# Seasonal steroid hormone profiles in plasma and gonads of the tilapia, *Oreochromis mossambicus*

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## Abstract

Syferkuil Dam is situated 8 km NW of the University of the North and comprises a series of eight interconnected rectangular dams, having cement sides and mud bottoms. Throughout the experimental period, male and female adult specimens of the mouthbrooding tilapia, *Oreochromis mossambicus* were collected for further analysis. Aspects of the reproductive physiology of *O. mossambicus* that were investigated included reproductive hormone profiles in plasma and gonadal supernatant. This study has shown that three distinct stages - breeding season, resting season and a gonadal recrudescent season may be distinguished in both male and female *O. mossambicus*. During the female resting season there are generally low levels of steroid hormones. However, during ovarian recrudescence, there is an increase in trophic and steroid hormones. This relates to a period of endogenous vitellogenesis that occurs during winter. After winter, the photoperiod begins to lengthen leading the breeding cycle into a state of exogenous vitellogenesis, wherein a second steroid (predominantly estradiol) surge is observed. In males, testosterone peaks prior to the gonadotropins because the former hormone is more important for sperm development. The results imply a close interaction between environmental cues and endocrine control of reproduction. The endocrine control cannot continue without the appropriate environmental cues required to stimulate reproduction. This may be used as a starting point for breeding in controlled laboratory conditions when attempting to manipulate artificial breeding by hormonal intervention.

## Introduction

The association of changes in gonad condition with plasma levels of gonadal steroids has proven to be a valuable tool in the development of an understanding of endocrine control of reproduction in teleosts. Correlations between seasonal changes in plasma levels of gonadal steroids and gonad condition have been well documented in a number of freshwater fish species (Crim and Idler, 1978; Lambert et al., 1978; Fostier and Jalabert, 1982; Scott et al., 1980a,b; Lamba et al., 1983; Van der Merwe et al., 1987).

Histochemical research has shown that steroid hormones, which are important for reproduction, are formed in the adrenal glands and gonads of many freshwater fish species. Steroid production in the ovary has been observed in the granulosa and/or theca cells of developing and mature oocytes. Post ovulatory and interstitial cells are also sources of sex steroids in the ovary. The occurrence of steroid production in different cells of the ovary may be related to different phases of oocyte development. Adrenal steroids are secreted prior to gonad steroids to promote vitellogenin production for oocyte development. This was confirmed by many investigators who studied seasonal changes in the plasma levels of steroid hormones (Crim et al., 1973; Crim et al., 1975; Fostier et al., 1983; Kagawa et al., 1983; Kobayashi et al., 1986; Santos et al., 1986; Rosenblum et al., 1987; Pankhurst and Conroy, 1987).

Although it has been ascertained in cyprinids that final oocyte maturation and ovulation are induced by a preovulatory gonadotropin surge, little information on the plasma and gonadal changes in steroid hormone levels during the reproductive cycle in *O. mossambicus* is known.

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During vitellogenesis an increase in plasma estrogen levels, mainly estradiol 17-β that correlates with the growth of vitellogenic oocytes has been observed in many species. In the tilapia *Sarotherodon* (now *Oreochromis*) *aureus*, the initiation of spawning by increasing water temperature is followed by a rise in testosterone levels (Katz and Eckstein, 1974).

Rothbard et al. (1987) have examined the changes in steroid concentrations that occur during sexual ontogenesis in tilapia. Their results indicate that although both testosterone and estradiol levels increase during sexual ontogenesis, it appears to be the former that is responsible for the process of sex differentiation. Smith and Haley (1988), working on female *O. mossambicus*, have reported that the estradiol profile in tilapia is similar to that reported by MacGregor et al. (1981), whereby there is no decline in estradiol levels prior to oocyte maturation. Testosterone appears high in these mouthbrooders in the latter half of the brooding period. Testosterone levels fall upon the cessation of mouthbrooding behaviour. It has not yet been established whether testosterone is directly involved in mouthbrooding behaviour or not. In contrast to the testosterone levels, Smith and Haley (1988) found that progesterone levels in mouthbrooders only increase once mouthbrooding had ended. This rise in progesterone could be due to either a decrease in conversion to other steroids or an overall increase in hormone production.

In the present study, it was decided to consider only the physiological role of gonadal steroids in reproduction and that the steroids that would be examined were testosterone, estradiol 17-β and progesterone. The results were related to gonadosomatic index (GSI), dam water temperature and seasonal lipid levels.

## Materials and methods

Each Monday morning at 08:00, 10 adult male and 10 adult female *O. mossambicus* were collected at Syferkuil Dam, 8 km NW of the University of the North using a seine net. The period of collection lasted for a full calendar year. Before the fish were

transported back to the University of the North campus in oxygenated water containing 20 mg/ℓ neutralised MS222 according to the method of Smit (1980), a 2.5 mℓ sample of blood was collected at the dam using the cardiac puncture method. This method of transporting the fish would overcome the effects of handling stress that may have been encountered during netting. In the laboratory, the fish mass (g) and gonad mass (mg) were recorded. This data were used to calculate the GSI for each fish analysed throughout the sampling period according to the following formula of Roff (1983):

$$GSI = \frac{\text{mass of gonad}}{\text{mass of fish}} \times 100$$

The concentration of the steroid hormones testosterone in the male and estradiol 17-β and progesterone in the female were determined using appropriate FRANSA radio-immunoassay kits. (Cat Nos. Testosterone: CM-TESTO; Estradiol 17-β: SB-ESTR; Progesterone: CM-PROG supplied by FRANSA). Both plasma and gonadal homogenate supernatants were analysed. All FRANSA RIA test kits made use of $^{125}$I-labelled hormones, which are intended for use with human samples. All readings of radioactivity were taken using a Beckman Gamma 8500 Microprocessor Counter.

Total lipid concentrations were determined using a Boehringer Mannheim test combination (Cat. No. 124 842) using the UV-method. All readings as required when using Boehringer Mannheim test combinations were taken on a Beckman model DU65 spectrophotometer.

Statistical analyses were carried out using the SAS program. Due to this being a field study, which may not be controlled as in the laboratory, a large variation in the size of the experimental animals occurred and also a degree of stress may have been encountered, the significance of the variation is not as great as in controlled laboratory conditions.

## Results

Table 1 shows male *O. mossambicus* plasma and gonadal supernatant testosterone concentration (ng/mℓ) values for the entire experimental period. Male plasma testosterone levels peaked during September and dropped to a lower level from October till February. Thereafter it declined further. Gonad testosterone levels were higher only during November and December whereafter these levels remained almost constant. Gonad testosterone levels were also higher than their corresponding plasma levels.

Table 2 shows female *O. mossambicus* plasma and gonadal supernatant estradiol 17-β concentration (ng/mℓ) values for the entire experimental period. Female plasma estradiol levels gradually increased from May to July, reaching a peak during August. Thereafter they declined to undetectable levels in November and December. Gonad estradiol levels gradually increased from March to reach a peak in September whereafter a gradual decline was observed until February. Gonad levels remained almost ten times higher than plasma levels, throughout the experimental period.

Table 3 shows female *O. mossambicus* plasma and gonadal supernatant progesterone concentration (ng/mℓ) values for the entire experimental period. Female plasma progesterone levels were low from January to August whereafter they increased significantly to December. In general, gonad values were high from March to August and thereafter they showed four dips in concentration during September, November, December and February.

**TABLE 1**
**TESTOSTERONE CONCENTRATION (ng/mℓ) MEASURED IN PLASMA AND GONADS OF MALE *O. MOSSAMBICUS* (SAMPLES TAKEN PER MONTH, n = 40)**

| | Plasma (ng/mℓ) mean ± sd | Gonad (ng/mℓ) mean ± sd |
|---|---|---|
| May | 1.22 ± 0.26 | 3.64 ± 0.88 |
| Jun | 2.20 ± 0.56 | 4.04 ± 0.68 |
| Jul | 1.80 ± 0.78 | 4.92 ± 1.02 |
| Aug | 1.76 ± 0.28 | 5.88 ± 0.96 |
| Sept | 12.30 ± 2.27 | 4.34 ± 0.62 |
| Oct | 3.14 ± 1.01 | 3.06 ± 0.69 |
| Nov | 2.38 ± 1.55 | 12.30 ± 2.70 |
| Dec | 3.38 ± 0.89 | 9.62 ± 1.21 |
| Jan | 3.30 ± 0.59 | 3.82 ± 0.49 |
| Feb | 3.34 ± 0.63 | 4.34 ± 0.64 |
| Mar | 2.04 ± 0.83 | 4.50 ± 0.63 |
| Apr | 1.60 ± 0.29 | 4.62 ± 0.55 |

**TABLE 2**
**ESTRADIOL 17-β CONCENTRATION (ng/mℓ) MEASURED IN PLASMA AND GONADS OF FEMALE *O. MOSSAMBICUS* (SAMPLES TAKEN PER MONTH, n = 40)**

| | Plasma (ng/mℓ) mean ± sd | Gonad (ng/mℓ) mean ± sd |
|---|---|---|
| May | 0.26 ± 0.04 | 1.49 ± 0.07 |
| Jun | 0.48 ± 0.02 | 3.19 ± 0.09 |
| Jul | 0.56 ± 0.04 | 3.38 ± 0.09 |
| Aug | 0.68 ± 0.04 | 5.34 ± 0.06 |
| Sept | 0.24 ± 0.02 | 5.02 ± 0.12 |
| Oct | 0.50 ± 0.01 | 4.75 ± 0.09 |
| Nov | non-measurable | 4.03 ± 0.09 |
| Dec | non-measurable | 4.44 ± 0.11 |
| Jan | 0.26 ± 0.03 | 3.94 ± 0.23 |
| Feb | 0.78 ± 0.03 | 3.04 ± 0.10 |
| Mar | 0.42 ± 0.05 | 1.81 ± 0.04 |
| Apr | <0.01 | 1.13 ± 0.05 |

Figure 1 represents the relationship between GSI (%) and the concentration of the steroid hormone testosterone (ng/mℓ) in male *O. mossambicus* plasma and gonadal supernatant. The concentration of plasma testosterone reaches a peak of 12.30 ± 2.27 ng/mℓ during September (Table 1), which is two months prior to maximum GSI and gonadal supernatant testosterone levels in November.

Figure 2 represents the relationship between GSI (%) and the concentration of the steroid hormones estradiol 17-β and progesterone (ng/mℓ) in female *O. mossambicus* plasma and gonadal supernatant. In Fig. 2, the levels of progesterone in the gonadal supernatant have been divided by a factor of 10 in order to fit in with the axes used. Female GSI reaches a peak during September. Plasma estradiol 17-β levels are high (0.68 ± 0.04 ng/mℓ) during August, whereas plasma progesterone reaches its peak of 8.58 ± 2.89 ng/mℓ during October. A very good relationship exists

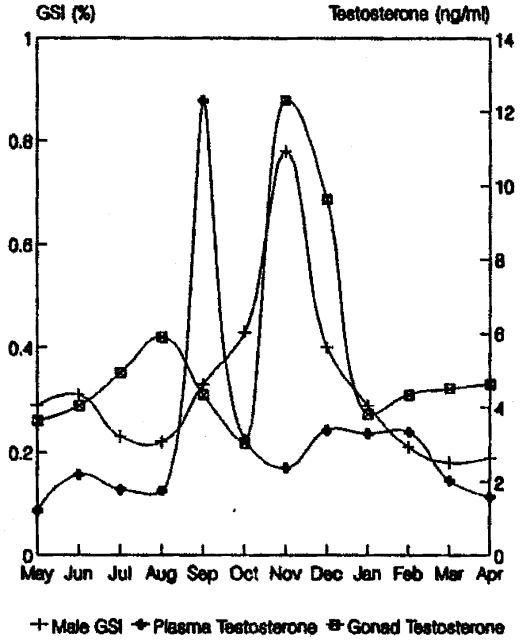
**TABLE 3**
**PROGESTERONE CONCENTRATION (ng/mℓ) MEASURED IN PLASMA AND GONADS OF FEMALE *O. MOSSAMBICUS* (SAMPLES TAKEN PER MONTH, n = 40)**

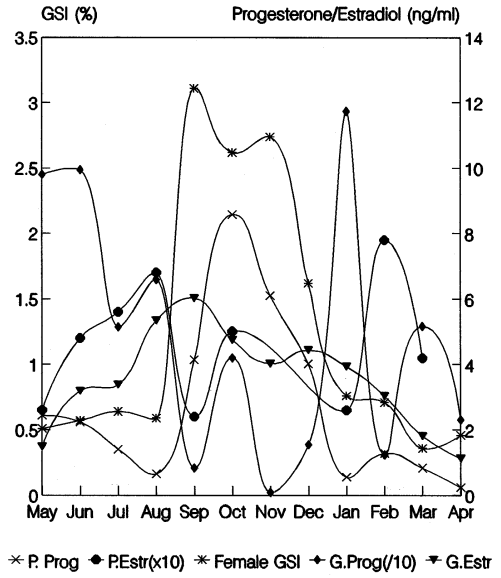
| | Plasma (ng/mℓ) mean ± sd | Gonad (ng/mℓ) mean ± sd |
|---|---|---|
| May | 2.44 ± 0.66 | 98.08 ± 10.66 |
| Jun | 2.24 ± 0.98 | 99.50 ± 11.85 |
| Jul | 1.40 ± 0.04 | 51.44 ± 4.46 |
| Aug | 0.66 ± 0.17 | 65.86 ± 5.83 |
| Sept | 4.14 ± 1.39 | 8.34 ± 0.68 |
| Oct | 8.58 ± 2.89 | 42.00 ± 8.75 |
| Nov | 5.10 ± 1.64 | 0.84 ± 0.36 |
| Dec | 4.02 ± 1.80 | 15.46 ± 1.89 |
| Jan | 0.56 ± 0.19 | 117.40 ± 5.63 |
| Feb | 1.28 ± 0.25 | 12.34 ± 2.74 |
| Mar | 0.84 ± 0.01 | 51.66 ± 4.70 |
| Apr | 0.24 ± 0.07 | 23.10 ± 2.81 |

between plasma progesterone concentration and GSI (r = 0.85) in female *O. mossambicus*. In the gonadal supernatant, a good relationship exists between estradiol 17-β and GSI (r = 0.67) with both reaching maximum values during September. Gonadal progesterone concentration appears to exhibit an almost inverse relationship with female GSI, although a small progesterone peak (42.00 ± 8.75 ng/mℓ) was measured during October. The highest level of progesterone (117.40 ± 5.63 ng/mℓ) is seen in January when GSI has fallen considerably from the high noted during September till November.

Figure 3 represents the relationship between dam water temperature (°C) and the concentration of steroid hormones (ng/mℓ) in male and female *O. mossambicus* plasma. The temperature of the dam water increases sharply during September and remains high until February (Cornish and Smit, 1995). Male testosterone also shows a peak during September and another from December to February. Female progesterone shows peaks in June, September to December and February reaching a maximum during October. In the case of female estradiol 17-β, the highest concentrations are seen during August, October and February. Male plasma testosterone levels generally peak when female estrogen levels are low.

Figure 4 represents the relationship between Syferkuil dam water temperature (°C), GSI (%) and male and female steroid hormone concentrations (ng/mℓ) in *O. mossambicus* plasma. High male GSI values are seen to extend from September till January with a peak during November, which is two months after the maximum testosterone peak, but at a time when dam water temperature is still high. In the female, estradiol 17-β reaches a



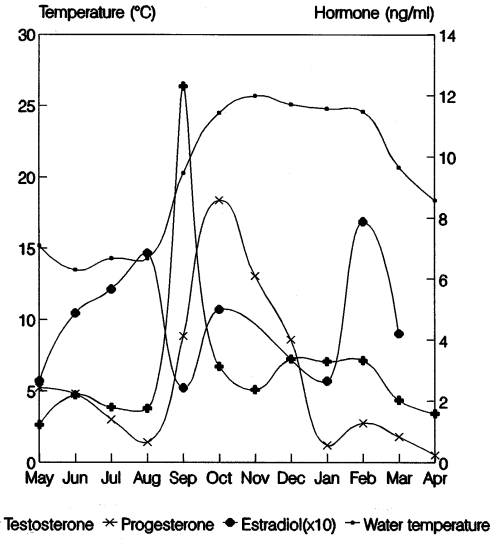




***Figure 1 (right, top)***
*Plasma and gonadal testosterone levels in male* O. mossambicus
***Figure 2 (right, middle)***
*Plasma and gonadal progesterone and estradiol 17-β levels in female* O. mossambicus
***Figure 3 (right, bottom)***
*Syferkuil dam water temperature and plasma steroid hormone levels in male and female* O. mossambicus

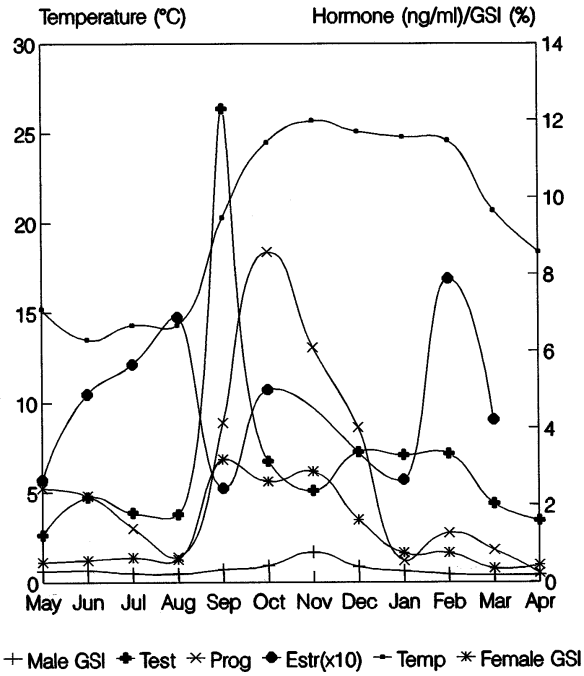



***Figure 4***
*Syferkuil dam water temperature, plasma steroid hormone levels and GSI in male and female* O. mossambicus

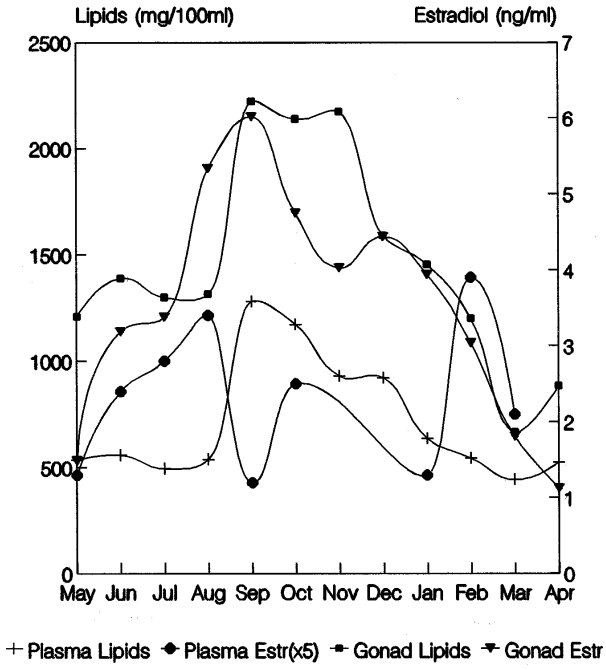



***Figure 6***
*Plasma and gonadal lipid and estradiol 17-β levels in female* O. mossambicus

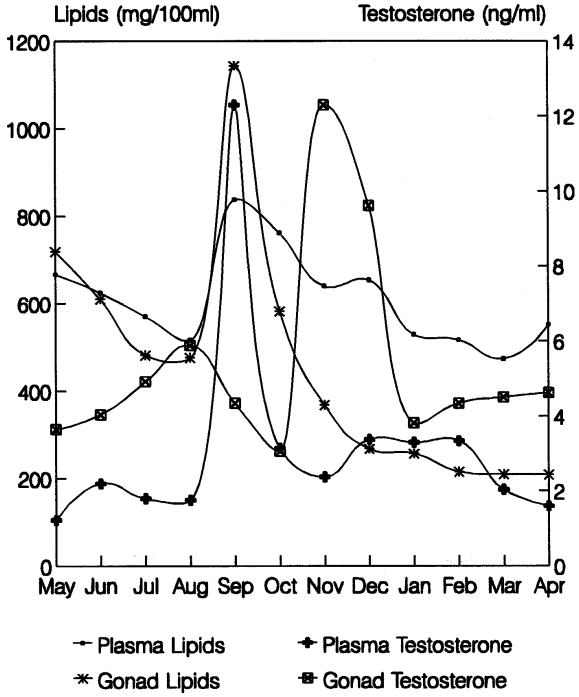



***Figure 5***
*Plasma and gonadal lipid and testosterone levels in male* O. mossambicus

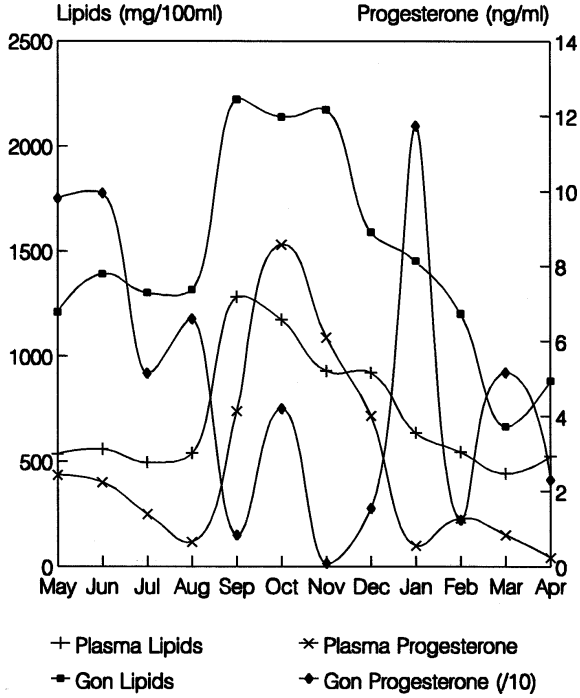



***Figure 7***
*Plasma and gonadal lipid and progesterone levels in female* O. mossambicus

high concentration during August, October and February. It is during this period that female GSI levels reach a maximum. Progesterone also reaches maximum levels during this period.

Figure 5 represents the relationship between lipid (mg/100 mℓ) and testosterone (ng/mℓ) concentration in male *O. mossambicus* plasma and gonadal supernatant. A good relationship exists between plasma lipid and testosterone (r = 0.67) concentrations, with both parameters reaching a high concentration during September, whereas this relationship appears to be one month "out of phase" in the gonad. The gonadal testosterone level peaks during November with the gonadal supernatant lipid peak coinciding with maximum GSI (see Fig. 1). Figure 5 shows that plasma testosterone, although initially lower than gonadal supernatant levels, reaches its maximum prior to the gonadal supernatant testosterone peak. There is an initial surge of testosterone in the gonadal supernatant during August. Thus the two gonadal testosterone surges have opposing effects on plasma testosterone levels.

Figure 6 represents the relationship between lipid (mg/100 mℓ) and estradiol 17-β (ng/mℓ) concentration in female *O. mossambicus* plasma and gonadal supernatant. There is an inverse relationship between lipids and estradiol 17-β in plasma during August and September when peak values are reached. This was followed by an increase and subsequent decline in estradiol 17-β levels a month later. In the gonads, however, the same positive relationship between lipids and estradiol 17-β was observed, but at much higher levels.

Figure 7 represents the relationship between lipid (mg/100 mℓ) and progesterone (ng/mℓ) concentration in female *O. mossambicus* plasma and gonadal supernatant. Fig. 7 appears to indicate an inverse relationship between lipid and progesterone concentration in the gonadal supernatant of female *O. mossambicus*. Both plasma and gonadal lipid levels reached a peak during September.

## Discussion

The concentration of a circulating hormone results from the rates of secretion into and the clearance from the plasma. Interpretation of plasma hormone fluctuations in fish appears to be linked with both pituitary and gonad secretion rates.

### Testosterone

Figure 1 shows that there is an increase in the level of testosterone in the plasma prior to the increase observed in the gonad. Figure 3 shows that this increase in testosterone in the plasma could be associated with the increase in the dam water temperature which occurs at the same time (September - spring). There is also an increase in daylength during this period, which has been shown to be an environmental cue to a preovulatory surge in hormonal secretion in cyprinids (Aida, 1988). This occurrence may create a false interpretation of the results which will be outlined below. The foregoing results suggest that an inverse relationship exists between male plasma and gonad testosterone levels. Two factors may be involved. Firstly, a time lag may occur between the testosterone production in the testes and inter-renal tissue and their shift to the plasma before it may be measured at quantifiable levels. Secondly, the different peaks observed in the plasma, may be related to body size, i.e. the larger the specimen, the lower the testosterone levels (Cornish, 1993). This corresponds with the size of the males collected during the breeding period. It appears as if the bigger males spawn first, followed by the smaller males (Cornish et al., 1997). In addition this double testosterone cycle for each group, corresponds with ovarian development in females. The high testosterone concentrations correspond with female GSI development. Furthermore, the large testosterone surge in males during September, may result from a build up of testosterone in male plasma as a result of male testes being able to produce testosterone at a specific rate only. Thus, when female GSI reaches a peak and spawning occurs, an immediate decline in male plasma testosterone occurs. This observation is supported by the relatively low production of testosterone recorded in the testes during the same period. The biphasic cycle in males seems to be related to the biphasic cycle observed in females. Although it appears that the male cycle "lags" about two months behind the female in terms of peak GSIs recorded for both sexes, hormone levels measured suggest the opposite. Although the volume and mass of eggs is much higher than sperm, the synchronisation of both the male and female reproductive cycle is therefore closely related to the mouthbrooding period of the females.

The increase in September, which was preceded by a much smaller peak during June suggests that the testosterone levels indicate the commencement of spermatogenesis within the testis. It is also possible that spermatogenesis commenced in June to a specific level controlled by, amongst other factors, environmental stimuli and then further development of the gonads occurs in September as a result of a synchronised effect of testosterone and favourable environmental stimuli. The correlation of testosterone and GSI levels indicates that this androgen is associated with testicular development. Immediately prior to testosterone increasing, there is an increase in both gonadotropins measured, which may act as a stimulant, resulting in testosterone secretion. Both plasma and gonadal testosterone levels show a bimodal increase. These results would appear to correlate with those for the brown bullhead (Burke et al., 1984), the black goby (Bonnin, 1979) and the blue cod (Pankhurst and Conroy, 1987) who all exhibit this bimodal profile of gonadal steroids. The significance of the bimodality could be that recrudescence occurs rapidly (less than one month). The relatively high levels of testosterone measured in the gonad during November (Fig. 1) is most probably associated with the release of mature spermatozoa. Once the gonadal lipids reach a high during September (Fig 5), they could then lead to an increase in the testosterone levels and subsequent spawning.

In male teleosts, testosterone is typically elevated during spermatogenesis, and then falls at the onset of spermiation (Fostier et al., 1983). The lower levels of testosterone observed in this study, could reflect the synthesis of unmeasured metabolites.

It appears that a time lapse exists between testosterone production and the male breeding cycle, which is associated with female gonadal maturity. Thus temperature appears to be a possible cue causing testosterone to peak which leads to the gonads, and subsequently their gametes, reaching reproductive maturity.

#### Estradiol 17-β

This parameter was measured in females only. Estradiol 17-β is secreted by both the female gonads and inter-renal tissues. In general, estradiol is responsible for stimulating vitellogenesis and is also secreted by female gonads during the pre-spawning period. Evaluation of the results in Table 2 and Figs. 2, 3 and 6 reflects the importance of this hormone. Table 2 suggests that gonadal estrogen levels are generally higher than plasma levels.

Plasma estradiol levels suggest no major changes, except during November and December. The latter observation suggests that most females were in the immediate postspawning period prior to gonadal recrudescence at this time. From May until August a gradual increase in plasma levels was observed. This mild increase suggests a bimodal increase from both the gonads and the inter-renal tissues. It does, however, not explain why a major shift from the gonads to the blood occurs. This may be due to a decline in steroidogenic postovulatory follicles being present. It also suggests that this period corresponds with the major mouthbrooding phase of female *O. mossambicus*. Furthermore, plasma estradiol levels confirm an increase in the immediate pre-spawning activity when compared with female GSI values. Gonad estradiol levels reflect a continuous maturing of females to prepare for the following spawning cycle. Estradiol is known to be secreted by the cells of the ovarian follicles that promote the development and maintenance of the female sexual characteristics. In humans it is the hormone (together with other hormones) that is responsible for controlling the female sexual cycle. Thus the number of ovulating follicles would determine or at least contribute to the quantity of estradiol that is present in the gonads. Estradiol has been reported to stimulate vitellogenesis in teleosts (Campbell and Idler, 1976; De Vlaming et al., 1980; Smith and Haley, 1988). These authors have reported an increase in plasma estradiol levels once spawning commences, and that it remains high throughout the period of oocyte growth. These observations suggest that during this phase of undetectable estradiol levels, no vitellogenesis is required during the mouthbrooding period and that some females experience gonadal recrudescence. Another possibility to be considered, is that the mid-cycle decline in estradiol levels could be due to a rapid utilisation of the hormone in stimulating vitellogenesis.

The estradiol peak observed in February (Figs. 2 and 3) in female *O. mossambicus*, would correspond to the results of Smith and Haley (1988), who observed that the estradiol levels increase markedly toward the end of the ovarian cycle, after mouthbrooding has ceased and oocytes resume their growth. The initial estradiol peak may result in the oocytes being maintained through a "protective" effect similar to that suggested by Sundararaj and Goswami (1968) whereas the second estradiol peak corresponds to a rapid vitellogenic growth phase in the oocytes. This protection could be to prevent the oocytes from becoming atretic.

Rosenblum et al. (1987) have shown a good correlation between circulating estradiol-17β and calcium levels in female teleosts. In the present study, increases in plasma estradiol in female *O. mossambicus* paralleled increases in both GSI and calcium levels (Cornish, 1993), thereby confirming a role for estradiol in vitellogenesis.

Pankhurst and Conroy (1987) have shown in the blue cod, *Parapercis colias*, that the absence of high or detectable levels of estradiol may be due to only a proportion of follicles having oestrogenic capacity at that time. The occurrence of Stage 3 follicles throughout the entire period, suggests that oestrogenic activity will always be located in female gonads. This could also be true for the present study on *O. mossambicus*. At maturity, the relative proportion of estradiol synthesising follicles may be larger, and there may also be a stimulatory effect on steroidogenesis associated with preovulatory increases in gonadotropin.

Another factor to be considered, is the effects of a preovulatory increase in estradiol that may be excreted via the urine. It is suggested that the oestrogenic excretory products may act as a type of pheromone to prepare and attract males for the female ovulatory phase.

Although not the subject of this study, the role of estradiol has been stated to be important in sex inversion or reversal in teleosts (Rothbard et al., 1987; Kime et al., 1991). Further investigation on *O. mossambicus* is required in this regard, in order that this suggestion may be verified or rejected.

In general, the results recorded for *O. mossambicus*, correspond with those for most teleost fish and vertebrates.

### Progesterone

Table 3 suggests that plasma progesterone levels are generally lower than gonad levels. It also reflects an inverse relationship between blood and gonad values. During the period of September till February, the gonads show a relatively sharp decline in progesterone levels with some mild fluctuation corresponding with the bimodal breeding cycle. Such fluctuations also follow the estradiol levels recorded in the plasma and gonads. An inverse relationship was also noted between plasma and estradiol levels. Thus, when plasma progesterone levels are high, estradiol levels are low. These observations therefore give an indication of the stages of follicle development and gonadal recrudescence. Such levels also correspond with the bimodal cycle for the two age groups as suggested earlier.

Smith and Haley (1988) have shown that the progesterone levels in mouthbrooders do not increase until mouthbrooding behaviour has ended. Thus the sharp increase in gonad progesterone levels during the period of March to August, reflects the possibility of environmental factors inhibiting gonad development. It also confirms a resting period for this species before commencing the next spawning cycle at the end of August. This rise in progesterone could also be attributed to either a decrease in conversion to other steroids or to an overall increase in steroid hormone production. The present study on *O. mossambicus* indicates that the concentration of progesterone shows a marked increase during January which is after mouthbrooding has been completed. A progesterone peak some time after spawning has been shown by Smith and Haley (1988) to mark the time when steroidogenic-appearing postovulatory follicles begin to degenerate in mouthbrooders. The presence of two peaks for progesterone in the present study could be explained by the fact that fish of different sizes were sampled and that the younger fish complete their breeding prior to the older fish. The second peak is noted toward the end of the ovarian cycle. It is unknown whether progesterone is involved in final maturation in the tilapia.

Progesterone also seems to increase in concentration as a result of the increase in water temperature that is noted during September (spring).

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