheries. By presenting a clear-eyed synthesis of our knowledge and its gaps, this review also paved the way for a generation of researchers (and perhaps two or three) to continue examining the fascinating life history of salmon and the physiological challenges that it presents.

A Brief Biography of William Hoar

Professor William Stewart Hoar was born in Moncton, New Brunswick, Canada on August 31, 1913. He received a B.A. in Biology and Geology from the University of New Brunswick in 1934. After obtaining a Master’s degree in Zoology from the University of Western Ontario and a Doctorate in Medical Sciences from Boston University, Professor Hoar held academic positions at the University of New Brunswick (1939–42 and 1943–46) and the University of Toronto (1942–43). During this time he also worked for several summers for the Fisheries Research Board of Canada. In 1945 Professor Hoar was appointed Professor of Zoology and Fisheries at the University of British Columbia. Here he became well known as an excellent teacher and scientist and played a major role in shaping the Department of Zoology, particularly from 1964 to 71 when he was Head of Department.

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A Brief Biography of William Hoar

In addition to well over 100 scientific publications, Professor Hoar was the editor of the Canadian Journal of Zoology and coeditor of the multivolume series on Fish Physiology. In 1966 he wrote an influential textbook of General and Comparative Physiology which had three editions and was translated into a number of foreign languages. Professor Hoar has received no less than seven Honourary Degrees from Canadian Universities. In 1955 he was appointed a Fellow of the Royal Society of Canada (Academy III), received its Flavelle Medal in 1965 and was its president from 1971 to 1973. In 1974 he received the Fry Medal from the Canadian Society of Zoologists and in the same year became an Officer of the Order of Canada. Bill Hoar passed away in Vancouver on June 13, 2006.

Information obtained from the UBC Hoar Memorial Award website: <https://zoology.ubc.ca/events/special-seminars-and-events/william-s-hoar-memorial-lecture>.

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