ENVIRONMENTAL CONTROLS FOR INDUCED MATURATION

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INTRODUCTION

Reproduction in cultured finfishes is usually restricted to a specific period of the year when environmental conditions are favourable. The success of marine and brackishwater finfish breeding primarily depends on the availability of healthy breeders in sufficient numbers for use in induced breeding and thereby leading to large scale seed production. In India, in order to meet the growing demand for the seed of cultivable marine and brackishwater finfish for aquaculture practices, mass production of seed by induced breeding is an essential prerequisite. It is imperative to maintain brood-stocks in an environment which is conducive to them and one that promotes gonadal maturation. Many of the major current problems in marine and brackishwater finfish breeding relate to nutrition, reproduction and environmental requirements and hence the need for better understanding and control of these factors (Lam, 1983).

The major activities in finfish breeding involved are the raising and maintenance of broodstock, induced maturation of gonads, hatchery operations including spawning, fertilization and hatching, larval food production, larval and nursery rearing techniques and production of hatchery bred fingerlings. The influence of environmental factors on maturation of gonads has been studied in several species of freshwater fishes and not much work has been done on marine and brackishwater fishes. In this paper, the role of environmental parameters on gonadal maturation of finfishes in the three habitats are discussed.

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GONADAL MATURATION OF FINFISHES

Gonadal maturation process in fishes consists of two major phases (1) Gametogenesis and gonadal growth and (2) Completion of maturation and release of gametes. While the period required for the latter phase is much shorter than the first, most captive fish, particularly females fail to complete the final stage of maturation. The development of gonads could be induced by nutritional manipulation, environmental manipulation and hormone control.

The gonadal maturation of finfishes is basically controlled externally by environmental conditions and internally by the endocrine system (de Vlaming, 1974). Environmental stimuli and hormonal secretions influence maturation of gonads and there is interaction between the brain, pituitary gland and gonads of finfish. The right stimuli transmitted from the brain induce secretion of a releasing hormone (RH) from hypothalamus. The releasing hormone stimulates the release of gonadotropin from the pituitary gland into the vascular system. The gonadotropin is then carried to the gonads and it induces the production of steroid sex hormones. The latter, which include androgen, estrogen and progesterone are responsible for gonadal maturation (Aronson, 1959; Hoar, 1969; Lam, 1982).

INFLUENCE OF ENVIRONMENTAL PARAMETERS ON GONADAL MATURATION

The important environmental factors which control gonadal maturation and spawning of finfishes include photoperiod, temperature, floods, food availability and stress.

The effects of photoperiod and temperature have received much attention and are generally considered to be of great importance in the inducement of gonadal maturation and spawning (Shehadeh, 1970; Lam, 1983). In nature, gonadal maturation and spawning in most of the finfish species are regulated either directly by manipulation of day-length or temperature and providing optimum quantity of food. In some finfish species, gonadal maturation may be manipulated by photoperiod alone. For example, gonadal maturation is advanced with short light exposure in the blueback salmon, Oncorhynchus nerka and delayed by prolonged light in brook trout, Salvelinus fontinalis (Combs et al., 1959; Allison, 1951). Lowering of temperature alone can promote gonadal maturation in some tropical marine fishes. This may be related to the migratory behaviour. The fish migrate to cooler waters in deep sea for gonadal development and maturation and subsequently to warmer shallow waters for spawning. The gonadal maturation can also be regulated by combined manipulation of photoperiod and temperature. For example, the ovarian maturation of the grey mullet, Mugil cephalus can be accelerated at 21°C and 6 hr light, 18 hr darkness (Kuo et al., 1974a).

In the Ayu, Plecoglossus altivelis, a smelt-like fish cultured in Japan, manipulation of photoperiod resulted in the successful acceleration of gonadal maturation which enabled rearing of fry during period of abundance of natural food (Kuronama, 1968). Temperature and light intensity are important factors for seasonal peaks of gonadal activity in Tilapia leucosticta living in lacustrine habitat in Kenya. An increase in the reproductive rate has been observed in Tilapia mossambica with rise in temperature upto 28°-31°C (Mironova, 1977). Female Tilapia aurea reared at 17°C had regressed ovaries but exposure to 28°C for two weeks stimulated ovarian development (Terkatin-shimony et al., 1980). The reviews of Jhingran (1969) and Singh (1969) discuss the effects of various other environmental stimuli viz., rainfall, floods and hydrological conditions, pH, NH_3, CO_2 and turbidity on the controlled breeding of cultured food fishes.

Photoperiod

In fish species which spawn in spring or early summer, gonadal recrudescence is stimulated by long photoperiods

particularly in combination with warm temperatures. An abrupt increase in photoperiod is not ecologically helpful because fish are normally exposed to a gradually increasing photoperiod. In the laboratory conditions, a rapid increase in photoperiod from 8-16 hr within one week caused greater stimulation of vitellogenesis than gradually increasing photoperiod in Salmo gairdneri (Scott, 1979). In contrast, in species which spawn in autumn or early winter, gonadal recrudescence is often favoured by short or decreasing photoperiods (Htun Han, 1977). A decreasing photoperiod is much more effective than a constant short photoperiod in stimulating gametogenesis. In some populations, long photoperiods stimulate gonad development (Skarphedinsson et al., 1982). Light intensity is often not considered in photoperiod studies. The photoperiod effects are dependent on light intensity being absent or altered if the light intensity is too low or too high. Therefore, light intensity may be an important variable in experiments. The time measuring mechanism involved in photoperiodic responses appears to be based on circadian rhythm of sensitivity to light. Maximum response in terms of percentage of fish attaining gonadal maturity occurred when the light pulse fell between the hours 14 and 16 of the light cycle. A decreasing photoperiod from 16 hr of light to 10 hr during 6 months experimental period was stimulatory in rainbow trout (Billard et al., 1981b). It has been reported that light intensity plays a role in gonadal maturation of the milk fish, Chanos chanos (Kumagai, 1981).

Temperature

Temperature dependence of photoperiodism has been reported in a number of finfish species. Long photoperiods stimulate gametogenesis in some species like Gambusia affinis affinis, Culaea inconstans and Notemigonus crysoleucas only in combination with warm temperature (Sawara, 1974; Reisman and Cade, 1967; de Vlaming, 1975). However, in some fishes such as Gasterosteus aculeatus and Cymatogaster aggregata, long photoperiods are stimulatory in gonadal maturation at both warm and cold temperatures (Baggerman, 1957; Wiebe, 1968). In some finfishes decreasing or short periods or an accelerated light cycle stimulate gametogenesis regardless of temperature (Macquarrie et al., 1979; Henderson, 1963; Breton and Billard, 1977). In some other fish species, low temperatures promote sexual maturation regardless of photoperiod although the effect is enhanced by short photoperiod (de Vlaming, 1972b). Temperature has also been found to be more important than photoperiod for gametogenesis and oogenesis. It may exert its effects by (1) a direct action on gametogenesis (Lofts et al., 1968), (2) action on pituitary gonadotropin secretion (Breton and Billard, 1977; Peter 1981), (3) action on metabolic clearance of hormones (Peter, 1981), (4) action on the responsiveness of the liver to estrogen in the production of vitellogenins (Yaron et al., 1980) and (5) action on the responsiveness of the gonad to hormonal stimulation (Jalabert et al., 1977; Bieniarz et al., 1978). In majority of finfishes there is a maximum and minimum limit of temperature range within which the fishes usually breed. The critical temperatures above and below which the fish will not reproduce vary from species to species (Kinne, 1964; de Vlaming, 1972a).

Salinity

A rise in salinity has led to regression in gonads in the South American gymnotoid fish, Eigenmannia virescens (Kirschbaum, 1979). In the wild fish, Gillichthys mirabillis, there is regression of gonads, when salinity rises in the estuarine habitat of the fish (de Vlaming, 1971). Regarding the effect of low salinity on gonadal maturation and reproduction in euryhaline mullets, Mugil cephalus and Mugilcapito, vitellogenesis is inhibited in freshwater (Abraham et al., 1966). But Eckstein and Eylath (1970) have reported that reproduction is not disturbed if these species are reared in freshwater from fry stage to maturity in the same environment. The grey

mullets, Mugil cephalus, Liza parsia and Liza tade have been raised from maturity stage I - III in ponds at salinity range of 25-30% (Nammalwar et al., (MS).

Other factors

It has been shown that factors like O_2, pH, food availability, stress and pollutants also have influence on gonadal [redacted] of fishes. It has been reported that increased [redacted] oxygen concentration accelerates or induces ovulation [redacted], Cyprinus carpio (Billard and Breton, 1983).

Reproduction of the pupfish, Cyprinodon neradensis is [redacted] inhibited when the pH is lowered from the normal [redacted] level of 8.3. Egg production was reduced by 50% at pH 7.0. Food availability is closely related to maturation [redacted] up of gonads of finfishes. A reduction in the [redacted] has been found to result in regression of gonads [redacted] mirabilis (de Vlaming, 1971). Decrease in food supply has inhibited gonad development in Salmo gairdneri and Salmo trutta (Scott, 1962; Bagenal, 1969). Improved feeding accelerated maturation time of gonads in a year in the flounder, Pleuronectes limanda and the herring Clupea-harengus (Woodhead, 1960). In the temperate golden perch, Plectoplites ambiguus of Australia, the yolk-laden oocytes do not become mature if there are no floods (Mackay, 1973).

Stress is recognized as a factor affecting gonadal maturation in fishes (Gerking, 1960; Billard et al., 1981). The gonads of mature wild fish often undergo rapid atresia on capture and transfer to an aquarium tank (De Montalambert et al., 1978; Scott 1979; Lam, 1982). Handling stress has also been considered to be responsible for the failure to induce maturation in milkfish, when hormone treatment was given (Lacanilao et al., 1983). Pollutants such as heavy metals, pesticides and oil have assumed increasing importance as environmental inhibitors of gonadal activity of fishes (Donaldson, 1975; Donaldson and Scherer, 1982).

INDUCED MATURATION OF FISHES BY CONTROL OF ENVIRONMENTAL FACTOR

There have been several attempts to induce gonadal maturation in captive broodstocks through hormone and environmental control. The approach of hormone manipulation has encountered with many difficulties (Lam, 1982; Lacanilao et al., 1983). The approach of environmental manipulation is promising (Shehadeh, 1970; Pullin and Kuo, 1981; Billard, 1981; Billard and Breton, 1983). Environmental factors conducive to spawning once known can be manipulated to trigger natural spawning in gravid fish. Photothermal manipulation markedly enhances the reproductive capacity of the grey mullet, Mugil cephalus (Kuo and Nash, 1975). Another approach is to delay gonadal maturation so as to stagger fry availability outside the normal season. In some species, a prolonged or continuous photoperiod or a delayed rate of change in photoperiod delays sexual maturation by several weeks or months (Scott, 1979).

In tropical regions, photoperiod does not vary much generally during the course of the year, although temperature may change in summer and winter seasons. Tropical fishes tend to have an extended breeding period or even continuous breeding throughout the year, but spawning peaks do occur, which are usually associated with seasonal rainfall and or floods. Very little is known of the environmental factors responsible for such seasonal peaks in reproductive activity. Factors associated with rainfall or floods are more likely to be related to synchronization of final maturation and spawning.

The ovarian maturation of the grey mullet, Mugil cephalus has been induced out of season by environmental manipulation, photoperiod and temperature in controlled experiments by Kuo et al., (1974b). Female grey mullet adults have been selected from estabilished broodstock held captive for more than two years. In order to ascertain the effects of environmental parameters on ovarian oocyte development, all experiments have been conducted using early in the refractory period or primary oocyte stage. The effect of photoperiod cycle on the vitellogenesis have been examined by comparison of ovarian development, for different females exposed to (1) a condensed natural day light cycle (2) a natural day light cycle before a retarded light regime of 6L/18D, (3) a natural day light cycle acting as control. Constant temperatures between 17°C and 26°C have been maintained. In nature, vitellogenesis of ovarian oocytes begins shortly before the length of day light is minimal (11 hr). The same response in ovarian development was not found from the condensed day light cycles. The results indicated that a constant photoperiod regime of 6L/18D is effective in stimulating vitellogenesis irrespective of any preconditioning photoperiod adjustment within the temperature range examined. The experi- [redacted] conditions stimulated vitellogenic oocytes to develop within 49-62 days at the photoperiod regime of 6L/18D. No vitellogenic oocytes were observed in fish in controlled condition until 235 days by which time the ovarian development seemed to reflect the normal breeding cycle. For the temperature range, the progress of vitellogenesis was shown to be [redacted] upon temperature. Only fishes held in lower temperature range (17-21°C) attained functional maturity and were then [redacted] to spawn by injection of salmonid gonadotropin treatment and larvae were raised through metamorphosis. It is therefore possible to control ovarian development by proper combination of temperature and photoperiod regimes.

Several tropical fishes exhibit a distinct seasonal reproductive cycle (Lam, 1974; Payne, 1975; Johannes, 1978; Beumer, 1979; Kuo and Nash, 1979, Kumagai, 1981). The milkfish, Chanos chanos (Kuo and Nash, 1979; Kumagai, 1981) and the rabbitfish Siganus canaliculatus (Lam, 1974; Soh, 1976) are two examples. The environmental factors controlling the reproductive cycle of the two species have not been identified although some suggestions have been made (Soh, 1976; Kumagai, 1981).

Laboratory studies demonstrated that a long photoperiod of 18L-6D retarded gonadal maturation in S. canaliculatus compared to the natural photoperiod of 12L-12D (Lam and Soh, 1975). But long photoperiods of 18L-6D or 20L-4D and water temperature 12°C accelerated maturation of gonads of the temperate fishes, the turbot, Scophthalmus maximum and sole, Solea solea which resulted in early spawning (Htun Han, 1977). A short photoperiod (4L-8D/4L-8D) at 11±1°C stimulated ovarian development in the dab, Limanda limanda and spawning took place four months earlier to the breeding season (Htun Han, 1975). Temperature has not been studied but may be of importance for gonadal maturation as the fish appear to migrate to deeper waters, where temperatures are lower, and return to the coastal waters to spawn. Laboratory studies did not show difference in gonadal development between 3 year old immature milkfish reared at temperature ranges of 28°C-32°C and at 23°-26°C for six weeks (Lacanilao et al., 1983). Further, immature milkfish (2-4 year old) reared in a large floating net cage (10 m diameter x 3 m depth) at temperature of 25-31°C matured and spawned spontaneously after about 18 months. Wild milkfish in spent stage similarly maintained failed to remature (Lacanilao and Marte, 1980). Milkfish have matured sexually in large circular concrete tanks (8.25 or 12 m diameter in Taiwan at a temperature range of 21.4-30.7°C (Liao and Chen, 1979; Tseng and Hsiao, 1979).

Another common feature is that fish are fed a high protein diet. The role of nutrition in fish gonadal development has received little attention. Nutrition may be an important environmental factor in terms of seasonal changes in abundance and quality of food. Adult milkfish, feed on one of the species of macroplankters (Lucifer sp; Acetes sp; Stolephorus s at a time (Kumagai, 1981). Salinity is not apparently important for milkfish gametogenesis at least within the ranges of 7-12‰ (Nash and Kuo, 1976; Kuo et al., 1979), 13.7-29.8‰ (Liao and Chen, 1979; Tseng and Hsiao, 1979) and 28.35‰ (Lacanilao and Marte, 1980). The gonads of red

snapper, Lutjanus capechanus were induced to attain maturation and spawning occurred spontaneously in captivity by photoperiod and temperature regime control (Arnold et al., 1978). The John's snapper, Lutjanus johni and sea bass Lates [redacted] were raised in floating net-cages (5 m x 5 m x 3 m) to sexual maturity at temperature and salinity ranges of 28-31°C and 27-31‰ respectively at Singapore (Lim et al., [redacted] Anon, 1988). In the sea bass, Lates calcarifer, natural breeding is often facilitated in captive conditions by mani-[redacted] the environment to provide the natural conditions [redacted] prevail during the spawning season and it involves tidal [redacted] and adjustment of temperature and salinity (Wongsumnok and Manevonk, 1973; Kungvankij, 1987). The grouper, Epinephelus tauvina also reared at Singapore in [redacted] net-cages (5 m x 5 m x 3 m) at a temperature range of [redacted] matured at the age of 2 years (Chen et al., 1977). In U.S.A. finfishes such as striped bass, Morone saxatilis, Channel catfish, Ictalurus punctatus, Pacific salmon, Oncorhynchus kisutch, rainbow trout, Salmo gairdneri and brook trout, Salvelinusfontinalis were raised to gonadal maturity in net-cages. In Japan, red seabream, Pagrus major black seabream, Acanthopagrus schlegeli, striped knife-jaw, Oplegnathus fasciatus, flounder, Paralichthys olivaceus, yellowtail, Seriola quinqueradiata, grouper, Epinephelus akaara and seabass, Lateolabrax japonicus are reared in floating net-cages for gonadal maturity (Shepherd and Bromage, 1988).

Sexual difference in gonadal response to environmental factors is not evident in many species. In some species, like Cymatogaster aggregata males respond mainly to photoperiod and females predominantly to temperature (Wieb, 1968). In the stickleback, spermatogenesis appears to be independent of environmental factors (Craig-Bennett, 1931; Baggerman, 1980) but, functional sexuality of males and vitellogenesis in females depends on photoperiod and temperature (Baggerman, 1980).

The maturation of gonads of females of the Gulf Croaker, *Bairdella icistia* has been found to be influenced by photoperiod and temperature and the gonads of males attained maturity independent of the factors (Haydock, 1971).

The application of induced maturation techniques in fish falls into two basic categories. The first involves the induction of maturation and spawning in fish which would not otherwise reproduce in captivity : the second involves the manipulation of spawning time in fish which do normally breed in captivity (Donaldson and Hunter, 1983). A number of finfish species that are currently of great economic significance or of potential for marine and bractishwater aquaculture do not reproduce spontaneously in captivity. It is possible to control the environment of the broodstock enclosure to permit completion of gonadal development and normal spawning.

GENERAL CONSIDERATIONS

The environmental factors play a defenite and varying role in the gonadal maturation of fishes. The influence of the various factors in marine and brackishwater finfishes, especially in tropical fishes has received very little attention. In India, there is great interest to develop aquaculture on scientific lines. In this context, there is need for investigations on the control of environmental factors on maturation of gonads of cultivable finfishes like milkfish, *Chanos chanos*, grey mullets, *Mugil cephalus*, *Liza macrolepis*, *Liza parsia* and *Liza tade*, sea bass, *Lates calcarifer*, grouper *Epinephelus tauvina* and red snapper, *Lutjanus johni*, rabbit fishes, *Siganus oramin* and *Siganus canaliculatus*, pearl spot, *Etroplussuratensis* and sandwhiting, *Sillago sihama* which are of commercial importance. There is need to carry out investigations on the exact relationship between factors like photoperiod, temperature, salinity, pH, oxygen and food availability and gonadal maturation.

Environmental factors function as selective forces in [redacted]olution of reproductive strategies. They influence both quantitative and qualitative components of reproduction by [redacted]fying the partitioning of time and resources between [redacted]oductive and non-reproductive activities (Wootten, 1982). The confident prediction of the effects of such factors requires a thorough study in the case of individual species of fishes. In fish reproduction, it is important to study the quantitative relationships between environmental factors and the reproductive activity of the fish. The gonadal maturation and reproductive success in relation to environmental factors can be predicted from such studies.

Studies carried out so far indicate that the effect of individual environmental factors like photoperiod, temperature on fishes varies considerably. For instance, long photoperiod is favourable for initiation of gametogenesis and maturation of gonads in some fishes like salmonids, turbot and sole. On the other hand, short photoperiod induced maturation in the dab. Low temperature stimulates gonadal maturation in *Gillichythys mirabilis* and rainbow trout, while the rise in temperature leads to reproductive activity in killifish and minnow. A combination of long or short photoperiod with either high or low water temperature stimulates gametogenetic activity in different species of fishes. A prolonged photoperiod of 18L-6D also retards gonadal maturation in the rabbitfish *Siganus canaliculatus* (Lam and Soh, 1975).

Environmental factors may limit the reproductive output not because of any direct effect on the reproductive system but because of their effect on other processes like rate of feeding. Temperature has a strong effect on the rate of feeding in fishes (Elliott, 1981). In the stickle-back *Gasterosteus aculeatus*, the scope for growth increases with temperature and hence the scope for the transfer of materials to the gonads for maturation (Allen and Wootton, 1982).

Environmental factors influencing gonadal maturation and regression could be controlled successfully to accelerate or delay gametogenesis in the broodstock, so that spawning could take place and fry produced whenever needed. Environmental factors responsible for spawning may be manipulated to induce or inhibit spawning. Environmental factors which result in gonadal regression may be manipulated to inhibit gametogenetic activity in growing fish so that somatic growth is accelerated instead of gonadal development. Environmental factors involved in gonadal maturation and spawning could also be manipulated to advance spawning and reduce the duration of reproductive cycle.

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