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THE UNIQUENESS OF THE SALMONIDS: A MINI-REVIEW ON ITS SMOLTIFICATION

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ABSTRACT

Salmonids have a distinct lifecycle, progressing from freshwater-dwelling fry and fingerlings stages to saltwater-dwelling juveniles. This migration, known as catadromous movement, varies in duration according to species. Environmental and physiological factors have a considerable impact on this movement, with temperature and photoperiod playing crucial roles in the smoltification process. Smoltification is the process by which a juvenile salmon prepares to migrate to marine water. This process includes a change in coloration (from cryptic to silvery), osmoregulatory structures and processes to keep physiologically appropriate water and salt concentrations in the tissues, and an increase in growth rate. Smoltification in salmonids being a complex change engineered by its endocrine is geared towards the adaptive migration from freshwater into saltwater for development is a very important aspect of its life cycle. The understanding of this phenomenon is however paramount to ensure optimal productivity and sustainability of this unique fish species (salmonids) in culture systems. Hence, this paper reviewed the basic factors that influence the smoltification process as well as the relevance of the knowledge to salmonid farming.

Keywords: Catadromous migration; Enzymatic assays; Metabolic profiling; Osmoregulatory capacity; Photoperiod; Salmonids.

INTRODUCTION

The family salmonids have a unique lifecycle. The early fry to fingerling stages are known as freshwater dwellers while the juvenile stage is spent in saltwater. Freshwater to saltwater migration also known as the catadromous movement could be a lengthy or brief period depending on the purpose. The saltwater tolerant level in salmonids is species-bound as some species in their early life stagehave already entered the ocean. Pink salmon (*Oncorhynchus gorbuscha*) and Chum salmon (*Oncorhynchus keta*), are very good examples of such species having great tolerant levels for saltwater from hatchlings (Li *et al.*, 2019; Paulsen*et al.*, 2022; Abramova & Kozin, 2023). Although, species like Atlantic salmon (*Salmo salar*), Coho salmon (*Oncorhynchus kisutch*), Chinook salmon (*Oncorhynchus tshawytscha*), Masu salmon (*Oncorhynchus masu*), Amago salmon (*Oncorhynchus rhodurus*), Steelhead trout (*Oncorhynchus mykiss*), Brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*), spend their early stages even with some growing to very appreciable sizes of 10-15cm in body length in freshwater before migrating into saltwater (Handeland*et al.*, 2014; Hecht *et al.*, 2015; Kimoto *et al.*, 2015; Tacchi*et al.*, 2015; Christensen *et al.*, 2018; Nevoux*et al.*, 2019; Damsgaard*et al.*, 2020; Kaeriyama and Sakaguchi,2023).

The catadromous migration of salmonids at that stage is influenced significantly by some factors classified under environmental and physiological factors. Some of these factors such as temperature, photoperiod,growth rate, latitude, and food availability at that stage of their lives, bring about the smoltification process and the necessary movement of the fish from freshwater to saltwater (Langdon, 2019; Morera *et al.*, 2021). In the various life stages of salmonids, there are a lot of mechanisms that are developed to live and survive in both freshwater and saltwater. These biological mechanisms that enable the species to dwell in both water bodies conveniently are known as smoltification or parr-smolt transformation (Ugachi*et al.*, 2023).

Numerous endocrine systems combine functions to bring about smolt development, and this endocrine system such as cortisol, thyroid, and prolactin are manipulated significantly during the process of smoltification. This is to enhance the growth of the branchial, saltwater-type chloride cells and adjustment in the intestinal osmoregulatory capacity and performance (Langdon, 2019). During the catadromous migration and environmental changes that are accompanied, there is a major osmotic water loss and this is tackled by the changes in the function of the osmoregulatory system through much saltwater intake, where the gill functions in expelling single bond ions while the kidney expels double bond ions.

Also, theirmorphological changes and well-organized hypoosmoregulatory capacity add to the fitness for the present zone being occupied. Some of these noticeable morphological changes are the increased length of the caudal peduncle, which brings about a better swimming ability (Matthews *et al.*, 2022), accompanied by an adjustment in haemoglobin isoforms, which encourages the ability of the blood to carry more oxygen (Storz, 2016). The lightening of colour from dark parr to a shinier and brighter colour like silver (Pireddu, 2022), and theindividual struggle for feeding changes to the formation of schools of fish to secure food (Charlton *et al.*, 2016). This is also used to prevent being preyed on by larger carnivores and creates the opportunity for them to prey on vulnerable smaller species during the catadromous migration and while living in the marine environment.

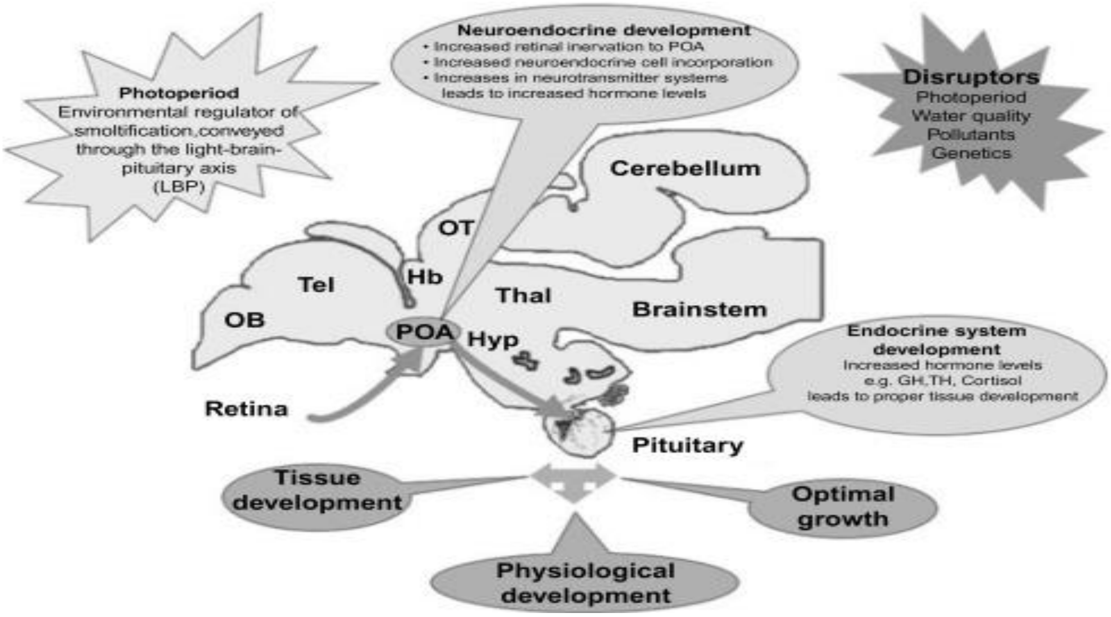

Figure 1: An overview of the light-brain-pituitary axis that illustrates the role of brain changes during smoltification on endocrine and physiological development. *Abbreviations*: OB, olfactory bulb; Tel, telencephalon; Hb, habenula; POA, preoptic area; OT, optic tectum; Hyp, hypothalamus; Thal, thalamus; GH, growth hormone; TH, thyroid hormone.

Source: Stefansson et al., 2008.

Smoltification is one of the known uniqueness attributed to the salmonids and a prior knowledge of the processes involved contributes to the successful culture of the salmon species especially the Atlantic salmon with high commercial value. Also, the understanding of the relevance of environmental, physiological, physicochemical, and biological factors such as temperature, pH, dissolved oxygen, turbidity, acidity, magnesium, potassium, and zooplankton and phytoplankton together with other anthropogenic factors is imperative. Therefore, this study reviewed the uniqueness of the salmonids with a pinhole focus on its smoltification.

ENVIRONMENTAL FACTORS

Environmental factors known to mainly affect the smoltification process in salmonids are temperature and photoperiods; these factors are linked together as a result they both bring about the success or failure of smoltification. The annual temperature alongside other factors such as available feed and space determines the growth rate and minimum attainment of the salmon before smoltification takes place. Catadromous migration of salmon is instigated by the temperature level at a particular time. The temperature range for optimal smoltification process is however species dependent although it has been established that a temperature between 12 – 15°C is suitable for a successful smoltification process (Stefansson *et al.*, 2020). A higher temperature on the other hand is known to influence negatively the growth rate and smoltification process, while regular fluctuation in temperature brings about a stop to the various migrations in turn also affecting the smoltification process (Mugwanya*et al.*, 2022). The temperature tolerated by different salmon species is presented in Table 1.

Adapting to the change in temperature of the marine ecosystem is challenging for smolts, especially in the first few days of entering the saltwater, hence, adjusting its morphological and physiological features during smoltification has a level of proportionality to the presiding temperature (Vehanen *et al.,* 2023). (Bernard *et al.,* 2019) also confirmed that high temperatures if not regulated may hinder the smoltification process the same way as temperatures below the recommended range. The temperature tolerance level of various species differs as some can undergo smoltification at a higher temperature while others may require a lower temperature level within the acceptable range; these also bring about the distinctive features developed in the process (Brauner and Richard, 2020).

The growth rate of salmon species slightly depends on the temperature of the waterbody (as shown in Figure 2), however, the duration it is exposed to light is considered a priority in this context; photoperiod significantly influences growth rate and coloration compared to temperature. Increased feeding and survival rates are also influenced by photoperiod, the presence of light makes salmon juveniles feed more since they can locate feed in the water body, keeping them active all day.The metabolic processes that bring about growth and smolt size are also enhanced by the photoperiod. However,the source of light is preferably sunlight since it has been reported that the usage of artificial light sources hinders the actualization of smoltification (Lall and Kaushik, 2021). This hindrance is sometimes a delay in the completion of the smoltification process or most cases a speedy completion leading to deformity.

In studies where alterations in the early stage of the smoltification were evident, even with maximum photoperiod, no success was observed (Pino Martinez *et al.,* 2021). In some cases, the deformity resulting from the alteration in the early stage of smoltification observed in parr salmon wasa poorly developed inner eye structure. This was attributed to excessive exposure to light as observed by (Smedley, 2016). (Morera *et al.,* 2021) stated that the smoltification process in salmon that had insufficient photoperiod produces parr salmon lacking the required features for adaptation in saltwater.

Also, the necessary factor that brings about sexual maturation in salmon species occurs sufficiently during the photoperiod (Good and Davidson, 2016). Changes in the reproductive processes of pelagic fish such as salmonids alongside favorable environmental conditions specifically photoperiods bring about the well-being of juveniles (Newman, 2015). There has been a wide range of studies on salmon smoltification linked with environmental factors (Mobley *et al.,* 2021). Decades ago, research carried out revealed the influence of photoperiod on the physiological and sexual maturation of salmonids. Changes were observed in the growth rate, size, and genetic makeup of the species (Fjelldal *et al.,* 2011; Rousseau *et al.,* 2012; Imsland *et al.,* 2014). Photoperiod plays significant roles in some biological processes such as spawning duration and readiness of reproductive organs (Polat *et al.,* 2021).

The smoltification process in salmon is also affected by seasonal variation as the temperature of water bodies fluctuates across months of the year. The decrease in temperature has been attributed to high osmotic disturbance which affects negatively the well-being of these fish species as well as the smoltification process (Swirplies *et al.,* 2019). To stabilize the osmotic level and encourage the condition of salmon, there is a need for the movement of smolts to saltwater bodies when salinity is at its minimal to enable smooth acclimatization (Calabrese, 2017). The need to ensure a good environmental condition (temperature and photoperiod) to facilitate the smooth and successful smoltification process is paramount; however, other factors such as the physiological mechanisms still contribute significantly.

Table1: Temperature tolerated by different Salmon species

S/N	SPECIES	TEMPERATURE	REFERENCES
1.	Chum salmon (*Oncorhynchus keta*)	12◦C-15◦C	(Richter and Kolmes, 2005)
2.	Atlantic salmon (*Salmo salar*)	12.7 ◦C	(Imsland *et al.,* 2014)
3.	Coho salmon (*Oncorhynchus kisutch*)	15◦C	(Richter and Kolmes, 2005)
4.	Chinook salmon (*Oncorhynchus tshawytscha*),	14◦C-15◦C	(Jamilynn *et al.,* 2017)
5.	Steelhead trout (*Oncorhynchus mykiss*),	13◦C-15 ◦C	(Stefansson *et al.,* 2020)
6.	Arctic charr (*Salvelinus alpinus*),	12◦C -13◦C	(Aas-Hansen, 2004)

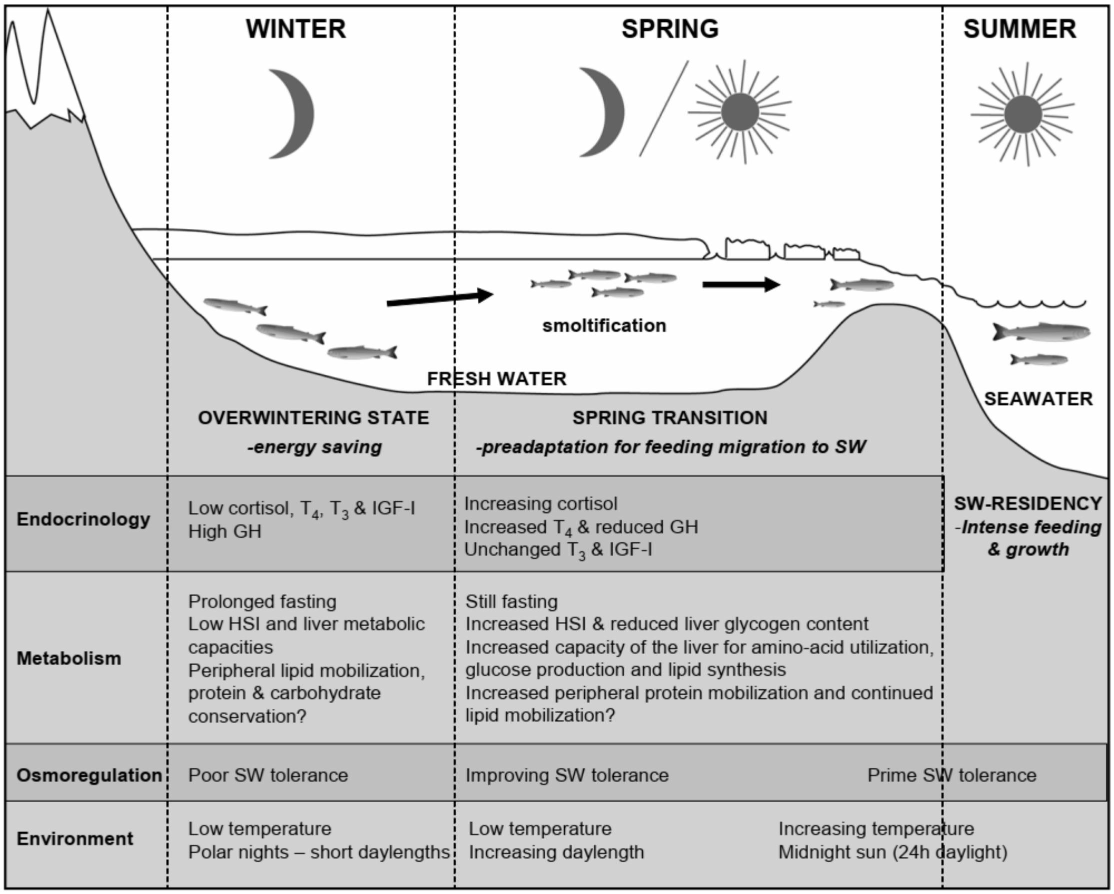

Figure 2. Schematized diagram showing a proposed seasonal pattern changes (photoperiod) in endocrinology, metabolism, osmoregulation, and associated environmental conditions (**Source**: Aas-Hansen, 2004).

PHYSIOLOGICAL MECHANISMS

The freshwater body is known to be a breeding ground for salmon species before the catadromous migration takes place at the juvenile stage which is influenced by the presence of the required food supply in the saltwater body. In line with this, adaptive features are developed to help the well-being of these juveniles to physicochemical and biological changes in their new environment.

In the catadromous migration of salmon species, they are subjected to high levels of hyper-osmotic stress caused by high concentrations of plasma ions and lack of water in the tissues at the early time spent in saltwater (over 30 ppt of salt) (Anand *et al.*, 2022). During this period, the species adjust to the new environment and the ease of adjusting is determined bythe size of the species, biological process, and temperature level (Islam *et al.*, 2020). The gill Na^+/K^+-ATPase regulates the osmotic level shift caused by the influx of saltwater (Mozumber*et al.*, 2023). The acclimatization process of salmon in the saltwater body after a few days of migration influences the optimal function of the gill Na^+/K^+-ATPase (Lokshall, 2023).

The change in the gut is also relevant in this smoltification process. Smolts in saltwater consume more than freshwater smolts to replenish water lost to the hyperosmotic medium. To absorb water, the gut first absorbs Na+ and Cl to lower the osmotic stress of the gut fluid. This is achieved by the cooperative action of an apical, absorptive Na+/K+/ 2Cl co-transporter (NKCC2) and a basolateral NKA. Active alkalinity (6.5 – 8.0) lowers the pH levels of the gut even more by precipitating $Mg^{2+,}$ Ca^{2+}, and SO_4^{2-}(Siwelane, 2023). Most species absorb water via paracellular and transcellular pathways in the anterior gut (Karasov, 2017). Some studies have reported the changes observed in some salmonids during the acclimatization process. Fluid transfer of the isolated posterior gut rose in Coho and Atlantic salmon during smolting and following sudden exposure to saltwater (Finlay *et al.*, 2021). Both water transport capacity and NKA activity increased in the anterior (*Pyloric ceca*) and posterior portions of the gut of yearling Chinook salmon during the early sunny season, before the establishment of salt tolerance (Vargas-Chacoff *et al.,* 2015). In a smolting population of brown trout (*Salmo trutta*), gut water transport capacity rose fivefold but was not accompanied by enhanced gut NKA activity (El-Leithy *et al.,* 2019). Increased gut NKA activity and paracellular permeability (as assessed by transepithelial resistance) in connection with higher fluid transport in Atlantic salmon smolts' anterior gut was reported by (Sundell *et al.,* 2022). After saltwater exposure, it was noticed that a reduction in transepithelial resistance indicated a shift from paracellular to transcellular water absorption mechanisms.

Furthermore, one of the mainphysical changes observed is the silvering of the body colour from dark, caused by constant and excessive disposal of guanine and hypoxanthine on the skin layer and scale of the fish (Yang *et al.*, 2021) which are softer in parr than smolt. However, the visibility of such coloration in parr depends solely on the eroding of the outer skin with time. The translucent nature of the fin is a result of the development of a dark fin margin on the dorsal caudal and pectoral fins. This feature remains very difficult to observe only when in a culture medium.

Figure 3: Morphological differences between Atlantic salmon parr (A) and smolt (B) reared in the wild. Note the vertical bands and spots on the sides of parr, and the presence of intense silvering and darkened caudal, pectoral, and dorsal fin margins in smolt. Photo credit: S.D. McCormick.

There are numerous speculations about the caudal fin margin considering that it is used for communication during schooling (Ferron *et al*., 2017). The scattering of the scales of smolts is a result of the loss nature of theirscales and is observed during handling. Furthermore, the loosened scale has been attributed to the massive growth rate observed in Atlantic salmon, where tissue exertion (contraction) to accommodate the changes in the size was observed by (Lovett, 2020).

Parts without scale can serve as a medium through which salt water penetrates the body thereby hindering osmotic function and creating an irregular adjustment in osmoregulation. Jehannet *et al.* (2019)suggested from their observation in eels the rapid increase of silvering was encouraged by hormones (such as pituitary gonadotropin)responsible for growth.

IMPORTANCE OF SMOLTIFICATION IN SALMONID AQUACULTURE

Fishfarmers' in a bid to optimize production, adopt measures to replicate the natural environment and its attributes in culture media. In the culture of salmonids, smoltification is a process that involves the utilization of both freshwater and saltwater. It is known to be seamlessin the wild, where both water bodies can be easily accessed by the species (Chan, 2018).

According to Langddon, (2019), the importance of smoltification to the growth and development of salmonids has made it a necessity that the aquaculture system needs to be adjusted to enable such processes to occur while in culture medium through human interference. The various mechanisms required for smoltification are within the reach of culturists which makes such important measures achievable in aquaculture systems. It is easier to practice such in a closed system of aquaculture than in an open system where atmospheric conditions such as light penetration, and temperature cannot be regulated (Colt and Huguenin, 2002; Good and Davidson, 2016).

Early maturation of salmon species reduces the growth efficacy of such species because the energy for growth will be converted for reproduction. But with photoperiod, such can be controlled by reducing the light intensity and penetration as well as the temperature of the water body, throughout the life cycle of salmonids as reported by (Good and Davidson, 2016). With the firsthand knowledge acquired from the various studies carried out onthe aspects of salmon smoltification (the development of adaptive features), modern-day aquaculture has been able to adopt and manipulate cultured salmon species to perform like their wild counterparts. Activities such as schooling, catadromous migration, and morphological changes associated with it through the adjustment of culture medium (Chaudhuri, *et al*., 2021).

Also, with experiments on gill salt ions test to evaluate salinity tolerance (salinity levels ranging from freshwater to seawater of 0 to 35 parts per thousand, or ppt) and water flow, large salmon farms have been able to devise means to actualize the freshwater to saltwater migration of salmon and when necessary through crude indication methods (Ytrestoyl *et al.*, 2020). The transformation into a silver colour is one of the indicators strongly adhered to by these farmers. Kolarevic *et al.* (2018) penned that innovations have been adopted to manipulate the smoltification of salmon in a culture medium, as smoltification results from the migratory process, Aquaculturists have been able to devise means where salmon at the juvenile stage are transferred to cages installed in saltwater bodies, this gives them a sense of being in their natural environment and with the right temperature and photoperiod complete smoltification is achieved (Morro *et al*., 2019).

CONCLUSION

Smoltification in salmonids is an essential part of its life cycle and development consequently ensuring its optimum performance in saltwater bodies where it attains some level of maturity. Factors such as environmental (temperature and photoperiod), and morphological changes (skin colour from dark to shiny silver) are known to influence and be influenced by this activity. Hence, to be a successful salmonid farmer, it is imperative to establish excellent manipulative culture media and practices to aid such activity even while in an artificial environment (culture media). Therefore, the productivity and sustainability of salmonids production depends greatly on the verse knowledge of its smoltification.

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