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SEASONAL REPRODUCTION IN FISH: A FUNCTIONAL INTERPLAY BETWEEN THE PINEAL ORGAN AND PHOTOPERIODS

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SUMMARY

Reproduction in most fishes is discontinuous or seasonal. Rhythms with a periodicity of one year represent major components in the adaptation of concerned fish to their environment. Environmental factors, such as light and temperature, play an important role in the synchronization of this rhythmic activity of reproduction. In vertebrates, synchronization is mediated through the system which is composed of sensors and circadian oscillators like the pineal organ, the lateral eyes and the suprachiasmatic nuclei of the hypothalamus. The fish pineal seems to be involved in the timing and control of reproduction. On the basis of several experimental evidences, it is believed that the pineal is able to translate environmental information (photoperiod, temperature) into rhythmic messages. To date, two kinds of signals have been clearly identified, a nervous signal and a neurohormonal signal, i.e., melatonin. Whereas the functional significance of the nervous signal is not yet clearly understood, there is increasing evidence that in at least temperate zone vertebrates, melatonin is the chemical messenger of photoperiod (Zeitgeber). In contrast to the neuronal message, elaborated mainly (if not exclusively) by the pineal of ectotherms, melatonin appears to be a conservative signal in the vertebrate phylum. In all the species investigated so far, melatonin production is high during nighttime and low during daytime. Despite this apparent homogeneity, the involvement of the pineal in the temporal organization of reproduction, as well as the mechanisms by which the photic information is processed in the control of gonadal germ maturation in fish have been the matter of great interest. Molecular mechanism involved in photoreceptor-induced pathway in fish is yet to be known, without which benefit from such information remains unveiled.

Key words : fish; light; pineal; reproduction

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INTRODUCTION

Majority of teleosts all over the world are discontinuous or seasonal breeders, showing their peak reproductive activity or act of spawning for a short period which is preceded by a long and complicated process of preparation. The temporal organization of annual reproduction is species specific and in most cases influenced by one or more components of the environment in which the fishes live in. The major environmental factors which in broad sense form the battery of information used by a species in determining its breeding periodicity include light, temperature, rainfall, abundance of food, and availability of nutrients. Among the components of the environment, annual changes in the duration of solar day has been proved to be the primary and regular variable that individually, or in combination with water temperature, impel the "driving function" in determining the sexual periodicity in most of the vertebrates including fish. However, the use of photoperiods as the environmental cue in determining sexual periodicity in fish varies not only with the species, but also with their distribution (1-4). A successful interaction between the environmental factors and the endogenous body functions results in appropriate timing of seasonal reproductive events and thus choosing the suitable condition for rearing of their offspring.

The physiological response in any animal to either a single or a group of environmental component(s) has evolved a precise mechanism for processing of environmental information. Available information suggests that synchronization of body functions with the environmental information is mediated through the system composed of sensors and circadian oscillators (5). This circadian oscillator system among the fish species is located in the pineal organ and the eyes (6), among which the pineal organ is considered as the most important component for its responsive mechanism to the changes in environmental light and darkness (7-10). The present review is an attempt to understand a possible interplay between the pineal organ and photoperiods in the regulation of seasonal reproduction in fish.

I. The Pineal Organ: A Photosensory Unit in Fish

On the basis of several lines of experimental evidence, it is believed that the pineal is able to translate environmental information (photoperiod and temperature) into rhythmic messages (5). To date two kinds of signals have been clearly identified, a nervous signal and a neurohormonal signal i.e., melatonin (5-6). Whereas the functional significance of the nervous signal is not yet clearly understood, there is increasing evidence that, in fish as well as in other vertebrates, endogenous level of melatonin is the chemical messenger of photoperiod (10).

In fish the pineal organ acts as a direct photoreceptor, tranducing light information into neural and hormonal (melatonin) signals (5). Melatonin acts as an internal zeitgeber or 'time-keeper' which is involved in the timing and control of a number of rhythmic physiological and behavioural functions including reproduction in vertebrates (11). Systems responsible for the rhythmic production of melatonin include a circadian clock which drives the rhythm, and a photodetector which mediates the effect of light. In fish the entire system (the photodetector, the circadian clock and melatonin synthesizing enzymes) is contained in the pineal organ (12) suggesting that the pineal acts as a transducer, responding to changing circumambient light by changing its rate of melatonin output.

In contrast to the nervous messages, elaborated mainly (if not exclusively) by the pineal of ectotherms, melatonin is a conservative signal in all the vertebrates. In all species investigated so far, melatonin production is high during nighttime and low during daytime (5). Considering this unique feature, melatonin appears to be the signal of darkness and the time keeping molecule of the organisms in most vertebrates (13). Despite this apparent homogeneity, the organization of the pineal and the melatonin synthesizing cells as well as the mechanisms by which the photoperiod controls melatonin production, have been greatly modified from fish to mammals (6).

The effects of different lighting conditions and physical parameters of light were investigated in the isolated pineal organ of the white sucker kept under static or superfusion culture (14). It was found that the secretion of pineal melatonin is directly controlled by the photoperiod and completely suppressed under constant illumination. The inhibition of melatonin secretion by unexpected light at night depends on the irradiance, duration, timing of the treatment and the lighting history of the pineal organ (14). The presence of an endogenous intrapineal oscillator driving the melatonin production has been detected in all fish species so far investigated except the rainbow trout (7). A study on the zebrafish has provided the evidence that this fish has a photosensitive pineal gland, which has an endogenous circadian pacemaker, entrained to environmental light dark cycles (8). Further study on this fish suggested strongly that exo-rhodopsin is a pineal opsin common to teleosts (9).

The question whether a pineal clock identified in the sailfin molly (*Poecilia velifera*) is also present in some other representatives of the teleostean family Poeciliidae was addressed by Okimoto and Stetson (15). The collected data suggested that a circadian oscillator residing in the pineal of the sailfin molly also appears to be present in all of the poeciliid representatives tested supporting the notion that the presence of a pineal clock occurs at every level of study (15).

A comprehensive study that combines anatomical and ultrastructural findings with cell and molecular biological results, confirms the functional significance of the melatonin-synthesizing pineal organ as an important component of the photoneuro-endocrine system and stresses the importance of this organ as a model of study signal transduction mechanisms both in photoreceptors and in neuroendocrine cells (16). While importance of melatonin as the most important candidate involved in the mediation of photic effects on piscine reproduction has been emphasized by several investigators, search for other molecules which may mediate similar functions of pineal has also got momentum. A novel opsin has been isolated (17)from the pineal complex of Atlantic salmon (*Salmo salar*) and from the brain of the puffer fish (*Fegu rubripes*). These extra-retinal opsins share approximately 74% identity at the nucleotide and amino acid level with rod-opsins from the retina of these species (17). However, role of these molecules in the regulation of fish reproduction remains as a topic of future research.

II. Photoperiodic Regulation of Reproduction: Involvement of the Pineal

A. In High Latitude Fish:

The question whether the effect of daily changes in the length of photoperiod influences the temporal organisation of reproductive seasonality in teleostean fish, and if so how that

happens, has been addressed in several studies on high latitude fish. Preliminary observations indicated that the gonadal recrudescence is stimulated by long photoperiods in several fishes like bridle shiner *Notropis bifrenatus* (18), the Japanese medaka *Oryzias latipes* (19), three-spined stickleback *Gasterosteus aculeatus* (20-21), the goldfish *Carassius auratus* (22), and the mosquito fish *Gambusia affinis* (23).

A stimulatory effect of light on the gonadal development in the blinded medaka *Oryzias latipes* was reported by Urasaki (24). In this species reproductive effects of long photoperiods (LD 14:10) has been reported to vary seasonally; ovarian enlargement is stimulated by long photoperiods most dramatically during the months of May and June (25), when blinding retards the galvanizing effects of a long photoperiodic schedule on ovarian size. Medaka pinealectomized in late February and exposed to continuous light or natural day lengths until nearly May have smaller ovaries than intact fish maintained under the same regimens (26). Therefore the medaka pineal organ appears to be a component in a pathway by which long photoperiods promote gonadal recrudescence (24,26,27).

The pineal organ, because of its photoreceptive properties in the teleostean fishes, transforms light stimuli into chemical stimuli into a chemical signal affecting gonadal maturation and reproduction, though the nature of such signal remains undefined (28). The pineal organ of *Fundulus heteroclitus* has been examined with reference to photoperiodic control of reproduction (29). Female fish collected in winter, spring, or summer were subjected to pinealectomy and maintained on short days (LD 9:15) or long days (LD 15:9) at 20^{0} C. Sexual maturity was determined after 6 weeks of exposure to the experimental light regimes. The fish subjected to surgical manipulations were capable of perceiving stimulatory or inhibitory photoperiods regardless of whether the pineal was intact or removed. Pinealectomized fish did not remain sexually active when exposed to short days. From these results, it was not possible to demonstrate an essential photoreceptive or endocrine role of the pineal organ in reproduction in *F. heteroclitus* (29).

Administration of melatonin to medaka is known to inhibit oocyte development and alter pituitary gonadotropin function in fish exposed to a LD 14:10, at 26°C regime during spring (30). During winter, ovarian size is larger in controls than in pinealectomized fish treated with melatonin and exposed to a LD 16:8 regime, but not a LD 8:16 regime (31). Such results could be obtained if short photoperiods evoke pineal organ and retinal melatonin production. *In vitro* experiments demonstrate that melatonin at relatively low doses (0.1 mm/ fish) slightly represses, but did not totally inhibit medaka oocyte maturation (32).

The study on rainbow trout (*Oncorhynchus mykiss*) suggests that the pineal gland may influence the hypothalamo-pituitary-gonadal axis by altering the maturation period and controlling gonadal axis by altering the maturation period and controlling spawning (33). Data presented by De Vlaming and Vodicnik (34) imply that the cyprinid teleost, *Notemigonus crysoleucas*, the pineal organ exerts its effects on reproduction via the hypothalamus and pituitary. The study on goldfish, *Carassius auratus*, lead one to consider the possibility that the pineal organ has an additive effect with regard to the stimulatory effects of long photoperiods on gonadal activity (35).

B. In Low Latitude Fish :

Light as a source of environmental cue in the use of regulation of reproduction in fish of low and middle latitudes has been considered by several workers, but the studies have been mostly confined to the Indian catfishes (*Heteropneustes fossilis; Clarias batrachus*), freshwater murrel (*Channa punctatus*) and an Indian minor carp *Cirrhina reba*, of which best studied is Indian Catfish, *Heteropneustes fossilis* (36-40). To utter surprise, none of the Indian major carps received proper attention for revelation of the photic influence on the reproductive performance of concerned fish.

Exposure to a daily schedule of long photoperiods (14L:10D) for six weeks resulted in stimulation of ovarian recrudescence (vitellogenesis) during the preparatory phase (February–April) in an annual gonadal cycle of Indian catfish, *Heteropneustes fossilis* (36-38). Ovarian development in *Heteropneustes fossilis* was found to be accelerated under the influence of long photoperiods, while a retardation was noted in short photoperiodic fish (41). Similar observations were made on a minor carp *Cirrhina reba* (42) and another catfish *Mystus tengara* (43) where acceleration of gonadal growth was noted under the different schedules of long photoperiods (14L:10D; or 18L:6D; or continuous light 24L:0D). Conversely, a regimen of short photoperiods (8L:16D) or total darkness (0L:24D) resulted in delay of reproductive maturation. A combination of long photoperiods and relatively high temperature regimen was also found to be effective in causing the maturation of gonad in another teleost, the Indian murrel *Channa punctatus,* (44-46). Nevertheless, no information is available on the relative influence of an identical regimen of altered photoperiods during the different phases of the annual reproductive cycle in any Indian major carp which has immense economic value.

Subsequently, the question whether the pineal organ is involved in the mediation of photoperiodic effects was addressed by Garg (47-48). To investigate the relative importance of pineal and eyes in ovarian activity; catfish were subjected to pinealectomy, blinding, or both were exposed to continuous light (LL) or continuous darkness (DD) during the different phases of the annual reproductive cycle (47). The observations that ovarian recrudescence occurred even in the absence of both pineal and eyes, indicated the involvement of extrapineal and extraocular photoreception in the regulation of reproductive activity in the catfish. Further study concluded that the role of the pineal in catfish (*Heteropneustes fossilis*) reproduction is variable and depends upon the photoperiod to which they are exposed as well as on the time of the year and the stage of the reproductive cycle (48). In another investigation on the same species (49) revealed that pinealectomy under normal photoperiods and temperature causes season-dependent effects on ovarian activity. When the fish were pinealectomized in the preparatory phase (early light-responsive period) and maintained until the early prespawning phase, there was an accelerated growth of the ovary, but the same treatment was ineffective in the presawning and spawning (late light-responsive phase) and postspawning (light refractory) phases.

In case of another catfish, *Clarias batrachus*, it has been shown (50) that 5-methoxy tryptamine (5-MT) is a physiologically active hormone that mimics the action of melatonin on gonads. Melatonin administration to this species in the afternoon prior to the diurnal dark phase increased the level of testosterone. However, its higher doses of 100 and 200 mg/fish

decreased the testosterone levels. But even more higher dose of 400 mg/fish again increased the testosterone levels in comparison to the dose of 200 mg/fish. Administration of melatonin and 5-MT decreased the estradiol-17b levels and estrone levels.

The inhibitory role of melatonin on gonadal activity has also been documented in *Channa punctatus* (51-52). It has been inferred that hypothalamic 5-HT may play a central role in photosexual mechanisms and mediate long photoperiodic effects on neuroendocrine-reproductive axis. The photoperiodic study on the same species revealed that a schedule of LD 16:8 is stimulatory whereas LD 8:16 regime is inhibitory to the testicular activity at 30^{0}C temperature (53-54). But the role of pineal in this phenomenon remains unknown.

Administration of melatonin at lower concentrations (25, 50 mg/fish) significantly lowered the 17-a-hydroxyprogesterone levels and higher doses (100, 200 and 400 mg /fish) further reduced it to non-detectable levels; however, 5-MT reduced the 17-a-hydroxyprogesterone level in *Clarias batrachus* (55). In connotation with the data available with the female Indian fishes, precocious recrudescence of seminal vesicle and testis has also been reported following the study on long photoperiods subjected catfish, *Clarias batrachus* (56). Recently, influences of long (LD 16:8) and short (LD 8:16) photoperiods have been studied in both the females (57) and males (58) of Indian major carp, *Catla catla* during the diferent phases of an annual gonadal cycle. Collectively, results of the undertaken preliminary studies demonstrated for the first time that environmental light has significant influences on the gonadal functions of *Catla catla*, but the nature of influence remarkably varies in relation to the reproductive status of the concerned fish (57-58).

III. Photoinduced Gonadal Maturation: An Insight

While photic influences on the gonadal maturation process has been taken into consideration by the studies cited above, the mechanism involved in the germ cell maturation of Indian fish has been the topic of research only in recent years. A maturation promoting factor (MPF) has been found to be involved in the process of germ cell meiotic maturation beyond the diplotene stage under the influences of progestogens (in fish it is mainly DHP or 17a,20b-dihydroxy-4-pregnen-3-one) released from the somatic cells of ovarian follicles by the induction of GtH or gonadotropic hormone (59). Evidences obtained in recent studies indicate that DHP in fish initially interact with the membrane receptor of oocyte to induce the cascade of cytosolic events including MPF formation which leads to the germinal vesicle breakdown (GVBD) (60). Nonetheless, it remains to be investigated how photoinduced gonadal maturation takes place at molecular level.

IV. Pineal in the Photoperiodic Regulation of Reproduction in Fish : Possible Mechanism of Action

The mechanisms underlying the photoperiodic entrainment of the endogenous circannual rhythm of maturation in the rainbow trout were investigated subjecting December-spawning fish to abrupt changes in daylength which varied in their timing or magnitude (61). These results indicated that photoperiodic history determines the reproductive response of rainbow trout to changes in daylength. A recent study (62) suggested melatonin to be one of the

factors that mediates the transduction of photoperiodic information to the brain-pituitary-gonad axis in gonadal maturation of underyearling precocious male masu salmon. But the mechanism by which melatonin performs this function remains speculative. On the contrary, study on rainbow trout suggested that the pineal may not be the site of pacemaker that controls rhythms, and further research is required to study the involvement of other photoperiod-transducing systems and melatonin (nonpineal origin) in the regulation and expression of circadian rhythm in this species (63). Likewise, a more recent study in female three-spined stickleback (*Gasterosteus aculeatus*) suggested that the major part of the photoperiodic effects is mediated via mechanisms other than circulating melatonin (3). However, the study on European sea bass provided the basis of a conclusion that plasma melatonin in this species reflect the pineal capacity to integrate seasonal information and supply precise calendar information, which may synchronize different physiological processes including reproduction (4).

V. CONCLUSION

Considering data available at this time, it may therefore be contended that some results on the study of few fishes are certainly ambiguous or conflicting, but in general substantial evidence coming especially from investigations with teleostean fishes compels us to the supposition that the pineal organ does modulate or 'fine tune' reproductive cycles in at least some teleosts (64). Notwithstanding, it is interesting enough to note that a molecular approach of understanding the photoinduced maturation in fish is yet to receive proper attention. But considering the recently available information (65) showing involvement of different peptides, commonly known for mammals, in the final fish oocyte maturation induced by gonadotropin and by maturation-inducing hormone (MIH), it may not be unwise to search a role for substances in the mechanism of photoinduction.

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