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Morphological and adaptational changes associated with fish migration from fresh to marine water bodies

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Abstract
Expansion of the aquatic industry and increased preference on white over red meat has resulted into intensification of aquaculture practices. Inland capture fisheries in Africa are also on the increase while marine capture has stagnated over the last 20 years. This has led to unconventional fish farming where by some marine and fresh water fish species are increasingly farmed in fresh and sea waters respectively. Although some fish species can naturally survive on fresh and sea water environments, the transition between the two water bodies requires morphological changes to ensure survival and optimal productivity. Morphological changes take place concurrently, with the physiological adaptations which are critical for survival in the new environment. Artificial hatcheries can simulate environmental conditions which favour such transitions, and therefore proper understanding of the underlying anatomical and physiological changes is crucial. In this paper, we summarize and discuss available reports on the anatomical and physiological changes associated with migration of fish from fresh to sea water and vice versa. Understanding of species specific adaptational changes is crucial as farmers engage in intensive fish farming involving transfer from hypoosmotic to hyperosmotic water environments and vice versa.

Keywords: Smoltification, fish, fish hatcheries, parr.

Introduction

Some fish species inhabit both freshwater and seawater bodies and routinely migrates between the two environments [1]. The transition between water bodies lead to anatomical changes such as: change in pigmentation, body shape and length, emergence and growth of teeth on the maxilla, mandible and tongue; growth and changes in shape of integumentary folds adjacent to the cloacal opening; growth and change in shape of the auxiliary appendage of the pelvic fin; and growth in the scales with respect to radius and number of circuli. Additionally, adaptational morphological changes also occur in the gills, esophagus, kidney and intestines [1, 6-9]. Migration between fresh and marine water ecosystems is often associated morphological changes referred to as smoltification or parr-smolt transformation and the resulting migrant is termed a smolt, which is characteristic of juvenile fish. In this context there are two groups of fish namely as; catadromous and anadromous fish [2]. Catadromous fish are born in saltwater, then migrate to freshwater as juveniles where they grow into adults, before migrating back to the ocean to spawn. The catadromous fish include; true eels (*Anguillids spp*), thin-lipped grey mullets (*Liza ramada*) and European flounders (*Platichthys flesis*). This metamorphosis involve alterations in lipid metabolism, osmoregulation, oxygen transport, buoyancy, growth, colour, shape, rheotaxis and behavior are preparatory events to maximize survival during downstream migration, ocean entry and long distance feeding migrations in the marine environment [1].

In anadromous fish reproduction is limited to rivers which have few predators thus increasing chances of survival during the early stages. The river ecosystem supports limited growth rate and size of fish, therefore by leaving at a certain life stage and entering ocean which has rich marine food supply, they increase their reproductive success. The age at which smoltification occurs and its intensity differ among species. For example; in pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*) seaward migration takes place soon after emergence from the gravel and the rest of the life cycle and growth takes place in the sea. The Charr (*Salvelinus spps*) are entirely fresh water or spend only a few weeks feeding in sea water during summer.

In Atlantic salmon (*Salmon Salar*) and Coho salmon (*Oncorhynchus nykiss*) smoltification occurs after one year residence in fresh water. Movements are mainly associated with attaining maximum amount of food or a suitable habitat while avoiding predation or other sources of mortality. For example, movements of juvenile Atlantic salmon prior to the smolt transformation can be divided into five phases:

(i) movement of fry from the vicinity of their redds;
(ii) establishment and occupation of feeding territories;
(iii) spawning movements of sexually mature male parr;
(iv) shifting from summer feeding territories to winter habitat; and
(v) Descent from nursery streams to lower reaches of some rivers in late autumn as a forerunner of smolt migration.

Smolts face other challenges including; new food sources, diseases, parasites, and predators, which make the smolt stage a critical one, in which mortality can be high and variable. The much greater fecundity of anadromous females and reduced mortality of eggs and fry in fresh water allows them to overcome the risks. Multiple interactions between the environment and the fish lead to smolt development thus environmental conditions determine the age at which smolting occurs. Growth conditions such as temperature, food, photoperiod, and competition are crucial during the transition period. Once this developmental stage has been reached photoperiod and temperature regulate neuroendocrine changes, which result in physiological changes. Furthermore releasing factors such as temperature, flow, and turbidity may have direct effects to initiate downstream migration. However, development of the smolt physiological condition is necessary for releasing factors to initiate downstream migration. The possible neuroendocrine or physiological mediators of these rapid effects are not well characterized. Recent studies have suggested that the growth hormone, insulin growth factor-I, thyroid hormone (T4), insulin and prolactin are likely to be candidate molecules [3-5].

Certainly, some fish species can complete their life cycle without migrating. Several factors including growth conditions, cost of migration, mortality rate and fecundity determine whether an individual adopts an anadromous verses a resident strategy. Residency is a reproductive strategy for males and in many anadromous populations a portion of the males does not migrate to sea. Maturation of male as parr is common in many Atlantic salmon populations but there are also several populations of “dwarf” Atlantic salmon in which both females and males mature in streams. There are also “land-locked” populations in which smolts migrate downstream but reside in lakes rather than the sea. This capacity to complete their life cycle without anadromy demonstrates the plasticity of fish life history.

Recent advances in aquaculture have made it possible for hatcheries to artificially produce smolts by simulating the natural conditions and release them to marine waters to grow and mature, they then return to the hatchery environment to spawn. Other studies have gone further by conditioning naturally fresh water fish to marine environment and vice versa. This may involve raising fish in special tanks. In the present review, we summarize and discuss available reports on the anatomical and physiological changes associated with migration of fish from fresh to sea water and vice versa. Such changes are critical for survival in the new environment. Understanding of species specific adaptational changes is crucial as farmers engage in intensive fish farming involving transfer from hypoosmotic to hyperosmotic water environments and vice versa.

Morphological adaptational changes

External silvering

The deposition of purines (guanine and hypoxanthine) in epidermal tissues in the skin and scales covers the parr marks and results in external silvering that is characteristic of smolts. Endocrine basis for change in protein metabolism which causes silvering is not well resolved [4, 5]. However, growth and thyroid hormones have been implicated to play a role. Parr marks remain in the deeper skin layers and become visible if outer skin is eroded [6]. This is an adaptation for predator avoidance.

Change in body shape and length

When fish migrate from fresh to sea water and vice versa they undergo extensive morphological, physiological and behavioural changes [6-9]. Smolts grow more in length than weight, resulting in reduced condition factor (weight relative to length) [10]. Changes in body shape and length depends on the season of the year and availability of nutritional resources [10, 11]. The streamlined body allows the fish to move fast and evade obstacles during migration. Recent results from studies involving three groups of fish, which were sampled from seawater demonstrated changes in pigmentation, body shape and length [7, 8, 12]. The characteristic features that distinguished the fish in the various groups were as follows. *Parr:* light brown to yellowish overall color, yellow to brownish-orange fin. *Seawater parr (revertant):* parr marks faintly to boldly evident; fins yellow to orange-brown, often with a white margin on the anal fin; dorsal surface brown; ventral surface gray with a strongly mottled appearance; external sheen bronze or absent; and fish generally very thin and "pinheaded" (relatively microcephalic). *Seawater transitional:* parr marks partially distinguishable, yellow pigment evident in fins, dorsal surface faded from metallic blue to green-brown, faintly speckled on ventral surface, and overall sheen no longer silver but golden to bronze. *Condition factor is* less than that of a parr. *Seawater smolt:* externally the same as freshwater smolt, dorsal surface is a bold metallic blue, and body form is again robust after a month or two of seawater residence.

The emergence and growth of teeth

Studies in hatchery conditions have demonstrated that development of teeth also takes place as one of morphological and adaptational changes [10, 11]. Teeth develop on the maxilla, mandible and tongue. The teeth are adaptive for feeding as fish migrate into a new habitat in the deep marine waters [10, 11].

Para-cloacal skin folds

There are progressive changes in integumentary folds that surround the cloacal opening as shown in a study on Coho salmon [10]. In the 16-month-old parr the cloacal termination itself is rounded and it is flanked on either side by two stubby rounded protuberances. With time, the cloacal opening becomes more elongated antero-posteriorly. The two lateral integumentary structures grow posteriorly and medially and thinner at the same time. During the elongation the medial posterior portion of this fold becomes lobulated. In the 22-month-old smolts the two folds almost meet in the midline, posterior to the cloacal aperture and their ventral surfaces develop secondary "sculptured" or scale-like structures. The area of the ventral body wall posterior to the cloacal aperture becomes hollowed out in a shallow bowl-shaped form to contain these integumentary folds in the older parr and smolt. In the 22-month-old seawater parr the cloacal opening is more rounded than in the silvery smolt of the same age, but the para-cloacal folds are well developed to a much greater extent than in parr at 16 months [10, 11]. The changes are considered to be important presumably for streamlining.

Auxiliary appendages of the pelvic fins

The axillary appendage is another morphological change, which occur during smoltification. It is a small fleshy protuberance at the base of the pelvic fin of salmon and trout that is used to distinguish salmonids from other fishes with adipose fins. In a study on Coho salmon, it appeared as a small rounded fleshy lobe in 16 month-old parr lateral to and extending posteriorly to the attached base of each of the pelvic fins was seen [10]. In 22 month old smolt this structure was elongated and become pointed at its posterior tip. It then becomes wedge-shaped or prismatic in its cross section in the seawater smolt. In adult salmonids this structure is not much more fully developed, though it is larger than in the smolt.

Growth of scales

During smoltification the skin and scale layers are thicker in smolts than in parr. However studies carried out in plotted scale measurements taken from fish kept under hatchery conditions showed no clearly consistent patterns [10]. It has been reported that scales of the smolts are looser than spars and they easily dislodged during handling. Loose scales are an indication of growth and adaptation to osmotic disturbances and increase the osmoregulatory challenges associated with saline water [6].

Changes in the gills

One of the most critical adjustments allowing such successful migrations from fresh to sea water is the remodelling of gills in which a suite of morphological and molecular changes ensure optimal function in the face of reversing requirements for salt and water balance. The remodelling leads to specific freshwater and seawater gill phenotypes that are readily identified by the orientation and/or quantities of specific ion transporters and the presence or absence of specific cell types. The most important changes include:

Increased number and size of gill chloride cells.

In sea water smolts chloride cells are larger with a deep apical crypt for ion release while in freshwater they have a broad apical surface with numerous microvilli for ion uptake [13]. During sea water adaptation chloride cells show both hyperplasia and hypertrophy. Hypertrophy is due to increased differentiation of mitochondria and increased synthesis and incorporation of plasma membrane into the baso-lateral tubular system paralleled by increase in Na^+ K^+ ATPase activity [14, 15]. Studies in tilapia opercular membrane suggested existence of two phases: proliferation followed by differentiation. During the first three days existing chloride cells are activated and proliferate, then proliferation stops and cells enlarge for three weeks together with development of baso-lateral tubular system and mitochondria. The chloride current through these cells is activated within 24hrs following transfer and increase steadily during the two phases reaching fully adapted levels after two weeks [14, 16]. Apical surface of chloride cells also change following seawater transfer. In freshwater the apical membrane of chloride cells is either in alignment with or slightly above that of adjacent pavement cells while in seawater it forms an apical crypt reducing the area exposed to external medium to a narrow apical crypt. This is to prevent passive inward diffusion of electrolytes by restricting water convection in this area. This is adaptive for increased salinity tolerance which permits decreased estuarine residence and improved swimming performance in seawater.

Development of leaky junctions

Leaky junctions are highly permeable to electrolytes and join chloride cells and accessory cell membranes [17]. Development of these junctions is a prerequisite for successful transfer from fresh water to seawater and plays a pivotal role in efflux of sodium [13].

Increased rate of renewal of pavement and chloride cells

The increased rate of cell turnover is a result of accelerated differentiation and apoptosis. For example, in rainbow trout a "flattening wave" along primary and secondary lamellae has been described [18, 19]. It is thought to be a degenerative process associated with replacement of freshwater adapted chloride cells with seawater adapted ones [20].

Changes in the oesophagus

Changes in the structure of the oesophagus have been studied in Japanese eel (*Anguilla japonica*) [21]. Esophagus of freshwater adapted eel has a stratified epithelium rich in mucus cells impermeable to both water and ions [20, 22]. Following transfer to seawater, esophageal epithelium is replaced by a single columnar epithelium free from mucus cells permeable for ions but impermeable for water [20]. Its surface area is increased by enhanced folding and a high vascularization of the connective tissue layer develops beneath the columnar cells. About 3-4 days after eels transfer to seawater, large amounts of cellular debris from mucosal surface, blood cells and mucus were observed in esophageal lumen. One week after transfer, columnar epithelium was present in several places while two weeks after transfer most of mucosal surface was composed of columnar epithelium.

Changes in the kidney

Main function of the kidney is excretion of large amounts of diluted urine in freshwater and the excretion of divalent ions with minimal water loss in seawater. Histological changes have been reported in the eel during the first two days following seawater transfer [23]. The changes include: a slight decrease in glomerular size with increased amount of mesengial tissue and marked reduction in epithelial height along the nephron [22, 23]. The brush borders become thinner and basal folds and mitochondria volume are reduced. These changes are adaptive for osmoregulation as more water is retained and high concentration of ions secreted [24].

Changes in the intestines

Morphological changes have been reported in the middle intestine in rainbow trout following seawater transfer [25]. After two days, significant distentions of intercellular spaces were observed together with increase in intestinal absorption of sodium and chloride suggestive of increased paracellular water and ion flow from the lumen to the blood. Numerous tubular invaginations of the baso-lateral membrane also appeared. After adaptation in seawater for one month, both the distension of intercellular spaces and tubular invaginations had disappeared. The middle intestine had recovered a structure similar to that of fresh water adapted fish except that the number of mucus cells had decreased [21]. It was then suggested that long term intestinal adaptation to a hypertonic environment could be based on renewal of membrane components rather than development of cellular structures. In seawater there was a shift in intestinal water uptake from paracellular to intracellular pathway resulting in increased water uptake via intestines due to increased epithelial paracellular permeability [21].

Visual adaptation

Freshwater fish use vitamin A_2 (porphyropsin) based visual pigments for sensitivity to longer wavelength of light whereas marine fish use vitamin A_1 (rhodopsin) for shorter wavelength sensitivity [26]. Eels, lampreys and salmon switch the ratio of A_1 and A_2 pigments in their photoreceptors with vitamin A_2 pigments predominating in freshwater and vitamin A_1 predominating in marine habitats. These changes are part of endocrine induced physiological changes needed to move from shallow fresh water to deeper open sea. Changes also occur in UV light sensitivity of salmonids as they migrate to sea water. The UV light sensitive cones disappear as the fish approach smoltification and head to the sea but reappear when they return to freshwater to spawn [27]. The UV light cones are only lost in ventral retina and retained in the dorsal retina but it is not known why the UV light cones disappear.

Change in haemoglobin

Migration from fresh to sea water is also accompanied with change of hemoglobin to adult isomers [28]. Increase in levels of hemoglobin at metamorphosis has been reported and this phenomenon allows the adult fish to exploit warmer and more saline environments with less oxygen requirements [29].

Darkened fin margins

Changes involving darkening of fin margins occur on dorsal, caudal and pectoral fins while the fins become lighter almost translucent [30]. This develops gradually over several weeks owing to expansion of melanophores. There is no evidence of the significance of colouring but it is hypothesized that this darkening especially in caudal fins contributes to visual signaling within a pool of molts [11].

Desmoltification

Desmoltification refers to abandoning of preparatory adaptation changes to marine life in Atlantic salmon or parr-reversion in pacific salmonids. This phenomenon occurs if the fish is unable to enter marine environment during the period of complete smoltification (the smolt “window”). Desmoltification is accelerated by short photoperiod and abnormal variations in water temperatures [31]. The process is characterized by partial loss of morphological smolt characteristics for example fish again taking the darker appearance although not reverting to parr morphology despite loss of critical physiological functions. Other characteristics include loss of hypo osmoregulatory ability, critical metabolic adaptations, behavioral changes like re-establishment of positive rheotaxis and endocrine changes.

Smolts production in hatcheries

It is possible to produce smolts in artificial hatcheries. These smolts can then be introduced in new places, replacing or enhancing natural fish runs which are extinct, increasing abundance for sport fisheries and increasing commercial fisheries [32]. In order to achieve the desired purposes, conditions in the hatchery environment should promote morphological fitness by emulating natural fish body size, body shape, and coloration. Hatcheries can therefore simulate both fresh and marine water conditions through dietary salt, growth modulation, rearing density and environmental enrichment. Fresh water phase consist of spawning, cycle, egg production, hatching and first feeding stages. Breeding stocks selection is done from adults returning to the hatchery.

Conclusion

Migration from fresh to marine water is accompanied by morphological and physiological adaptation. Development of such features in parr and smolt is gradual and continuous. These features can be used to identify resident, transitional and reverting parrs and smolts. In general, wild smolts differ from hatchery smolts in four ways; wild fish are generally smaller than hatchery fish; show more rapid growth rate during the smolting period; have less body fat than hatchery smolts; and show a more dynamic change in physiological and metabolic status from over-wintering to the spring smolting period. Further research should be done to establish the importance of the auxiliary appendages on pelvic fins of salmon smolts, the reason why UV cones disappear in smolts as the fish approach smoltification and how fish increase buoyancy as they move to deep marine waters.

Conflict of interest

The authors declare to have no financial or personal relationships which may have inappropriately influenced the writing this article.

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