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Reproductive Physiology in Cichlid Fishes, with Particular Reference to *Tilapia* and *Sarotherodon*

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Works dealing with the external and internal factors which regulate reproductive efficiency in *Tilapia* and *Sarotherodon* are reviewed. Gametogenesis, although presenting the same general features as in most other teleosts is characterized by a low production of gametes related to the high efficiency of parental care: in substrate-spawners (*Tilapia*) the number of small sticky eggs is approximately related to the cube of body length, whereas in mouth-brooders (*Sarotherodon*), eggs are bigger, not sticky, and their number is related to the square of body length.

Both groups seem to exhibit a capacity for precocious sexual maturation, the reason for which is not clear. There is also unlimited successive breeding through whole populations in equatorial areas and an increased tendency for seasonal breeding with increasing latitude, with maximum activity during maximum temperature and light intensity. When temperatures exhibit seasonal variations of large magnitude, low temperature (15 to 22°C) inhibits reproduction during part of the year. Social factors have been shown to enhance spawning frequency and might also influence sexual precocity through mechanisms which need further work.

Despite some attempts, specific tilapia gonadotropins have not yet been satisfactorily purified; the ubiquity of specific prolactins in controlling both osmoregulation and parental care behavior must be confirmed, and their possible inhibitory action on gametogenesis need investigation. The precise nature of steroids which mediate the pituitary action during different phases of the reproductive cycle also needs more research.

Introduction

The efficiency of reproduction in *Tilapia* and *Sarotherodon* has paradoxical consequences: on one hand, this aptitude which allows easy and rapid propagation in various tropical and subtropical environments, partially explains the economic interest in these species for fish culture; on the other hand this reproductive efficiency can be a source of problems because

uncontrolled multiplication within a limited environment in situations of food competition is liable to produce dwarf fish populations, of little value.

The behavioral patterns which occur after spawning and which characterize substrate-spawners (*Tilapia*) and mouthbrooders (*Sarotherodon*) have been described and discussed by numerous authors (Lowe-McConnell 1959; Perrone and Zaret 1979). Whatever the role of each sex in brood care, which differs among species, this care provides an efficient protection for eggs and fry against predators, and contributes greatly to the reproductive efficiency of these species. However, the physiological mechanisms which control parental care behaviour are poorly understood.

Another aspect of the reproductive efficiency of tilapias is precocious sexual maturation which can occur as early as 3 months in some species (McBay 1961; Arrignon 1969) and depends probably, in addition to genetic factors, on environmental factors like temperature (Hyder 1970a; Siddiqui 1979a), food availability, social factors, etc. Precise data based on experimentation are generally lacking.

As soon as sexual maturity is attained, and provided temperature is suitable, most cichlid females are able to undergo successive breeding cycles, producing new broods at 4 to 6 week intervals. This usually results in a continuous production of fry throughout a population, with the exception of certain environments subject to substantial seasonal variations (Moreau 1979). But the relative asynchrony between the sexual cycles of individual females can be a problem when mass production of homogenous fry is required for intensive fish farming.

Thus, for practical reasons dictated by fish farming conditions, it would often be advantageous either to inhibit or delay sexual maturation, or in some cases to favor synchronous spawning and breeding for mass production of fry.

This paper reviews the external and internal factors which seem to be involved in the control of different stages of the reproductive cycles of cichlids, to suggest practical means for artificial control. As literature in the field of cichlid reproductive physiology is scattered, references will be made, when necessary, to the present state of knowledge in other teleosts. For more detailed information concerning reproductive physiology and endocrinology in fish, see recent reviews by Dodd (1975), Fontaine (1976), Jalabert (1976), Olivereau (1977), Callard et al. (1978), Peter (1978), Billard et al. (1978) and Breton et al. (1980).

General Characteristics of Gametogenesis

Sexual differentiation of the gonad into a juvenile testis or ovary with a characteristic morphology occurs very early in *Tilapia* (Yoshikawa and Oguri 1978) and in *Sarotherodon* (Nakamura and Takahashi 1973), around 15 to 30 days after fertilization (at 23 to 25°C). Sexual maturity can be then completed after a few months.

Gametogenesis in cichlids appears to present the same general features as in most other teleosts and lower vertebrates, whether in males or in females (Barr 1968; Hoar 1969). Thus some stages in the following de-

scription are taken from noncichlids. All the available information suggests that this is valid (Dadzie 1969; Hyder 1970a, 1970b; Polder 1971; Von Kraft and Peters 1963; Hodgkiss and Man 1978; Babiker and Ibrahim 1979; Moreau 1979b).

In males, the testis possesses a stock of undifferentiated gonial cells (type A) which originates from the primordial germ cells of the embryo through mitotic divisions. Active spermatogenesis begins with the isolation of type A spermatogonia, each one surrounded by a few somatic cells, followed by successive synchronous mitotic divisions of spermatogonia (type B), while surrounding somatic cells divide to form a continuous layer of cells, called "Sertoli cells". This process results in numerous cysts of cells throughout the testis. After an unknown number of spermatogonial mitotic divisions, meiosis occurs synchronously for each cyst, each spermatogonium then producing four spermatids which will differentiate into spermatozoa (spermiogenesis). Cyst evolution occurs along testicular lobules which are separated from each other by fibroblast cells and interstitial tissue. The latter is particularly well developed in cichlids in comparison with some other teleosts. Spermiation occurs when spermatozoa are released from cysts after separation of the Sertoli cells, first into the lobules and then into the vas deferens.

In female teleosts, the ovaries contain a stock of undifferentiated oogonia which seems to be renewed by mitotic divisions throughout life unlike higher vertebrates. For example, unilateral ovariectomy stimulates oogonial mitosis in the remnant ovary of *Sarotherodon aureus* (Dadzie and Hyder 1976). Some oogonia begin a meiotic division but remain at arrested prophase (primary oocytes). Each primary oocyte increases in size and is progressively surrounded by layers of somatic cells: inner granulosa cells which form a monolayer directly in contact with the thickening outer oocyte envelope (the zona radiata, i.e., the future chorion) and an outer theca, made of several layers of fibroblasts penetrated by capillaries. The theca forms the external cellular envelope of the ovarian follicle. The morphology of ovarian follicles in *Tilapia* and *Sarotherodon* has been well described by Von Kraft and Peters (1963).

Oocyte growth can be divided into two main phases: first, the previtellogenic phase when size increases (up to 0.6 to 0.9 mm diameter in *S. niloticus*) which is considered to be the result of synthesis occurring mainly within the oocytes (endogenous vitellogenesis) and second, the vitellogenic phase which results from the rapid accumulation, after minor biochemical modifications, of "vitellogenin": a lipophosphoprotein which is synthesized in the liver, released into the blood and incorporated into the oocytes by micropinocytosis (exogenous vitellogenesis or yolk deposition). At the end of vitellogenesis, meiosis resumes: a general process called oocyte maturation, characterized by completion of the first meiotic division, with first polar body emission, which is accompanied by important changes in the gross morphology of yolk and cytoplasm just before ovulation (expulsion of mature secondary oocyte from the follicle). Oocyte maturation ends only after sperm penetration with the second meiotic division and second polar body emission.

In contrast to the spherical shape of the mature egg in most teleosts, *Tilapia* and *Sarotherodon* eggs are ovoid. In substrate-spawners (*Tilapia*), ovulation is accompanied by the production of sticky material (probably mucopolysaccharides), which seems to be secreted by the granulosa, from light microscope evidence (Von Kraft and Peters 1953) and electron microscope observations (Nicholls and Maple 1972). This sticky substance is deposited around special threads emerging from the zona radiata of oocytes (Von Kraft and Peters 1963), and glues all the eggs into one mass which sticks to the substrate. In mouthbrooders (*Sarotherodon*) eggs are usually not embedded in these sticky threads, with the exception of *S. galilaeus* which leaves the eggs some minutes on the substrate before commencing mouthbrooding (Fishelson 1966b).

As discussed by Perrone and Zaret (1979), egg size and fecundity in fish are strongly related to parental care patterns. In *Tilapia* and *Sarotherodon*, whose behavior provides a high level of parental care, production of gametes is rather low. In males, testis weight is very low compared to that of other teleosts without parental care (Peters 1971), whereas in females the number of eggs per spawning is of the order of hundreds in *Sarotherodon*, and a few thousand in *Tilapia* (Peters 1963): very different from the millions of pelagic eggs produced by some species without parental care. In tilapias, as in other teleosts, fecundity, egg size and egg weight usually increase with female size: egg production increases approximatively in relation to the square of body length in *Sarotherodon* and in relation to the cube of the length in *Tilapia zillii* as discussed by Welcomme (1967b).

The temporal patterns and rhythmicity of gametogenesis have been much studied in *Tilapia* and *Sarotherodon*. Individual females spawn successively, either during a defined breeding season or year-round, with a few weeks interval between spawnings (Moreau 1979): this requires either rapid or continuous gametogenesis. In both sexes successive waves of gametogenesis have been demonstrated (Von Kraft and Peters 1963; Peters 1963; Dadzie 1969; Moreau 1971, 1979; Hyder 1970a; Bruton and Bolt 1975; Siddiqui 1977b, 1979a; Babiker and Ibrahim 1979).

In females some doubt remains as to the stage from which a new wave of oocytes develops to prepare for the next spawning. Some authors (Von Kraft and Peters 1963; Peters 1963; Hyder 1970a) have reported that the next wave of oocytes is already in the process of active vitellogenesis in spent fish just after spawning, but some other evidence suggests that each new batch arises from a stock of previtellogenic oocytes (Silverman 1978a, 1978b; Moreau 1979). This dubious point may be due to imprecisions in the exact definition of active vitellogenesis (or exogenous vitellogenesis, i.e., under pituitary control), to differences in species, and to environmental differences. For example, Moreau (1979) showed that the mean interval which separates the last two successive waves of oocytes in *Tilapia rendalli* is different in two different lakes. This point, however, would need more precise observation and experimentation to understand the underlying endocrinological mechanisms (see below), particularly in species where the female exhibits brood care behavior after spawning, during which ovarian growth might be inhibited.

In males, spermatogenesis is reported to occur continuously, the testis containing cysts at all different stages, in both *Sarotherodon* (Dadzie 1969; Hyder 1970a, 1970b; Moreau 1979) and *Tilapia* (Moreau 1979), but quantification reveals that substantial variations can occur in the intensity of spermatogenesis in marginal temperature conditions (Moreau 1979). Methods of quantification (Billard et al. 1974) should be used more extensively to assess spermatogenetic continuity. As in the case of females, this would allow investigation of the occurrence of any post-spawning inhibition in species where the male exhibits brood care behavior.

The Role of Environmental Factors in the Regulation of Reproductive Activity

In most teleosts, spawning periods appear to be adjusted to (and by) environmental factors (photoperiod, temperature, salinity, rainfall, etc.) so that they are suitable for rearing offspring (de Vlaming 1974). Fish of temperate zones, where photoperiod and temperature variations are of great magnitude, spawn during a limited period of the year, and only once in most cases. In equatorial and tropical regions, where these variations are more limited, temperature is rarely a limiting factor, but considerable environmental changes can occur which might inhibit or favor offspring survival, favoring related adaptations (for example rainfall and cloud cover during the rainy season).

Tilapia and *Sarotherodon* species are abundant in both equatorial regions and subtropical regions as well as the mediterranean and have even been introduced into environments which can be considered as marginal, for at least a part of the year, especially with respect to low temperature tolerance. This is the case in lakes at high altitude in Madagascar (Moreau 1971, 1979). Here the low temperatures encountered are very different from those in the original habitats of tilapias and the response in breeding patterns may be considered as the limit of a tendency. *Sarotherodon* and *Tilapia* extend their breeding seasons for as long as temperature is favorable. During the cold season spermatogenesis is greatly retarded but all its developmental stages remain present in the testis. In females, on the contrary, exogenous vitellogenesis seems to be completely inhibited by low temperatures and all yolk-laden oocytes disappear.

In more appropriate environmental conditions, such as equatorial lakes and ponds, *S. niloticus* was found to breed throughout the year, though the number of breeding fish was slightly higher during the wet season (Lowe (McConnell) 1958). In areas distant from the equator, the same species exhibits a well defined breeding season, spawning mainly during the warmest and most sunny season (Lowe (McConnell) 1958). Among *Tilapia*, *T. zillii* in equatorial lakes shows no reproductive seasonality and individual fish spawn successively year-round (Siddiqui 1979a). On the other hand, the same species in northern areas presents a definite seasonal breeding, spawning during the period of maximum water temperature and maximum light (Ben Tuvia 1959; Fishelson 1966a, 1966b; Siddiqui 1977b).

However, the assumption that no reproductive seasonality occurs in equatorial areas might even be questioned in regard to the precision and the validity of the method of appreciation, if we consider the contradictions between Hyder (1969, 1970a) and Siddiqui (1977b) concerning *S. leucostictus* in the same equatorial lake: the first studies show a seasonal variation in breeding activity, while the latter denies this finding and concludes that breeding is non-seasonal.

It seems therefore that *Tilapia* and *Sarotherodon* have a capacity for unlimited successive breeding (at least when the whole population is considered) in equatorial regions and an increased tendency for seasonality with increasing latitude, with maximum reproductive activity during periods of maximum temperature and day light. The effects of seasonal rainfall cannot, however, be excluded (Aronson 1957; Lowe (McConnell) 1958; Lowe-McConnell 1959; Hyder 1969, 1970a; Marshall 1979a, 1979b; Moreau 1979) but these remain controversial, probably because of differences between species.

It remains difficult to assess which are the key factors to stimulate, inhibit, or exert any regulation on the various stages of the breeding cycles of *Tilapia* and *Sarotherodon*. This uncertainty is due in part to the absence of any experimental study to dissociate the role of separate environmental factors, and also part to the imprecise methods which have been used to determine the different parameters relative to the intensity of reproductive activity.

The Role of Social Factors in the Regulation of Reproductive Activity

Social interactions are known to influence some parameters of reproduction, particularly the timing of first sexual maturation, spawning frequency and fecundity. In cichlids, spawning frequency is increased by different sensory stimulations coming from conspecific fishes, e.g., visual stimuli, sound production, lateral line contacts and probably chemical communication (Aronson 1945, 1951; Polder 1971; Marshall 1972; Chien 1973).

In some *Sarotherodon* species the female is able to spawn regularly even when isolated, but shows increased interspawning intervals compared to non-isolated females (Aronson 1945; Marshall 1972; Silverman 1978a, 1979b). In *S. mossambicus* Silverman (1978a, 1978b) was able to dissociate the effects of different levels of social contact on separate parameters of the interspawning interval. He distinguished between unlimited contact (several fish in the same aquarium), medium contact (adjacent aquaria each containing one fish so that each fish can see into the other tank) and low contact (visually isolated fish in different aquaria) and showed that visual stimuli hastened mainly ovulation with little influence on oogenesis but that other non-visual stimuli (e.g., tactile or chemical) in unlimited-contact females were able, in addition, to advance yolk deposition by about 7 days. Males and females were shown to be equally effective as stimulus animals. This may reflect some "general conspecific effect" related to gregariousness of *S. mossambicus*, a species where "presence" within a social group is important, according to Silverman. He suggested that regular spawning in isolation

would most likely occur in species where males with ripe gonads are continuously available waiting for new females to encounter their nests. Although very interesting, these experiments concerning *S. mossambicus* should be performed on other species, and efforts should be made to look for the existence of pheromone-like substances which have been shown in other fish (Solomon 1977).

The Role of Internal Factors in the Regulation of Reproductive Activity

Numerous organs, endocrine glands, and hormones are involved, directly or indirectly, in the regulation of reproduction in fish as in other vertebrates (Fontaine 1976; Olivereau 1977). This complex control system is directed by the nervous system which integrates external stimuli together with ontogenetic and physiological constraints, and exerts its control mainly through the hypothalamo-pituitary-gonad axis. The following section will deal essentially with the functional modalities of this axis. Points which are still very controversial in other teleosts, and which have not even been studied in cichlids to our knowledge will be omitted: for example, the role of the pineal organ.

THE ROLE OF THE PITUITARY

Many works reviewed by Pickford and Atz (1957) have demonstrated how important the role of the pituitary is in the control of reproduction in fish. This role was confirmed in cichlids (*Sarotherodon spilurus*) by means of chemical hypophysectomy using methallibure and replacement therapy (Hyder 1972; Hyder et al. 1974; Hyder et al. 1979). Methallibure, which was shown to inhibit gonadotropin secretion by the pituitary in fish (Breton et al. 1973) as it is known to do in mammals, induces an effective gonadal regression in both male and female *S. spilurus* after 4 to 5 weeks of treatment with daily doses of 1 mg/l of aquarium water (Hyder 1972). This treatment results in an extensive resorption of yolk-laden oocytes and a complete inhibition of vitellogenesis in females and in the complete inhibition of two steps of spermatogenesis in males: the step between spermatogonia and spermatocytes (meiosis) and final spermiation. A similar effect was confirmed by Lanzing (1978).

The present state of knowledge of teleost fish reproduction tends to support the hypothesis that two different pituitary gonadotropins are involved in the control of gametogenesis. One purified at first from carp, *Cyprinus carpio* (Burzawa-Gerard 1971), trout, *Salmo gairdneri* (Breton et al. 1976) and in salmon of the genus *Oncorhynchus* (Donaldson et al. 1972) is characterized by its control over final intrafollicular oocyte maturation (Jalabert et al. 1974) and its effect upon spermatogenesis (Billard et al. 1970). A second kind of gonadotropin which seems necessary for vitellogenesis was recently purified from carp and salmon pituitaries (Idler and Bun Ng 1979).

In cichlids, some attempts have been made to purify and characterize pituitary gonadotropins. Farmer and Papkoff (1977) obtained two preparations from *S. mossambicus* which exhibited some biochemical characteristics similar to luteinizing hormone (LH) and follicular stimulating hormone (FSH) from higher vertebrates. The first preparation stimulated testosterone production in isolated rat testis Leydig cells, an assay which is considered highly sensitive and specific for mammalian LH. Neither of the two preparations was assayed for its activity on *Sarotherodon* gonads. More recently, Hyder et al. (1979) observed enhanced gonadotropic activity (as judged by testis stimulation in methallibure-treated *S. spilurus*) after chromatographic separation of a glycoprotein fraction from *S. niloticus*. The fraction was the same as that known to contain FSH when the same biochemical procedure is applied to pituitary preparations from higher vertebrates. Results are thus still confusing, and more work remains to be done in order to find specific bioassays for the gonadotropins of cichlids.

Another pituitary hormone, characterized as a "prolactin-like" hormone, is believed to play an interesting role in the reproductive physiology of cichlids, in relation to the regulation of breeding activity and parental care. Blüm and Fiedler (1964) found that injection of ovine prolactin induced behavioral and histiotropic effects in *Symphysodon aequifasciata axelrodi*. The behavioral reactions were of fanning movements with the pectoral fins orientated to a distinct reference point (normally associated with parental care towards the brood) and suppression of feeding and fighting tendencies. The histiotropic effect was an increase in mucous cell production on the body surface which normally serves to nourish the young in that species (Hildemann 1959), thus exhibiting a curious analogy with the secretion of crop-milk in pigeons and milk production in mammals.

In other cichlids, e.g., *Pterophyllum scalare*, *Aequidens latifrons*, *Cichlasoma severum* and *Astronotus ocellatus* (Blüm and Fiedler 1965) ovine prolactin induces similar effects, including increase in mucous cell production although to a lesser extent than in *Symphysodon* and here this is not related to nursing of the young in that species. It is possible that mucus secretion can be related to the osmoregulatory properties of prolactin in fish (Blüm 1973; Bern 1975). Isolation and purification of *Sarotherodon* prolactin was successively reported by Blüm (1973) using behavioral and histiotropic effects in *Symphysodon* and by Farmer et al. (1977) using specific assays for osmoregulation. Considering the pleiotropic action of prolactin, isolating the same molecule through different kinds of bioassays is not surprising, but a comparison of different preparations using the same tests would be of interest in assessing the reality of this pleiotropic role for the same hormone. Among the alleged multiple actions of prolactin in fish, one could be of interest for *Tilapia* and *Sarotherodon* culture if its mechanism could be elucidated: the inhibition of gonad development (Blüm 1976). In natural conditions, gonadal development after spawning might be inhibited during parental care, which is precisely the period when prolactin is supposed to be acting. In addition, some antagonism between prolactin and gonadotropins was found to occur regarding spawning behavior (Blüm and Fiedler 1965).

THE ROLE OF THE GONADS

In addition to the central role of gametogenesis the gonads possess complex endocrine properties which, under pituitary control, contribute to the regulation of reproductive cycles by direct action on gamete differentiation, by controlling the activity of different organs and tissues involved in reproduction (such as the liver, fat and bone mineral stores) and also by controlling the development of secondary sexual characteristics. Finally the endocrine secretions of the gonads participate in the regulation of pituitary activity (a feed-back mechanism) and also act on the central nervous system, allowing different kinds of behavioral patterns to occur during the successive periods of the sexual cycles.

Sexual steroids are the main hormones produced by the gonads, but other compounds, the occurrence of which have not been investigated in cichlids, must certainly be secreted (Breton et al. 1980). Steroids are generally considered to be produced by specialized cells presenting histochemical and morphological features common to all vertebrates (Hoar and Nagahama 1978).

In males these cells form a typical interstitial tissue which has been characterized as steroidogenic by demonstration of 3β -hydroxy-steroidogenase (Yaron 1966) and from ultrastructural evidence (Nicholls and Graham 1972). They exhibit increased activity (number, size, lipid concentration) during spermatogenetic progression, with maximum activity during spermiation, when there is also rapid development of sexual coloration, nest building activity and territoriality (Hyder 1970b), and when the testis contains high levels of testosterone (Hyder and Kirschner 1969). The fact that interstitial tissue activity is under pituitary control can be demonstrated by several methods. Treatment with human chorionic gonadotropin (HCG), which exhibits gonadotropic activity in some fishes, induces both stimulation of interstitial tissue and an increase in the testosterone content of the testes (Hyder et al. 1970). Conversely, methallibure inhibition of pituitary gonadotropin secretion lowers interstitial cell activity, an effect which can be overcome by administration of HCG or *Sarotherodon* pituitary extracts (Hyder 1972; Hyder et al. 1974). But testosterone is probably neither the only nor the main steroid mediator produced in the gonad, as testosterone propionate administered to methallibure-treated *Sarotherodon* failed to restore spermatogenesis, producing only some spermiation at high doses (Hyder et al. 1974). As a range of androgenic steroids has already been found in fish, like 11-ketotestosterone in female *S. aureus* (Eckstein 1970), further studies would be of great interest in attempting to identify the major active steroids in *Tilapia* and *Sarotherodon*, and to understand their action on the different steps of spermatogenesis, sexual behavior and secondary sexual characteristics: for example, the genital tassel of male *S. macrochir* which seems to be an important signal in the spawning behavior of that species (Wickler 1965, 1966b).

In female cichlids both histochemistry (Livni 1971; Yaron 1971) and ultrastructural morphology (Nicholls and Maple 1972) show that most ovarian steroidogenesis is probably located in two kinds of follicular cells: the granulosa cells (although the ultrastructural evidence is here somewhat equivocal) and special theca cells, located mainly close to capillaries.

Estradiol-17- β (E2) seems to be of general occurrence in fish. It is mainly involved in the control of vitellogenin synthesis in the liver and of mobilization of mineral and fat stores (Olivereau and Olivereau 1979; Mugiya 1978). This seems to be true also in *S. aureus* where estradiol-17 β was identified in the ovary by Katz et al. (1971). Later a positive correlation was found between plasma E2 concentration and ovarian weight, i.e., the stage of vitellogenesis (Yaron et al. 1977; Terkatin-Shimony and Yaron 1978). In the same species, some ovarian steroidogenic pathways were investigated by Eckstein (1970) and Eckstein and Katz (1971), leading to the identification of new steroid metabolites like 11-ketotestosterone and 11-hydroxytestosterone among others which are more classical (testosterone and progesterone). Their exact function, although related to sexual activity (Katz and Eckstein 1974) is unknown. Deoxycorticosterone, a corticosteroid which can be synthesized either in the interrenal tissue or in the teleost ovary (Colombo et al. 1973) was found to increase 38-fold in the blood of *S. aureus* between a sexual resting phase at 18 to 20°C and sexual activity at 30°C. As this steroid is assumed to be one of those mediating gonadotropin action on final maturation and ovulation in catfish, *Heteropneustes fossilis* (Sundararaj and Goswami 1977), it is tempting to propose a similar model for final maturation control in *Sarotherodon*. However, the state of "sexual activity" (stage of ovarian development) at which the blood of female *Sarotherodon* was collected by Katz and Eckstein (1974) was not known precisely and further work is needed to find out which steroids mediate pituitary gonadotropin control over final oocyte maturation and their mechanism: for reviews on this problem in other teleosts, see Jalabert (1976) and Sundararaj and Goswami (1977).

Prolactin also has some control over ovarian steroidogenesis as can be inferred from the observation of Blüm and Weber (1968) that ovine prolactin greatly stimulates the activity of 3 β -steroid dehydrogenase in ovaries of the cichlid *Aequidens pulcher*. This observation suggests that inhibition of ovarian growth by prolactin is mediated through steroid action. An understanding of the precise mechanism for this action would be of great interest.

REGULATION OF PITUITARY ACTIVITY

As in higher vertebrates, gonadotropin secretion by the pituitary appears to be regulated by the nervous system through the hypothalamus which secretes a releasing factor first indicated in fish (*Cyprinus carpio*) by Breton et al. (1971) and Breton and Weil (1973). This factor is probably not very different from mammalian luteinizing hormone-releasing hormone (LH-RH) (Breton et al. 1972, 1975a) at least as far as the biologically active part of the molecule is concerned. Recent studies show that LH-RH's from lower vertebrates, including *S. mossambicus*, differ from those of higher verte-

brates both in immunological and biochemical characteristics (King and Millar 1979). Other experimental data in fish support the hypothesis that factors inhibiting pituitary gonadotropin secretion could be present in the fish hypothalamus (Peter 1978).

Ovarian endocrine secretions, particularly some steroids, seem to be able to exert positive or negative feed-back action upon the activity of the hypothalamo-pituitary complex in fish (Billard and Peter 1977; Breton et al. 1975b; Billard 1978; Jalabert et al. 1980) as they do in mammals.

A better understanding of all these controls over pituitary activity could provide practical means to manipulate some aspects of reproduction in cultured fish.

Conclusion

Some *Tilapia* and *Sarotherodon* species are well-suited for experimental work in reproductive physiology. They perform gametogenesis and regular spawning in aquaria, where external factors (light, photoperiod, temperature) can be easily controlled and they are of a convenient size for endocrinological studies involving blood sampling on living cannulated fish at different stages of the sexual cycle. Experimental data are rather scarce, however, making it very difficult to propose any techniques immediately applicable in tilapia culture. Thus, experimental research is still greatly needed to determine the respective roles of internal and external factors on first sexual maturation in the different steps of gametogenesis and on spawning frequency. Concerning the role of hormones, important results may come from work on other groups of fish and other vertebrates, concerning, for example, the hypothalamic regulation of gonadotropin secretion and non-specific means to control this activity. The development of specific methods to manipulate reproduction in tilapias requires better knowledge of their specific protein and steroid hormones involved in the control of sexual differentiation, gametogenesis and sexual and brooding behavior.

Discussion

NASH: I agree with you on the importance of egg quality. For example, salmon hatcheries tend to discard the first and last eggs available in a spawning season as they are invariably of poorer quality than those taken in the middle. Do you recommend for describing oogenesis in tilapias your six-part scale or Yamazaki's five-part scale? In your six-part scale, stages 3, 4 and 5 appear to be stages IIIa, IIIb and IIIc of the five-part scale. I assume that your stage 6 is atresia?

JALABERT: The important point is that we find oocytes at all stages in just about every fish in the population.

HEPHER: In temperate regions, it is found that vitellogenesis in fish is affected very much by day length. You haven't mentioned this at all. Is this because tilapias are from the tropical regions where there is little change in day length?

JALABERT: Some people say that there is a daylength effect even in equatorial regions, others say there is none. In tilapias, there is no clear evidence for such an effect and it

would need very precise criteria to assess small variations in the intensity of gametogenesis to investigate this. I remember for instance the contradictions between Hyder (1970a) and Siddiqui (1977b) concerning the seasonality of *S. leucostictus*. Such contradictions probably indicate the lack of precise criteria.

HEPHER: The works I know show that, for fish in general, day length affects vitellogenesis more than the other stages of oogenesis, but since you didn't mention this effect at all, may I assume that it does not exist in tilapias?

JALABERT: I don't know. We have to make controlled environment experiments to investigate this. The same is true for the effects of salinity on reproduction and growth. The evidence seems to be that in tilapias, responses to environmental changes are very variable indeed and may differ even within the same species. We conducted some recent experiments with trout to try to select for early and late reproduction to spread availability of eggs. We observed a shift in the timing of reproduction after only one generation. For tilapias, therefore, we can expect different responses for different species and strains.

NASH: We cannot generalize about reactions to environmental stimuli with subtropical and tropical fish. In mullet it is the light stimulus that triggers oogenesis and then the temperature takes control. And, although you cannot suppress development completely, you can delay it by temperature control even after triggering by light. There are groups of fish for which the opposite is the case. The temperature acts as the trigger and the light control acts as the monitor.

MORIARTY: I would like to ask a question from the point of view of the fish culturist. Is it going to be of any practical benefit to have a much more detailed knowledge of the reproductive hormones of these fish, or do you think that this is so complex that we would be better advised to study environmental and social factors?

JALABERT: Although the practical applications are not evident now, we do need more work on the reproductive hormones of fish and on their modes of action, in order to understand how environmental and social factors interact to modulate sexual activity. I believe that management decisions could be more efficient if based on such basic knowledge. But, from a strategical point of view, I feel that some fundamental questions are closer to application than some others; for example, are pheromones important in tilapia reproduction?

GUERRERO: In one experiment you described the separation of the two sexes of tilapia. You say that there was no pheromone action because the fish still spawned.

JALABERT: In this experiment the isolated females spawned anyway, or, more exactly, released their eggs, but the interval between successive spawnings was increased. When fish were together, this interval was reduced. We cannot rule out pheromones here, among the other factors. On the other hand, spawning in artificial environments can be affected by many stress factors which are not necessarily specific.

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