Research Article

Prolactin Influences Different Aspects of Fish Biology

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ABSTRACT

Prolactin (PRL) is a 198 amino acid long polypeptide hormone, structurally similar to growth hormone, secreted by adenohypophysis in the vertebrates. The full-length amino acid sequence of PRL has been determined from a variety of teleost and non-teleost fish. Teleost PRL genes are shorter than mammalian. PRL exists in two forms, namely, PRL-1 commonly found in all vertebrates and PRL-2 found in several non-mammalian vertebrates including fish. This hormone binds to transmembrane Prolactin receptor (PRLR) which is a member of the class 1 cytokines receptor superfamily. We know that PRL has over 300 different functions in vertebrates. In fish, PRL plays an important role in migration, osmoregulation, parental behaviour, reproduction and development along with other hormones. Recent studies show prolactin has a role in cell proliferation in the gills of teleost fish. This review highlights diversified role of PRL in fish which may serve as avenues for further researches in near future.

Key words: Prolactin, Osmoregulation, Fish, Migration, Reproduction.

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INTRODUCTION

Prolactin (PRL) is a well-known regulatory molecule with diverse physiological functions (Freeman *et al.* 2000). It has been expressed in a variety of different organs and is highest in the pituitary. In fish, it is maximally expressed in specific cells of the adenohypophysis, from which it is released into the bloodstream. PRL gene structure was first discovered in the chum salmon fish (*Oncorhynchus keta*) and is similar to the human PRL gene.[1] In 1930, Oscar Riddle first found out PRL from the pigeon. Prolactin plays an important role in fish, which is a peptide hormone found in all vertebrates except the jawless fish. In the human body, this hormone helps in milk production.[2] Prolactin hormone belongs to the same hormone family of Growth Hormone (GH) and Placental Lactogen (PL).[3] PRL is 277 amino acid long with 28 amino acid long chain of signal peptide.[4]

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Different types of PRL sequence are found in several species of fish like Fugu, European eel and rainbow trout.[5-7] Most of the teleost and non-teleost fish can be identified by the length of the PRL sequence. In teleost, the PRL gene produces a short 12-14 amino acid signal sequence. Pars distalis of pituitary gland is made by a definitive mass of PRL secreting cells which are found in all teleost fishes.[8] Researchers suggested that extra pituitary PRL gene expression has been exhibited in the spleen and gonad of gold- fish[9] as well as in the liver and intestine of the seabream.[10] Here the review highlights the current state of knowledge on the role of prolactin in fish reproduction, osmoregulation, regulation of calcium secretion, migration, cell proliferation and parental behaviour. This review tries to provide knowledge about the multidimensional effects of prolactin, which can be taken up for researches to explore more on prolactin and its effect on fish under different experimental or stressed environmental conditions.

Structure of Prolactin Gene

Prolactin (PRL) is the part of a larger hormone family that includes other hormones like Growth Hormone (GH) and Placental Lactogen (PL).[1] The length of this

gene is approximately 10kb, and is made up of 5 exons and 4 introns.[8] We found different types of prolactin which in most cases are monomeric with a molecular weight of 23kDa and rest with a molecular weight of 50kDa. Molecular weight of macroprolactin is 150kDa is made of a prolactin-Ig complex. From the suggested research papers, the first discovered PRL gene structure was in Chum salmon (*Oncorhynchus keta*) from the piscine family.[2] About 400 to 800 million years ago, the ancestral gene of PRL produced by duplication, simultaneously borne some similarities with other hormones like growth hormone (GH), placental lactogen (PL) and somatolectin.[9] A difference in the disulphide bond of PRL is found between teleost and other vertebrates. The disulphide was lost from the n-terminal in the common ancestors of teleost where was maintained in the tetrapod and the lobe finned fish.[10] In cases three disulphide bonds are present in PRL-2. Two types of PRL namely PRL-1 is found in all vertebrates and PRL-2 found in fish and non-mammalian vertebrates.[11]

Prolactin Hormone Receptor

The prolactin receptor (PRLR) belongs to the class one cytokines located on the cell membrane. PRLR was discovered in the *Oreochromis niloticus;*[12] PRLR is made of 600 amino acid long chain which is as same as to mammalian PRLR. Alternative splicing occurs during the formation of PRLR, therefore different types of PRLR of different lengths can be found[10] Mainly two types of PRLR are found namely PRLR 1 and PRLR 2 in several teleost fish. The PRLR made of two disulphide bonds and a modified WS motif which is without N-glycosylation between conserved 2 and conserved 3 regions.[13]

Factors Affecting Prolactin Release

The prolactin is secreted by special cells from the anterior pituitary is called lactotrophs. On the cell membrane G-protein coupled receptors (GPCRs) that induced cellular activities are present.[14] In many fishes PRL secretion is regulated by a neuro hormone (GnRH) that is produced by the hypothalamus. Reproductive period and osmolality are the other factors that control the secretion of PRL.[2] In the Mozambique tilapia (*Oreochromis mossambicus*) the secretion of PRL is controlled by GnRH.[15] Another substance, the leptin regulates the secretion of PRL that comes from the liver. A high level of GnRH increases signalling by phospholipase - c and inositol triphosphate, leading to intracellular calcium movement.[16] In Masu salmon (*Oncorhynchus masou*) the GnRH increases the mRNA expression in the PRL gene promoter region, which act as a transcription factor.[17] The prolactin binds with the receptor via two binding sites, dimer form of PRLRs initiate Janus Kinase pathway and phosphorylates STAT transcription, where it stimulates PRL genes specific promoter that causes biological response[2] and may also activates MAP kinase pathway for cell proliferation.[5]

Influences of Prolactin in Fish

Regulation of Calcium Secretion

Marine and freshwater fishes face change in calcium concentration in the environment. Calcium is deposited in the bone by the intestine in form of ionized calcium.[18] Calcium is needed for maintaining skeletons of fishes.[19] PRL stimulates the calcium absorption through branchial tissue using ATP.[20] When *Oreochromis mossambicus* moves from seawater to freshwater unexpectedly plasma levels of prolactin rise to enhance the gill calcium influx and resist the calcium outflow generating a condition known as hypercalcemia.[18] However, PRL secretion increases during high extracellular osmolality, causing the opening of the ion gated channels.[21] Reports show that calcium is deposited in bones and scales of female gold fish (*Carassius auratus*) with the help of prolactin hormone.[22]

Effect on Osmoregulation

It is challenging for fishes to survive in a hypo-osmotic environment. But PRL controls the activities of gills whose main function is ion and water exchange. During freshwater adaptation, prolactin-releasing peptide stimulate prolactin expression in the pituitary and peripheral organs in fish. Several research papers suggested that when PRL concentration is lowered, then osmotic permeability of gills is reduced as well as mucus secretion is increased which contribute in maintaining ion and water balance.[23-25] Growth Hormone, which is similar to prolactin, promotes acclimation to seawater in several teleost fish through the action of Insulin-like Growth Factor I. It has been reported that in the sea water-type chloride cell the development and differentiation of branchial epithelia (and their underlying biochemistry) is regulated by GH, IGF-I, and cortisol whereas in the freshwater-type chloride cell, prolactin and cortisol help in development and differentiation of the chloride cells.[26] Levels of extracellular osmolality regulate PRL secretion by autocrine feedback. Receptor of PRL found in chloride cells of *Oreochromis mossambicus* help in the chloride ion balance of fresh water fish.[27] PRL regulates the Na^+/K^+ ATPase activity in *Sparus sarba* which is closely connected with hypercalcemic action.[28] It has been also reported that the glomerular filtration rate is controlled by PRL concentration decreasing the urine

osmolality.[29] Furthermore, prolactin at a low level can absorb intestinal fluid and salt in Japanese eel and trout.[30]

Role in Migration

The migration between the parental river and the sea, and the homing migration to the maternal stream is one of the most interesting and challenging phenomena in fish biology. PRL plays an important role during migration as its level increases in salmon under the anadromous migration regulated by the GnRH.[31] During the transition from salt water to fresh water during pre-spawning PRL maintains the ion balance in fish. When *Anguilla japonica* migrates from sea water to fresh water, the PRL mRNA expression is low.[32] These literature surveys suggest that PRL regulate the movement of fish during migration.

Role in Reproductive Cycle

PRL helps in the reproductive cycle and development of the sexual organ in fishes. PRL and GnRH levels are usually high at the time of gonadal development and spawning in the Japanese eel and cat fish (*Clarius batrachus*).[33,34] The gonads of various species of fishes like Mozambique tilapia, seabream and gold fish show mRNA of PRL receptor[35] suggesting that prolactin regulates the gonadal growth and development in fishes by binding to its receptors. On the other hand, PRL secretion increases after spawning during vitellogenesis in female tilapia.[36] The production of testosterone hormone in the Mozambique tilapia as well as the oocytes development in the Guppy fish are directly regulated by PRL.[37] It has been found that sex hormones like estradiol increase the PRL synthesis *in vitro* in the Mozambique tilapia cells whereas GnRH stimulates the PRL release.[38] It has been reported that PRL suppresses progesterone as well as oestradiol expression when it is at its peak after vitellogenesis and before ovulation.[39] Therefore, prolactin along with other sex hormones and neurohormones like GnRH may regulate reproductive cycles in fish.

Development of Parental Behaviour

Researchers suggested that oral egg carrying behaviour is developed by the combined effect of prolactin and estrogen[40] in tilapia. PRL secretion increases at the time of embryogenesis and somitogenesis in the seabream.[41] The hormone can maintain the osmoregulation of eggs through chloride cells which response to changes in salinity by autonomous regulation in embryonic condition.[42] Most of the research papers suggested that PRL secretion and brood care are interrelated with positive feedback but exceptions are found in *Neolamprologus pulcher*.[43] Most fishes develop nest building behaviour, secrete mucous to protect their eggs and hatchlings under influence of prolactin. It also induces fanning in wrasse males *Symphodus ocellatus* and stickleback males.[44]

Regulation of Cell Proliferation

In seawater-adapted euryhaline fish, the permeability of the gastrointestinal tract is generally greater than that of freshwater-adapted fish. The esophageal epithelium of sea- water fish is simple columnar, whereas that of freshwater fish is stratified. The number of these cells can be increased through three mechanisms: proliferation and differentiation of new cells, differentiation (or transformation) of existing chloride cells from one type to another and a decrease in cell death (necrosis or apoptosis).[45,46] These mechanisms of cell turnover and differentiation are regulated by the growth hormone, prolactin, and cortisol by governing chloride cells and the acclimating teleost gills. On the goldfish scales, PRL expanded the mucous cell layers, which may restrict efficiently water inflow by the mucous system.[47] However, the control of cell turnover is an important function of PRL in teleost. Furthermore, prolactin specifically inhibited the osteoclastic activities of goldfish scales and promoted osteoblastic activities *in vitro*.[48]

Regulation of Immunological Functions

The prolactin is capable of inducing the expression of the pro-inflammatory cytokines IL-1β and TNFα, and Reactive Oxygen Species (ROS) in leukocytes and macrophages found in head kidney of gilthead seabream.[49] It has been reported that PRL has immunomodulatory and immunostimulatory effects by targeting the lysozyme activities in the macrophages of the head kidney in Salmon and increasing the expression levels of Toll Like Receptors (TLR) during pathogenic infections.[50]

CONCLUSION

This brief review shows that PRL is a vertebrate-specific hormone whose functions have been studied for a long time. Indeed, immense knowledge been accumulated on prolactin secretion and function in a variety of different species. Thus, prolactin represents an exciting opportunity for evolutionary neuroendocrinology as its functions are compared between the different species and classes of vertebrates. We review the current state of knowledge on the role of prolactin in fish reproduction, migration, reproductive development and cycling, brood care behaviour, pregnancy, and nutrient

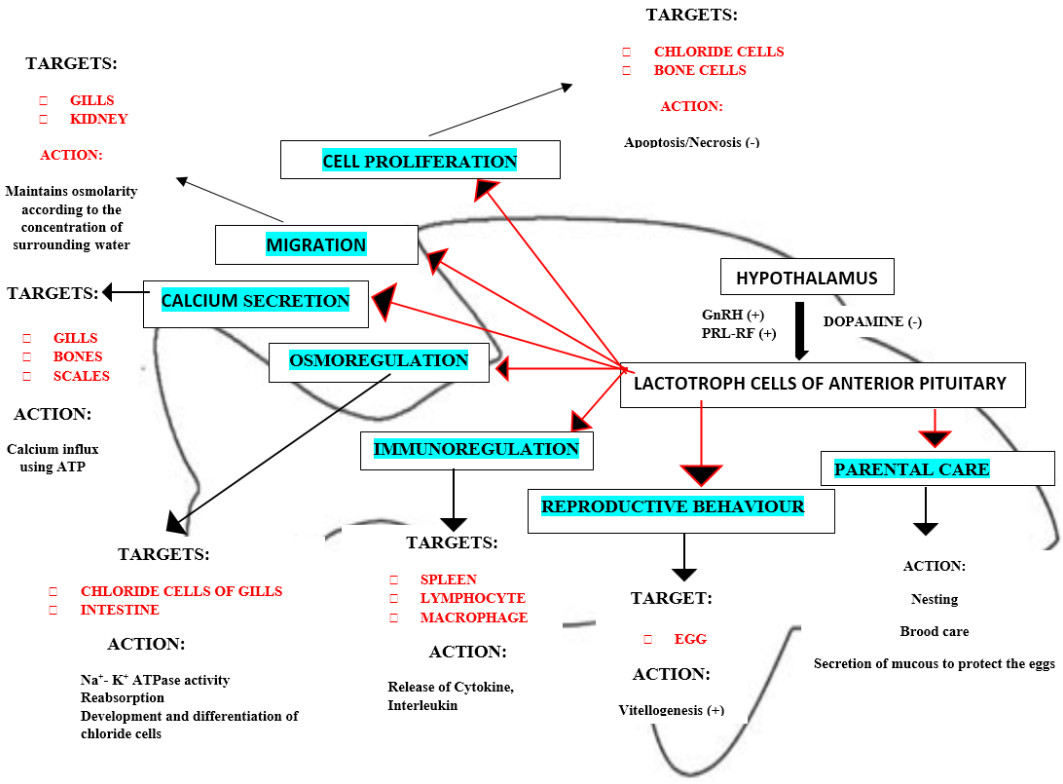

Figure 1: The flowchart depicts the multidimensional role of prolactin in fish biology. + indicates stimulation and – indicates inhibition. Blue highlighted boxes indicate multidimensional role of prolactin in fish followed by each of its targets and action.

provisioning to young and summarized it in Figure 1. We also highlight significant knowledge and specific action of prolactin in fish. It has a wide range of functions in fish physiology. Fish is a diverse group of species and comparative study on different aspects of fishes has clearly identified that PRL is a regulatory hormone for ion and water transport. In bony fish, PRL enhances calcium transport in the gills of both freshwater and euryhaline species, leading to hypercalcemia. Prolactin, a major osmoregulatory hormone in fish has evolved into a hormone that regulates lactation in mammals. In fact, both of these functions require the action of prolactin on epithelial cells and their proliferation. However, an intriguing change in the action of prolactin on parental behaviour in fish becomes prominent in birds and mammals with different brooding and nursing behaviours. The multifaceted role of prolactin in fish may be considered as different avenues for future researches.

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CONFLICT OF INTEREST

There is no conflict of interest between the authors.

Author's Contribution

Miss Chakraborty and Mr. Das, being undergraduate students, have contributed in literature survey and prepared a draft of the review. Dr. Saha corrected it and made necessary modifications of it and prepared the final manuscript.

ABBREVIATIONS

GH: Growth Hormone; **PRL:** Prolactin; **GnRH:** Gonadotropin Releasing Hormonr; **PL:** Placental Lactogen; **Ig:** immunoglobulin; **kDa:** kilo dalton; **IL:** Interleukin; **TNF:** Tumor Necrosis Factor.

SUMMARY

Prolactin is the well-known regulatory molecule with diverse physiological functions. In fish, it is maximally expressed in specific cells of the adenohypophysis. Prolactin maintains the blood calcium level in fishes

by changing the osmolality of blood that opens the ion gated channels creating a stable blood calcium level which is important for maintaining the skeletal structures in fishes. Prolactin helps in osmoregulation by controlling the activities of gill. The decrease in prolactin reduces the osmotic permeability of gills as well as increased mucus secretion. Prolactin causes migration as the level increases in salmon under the anadromous migration regulated by the GnRH. The current review shows a comprehensive role of prolactin in fish reproduction, migration, immunomodulation, cell proliferation and parental care.

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