Aquaculture, 63 (1987) 169–185
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

The Significance of Photoperiodicity, Water Temperature and an Inherent Endogenous Rhythm for the Production of Viable Eggs by the African Catfish, *Clarias gariepinus*, kept in Subtropical Ponds in Israel and under Israeli and Dutch Hatchery Conditions

C.J.J. RICHTER[1]*, W.J.A.R. VIVEEN[1], E.H. EDING[1], M. SUKKEL[1], A.J. ROTHUIS[1], M.F.P.M. VAN HOOF[2], F.G.J. VAN DEN BERG[2] and P.G.W.J. VAN OORDT[2]

[1]*Department of Fish Culture and Fisheries, Agricultural University, P.O. Box 338, 6700 AH Wageningen (The Netherlands)*

[2]*Department of Experimental Zoology, Research Group for Comparative Endocrinology, University of Utrecht, P.O. Box 80.058, 3508 TB Utrecht (The Netherlands)*

(Accepted 16 February 1987)

ABSTRACT

Richter, C.J.J., Viveen, W.J.A.R., Eding, E.H., Sukkel, M., Rothuis, A.J., Van Hoof, M.F.P.M., Van Den Berg, F.G.J. and Van Oordt, P.G.W.J., 1987. The significance of photoperiodicity, water temperature and an inherent endogenous rhythm for the production of viable eggs by the African catfish, *Clarias gariepinus*, kept in subtropical ponds in Israel and under Israeli and Dutch hatchery conditions. *Aquaculture*, 63: 169–185.

A comparison was made between the fecundity of female African catfish, *Clarias gariepinus*, transferred from their natural habitat in Northern Israel to nearby fish ponds and an indoor hatchery respectively, and conspecifics reared and kept in an indoor hatchery in The Netherlands.

The results indicate that an inherent endogenous rhythm rather than the natural light periodicity determines the cyclical changes in ovarian activity, and that this internal rhythm is determined by environmental factors at an early stage of development. High water temperatures and the presence of males seem to enhance ovarian activity and to shorten its resting period. The significance of gonadotropin secretion by the pituitary for the ovarian cycle is discussed.

It is concluded that for propagation of *C. gariepinus* throughout the year, independent of the seasons, broodfish should be reared and kept in hatchery tanks at a water temperature of 25 °C, with proper feeding, in the presence of males, and at any local light periodicity.

INTRODUCTION

The annual ovarian cycle of the African catfish (*Clarias gariepinus*) can be divided into three periods (Van Den Hurk et al., 1986; Van Oordt et al., 1987), i.e.:

0044-8486/87/$03.50

TABLE 1

Natural breeding cycles of different populations of the African catfish, *Clarias gariepinus*[a]

Place	Prespawning period	Spawning period	Breeding season (prespawning + spawning period)	Reference
Countries North of the equator				
Ghana (Lake Nunguna)			March–May	Thomas (1966)
Sudan (Jebel Aulia Dam reservoir)	April–July	August–September	April–September	Babiker (1984)
Israel (Hula reserve)	March–May	June–August	March–August	Van Den Hurk et al. (1986)
Countries South of the equator				
Zimbabwe			November–February	Holl (1966, 1968)
Malawi (Shire Valley)	November–December	January–February	November–February	Willoughby and Tweddle (1976)
Southern Africa (Lake Sibaya)	July–October	November–February	July–February	Bruton (1979)

[a]The nomenclature of African *Clarias* species used by Teugels (1984) is followed.

(1) a prespawning period or period of full gametogenesis, during which the ovaries gradually enlarge, with concommitant formation of yolk-rich oocytes (recrudescence of the ovary);
(2) a spawning or breeding period, which includes maturation of postvitellogenic oocytes, ovulation and oviposition;
(3) a postspawning or resting period, characterized by atresia of remaining follicles (regression of the ovary; Richter and Van Den Hurk, 1982) and previtellogenic oocytes in undeveloped ovaries.

In ecological field studies by Holl (1966, 1968), Thomas (1966), Willoughby and Tweddle (1976), Bruton (1979) and Babiker (1984) on the reproductive biology of the African catfish, the term breeding season often includes both the prespawning and the spawning period (Table 1). In populations north of the equator the breeding season seems to be restricted to the period March–August, and in populations south of the equator to the period July–February. They all have in common that spawning begins with the onset of the rainy season.

These field studies have led to the hypothesis that gametogenesis, or ovarian recrudescence, is controlled by photopheriod and water temperature, and that spawning is triggered by a combination of environmental factors such as a rise in water level and changes in the chemical composition of the water.

The discontinuity of oogenensis and the presence of a resting period in the annual ovarian cycle has caused problems in reproducing the African catfish under pond conditions. The breeding stock used by Micha (1974) in the Central African Republic and by Hogendoorn and Wieme (1975) in the Cameroons originated from a wild population of the Ubangui River. The fish showed gametogenesis and spawning during the period July–October, and during that period could be spawned artificially by stripping, following an injection of 11-desoxycorticosterone-acetate (DOCA) or carp pituitary suspension (cPS). With few exceptions, induction of spawning was difficult outside the natural breeding season, with small batches of infertile eggs (Micha, 1975).

In 1976, larvae of African catfish were transported from the Cameroons (Hogendoorn and Wieme, 1975) to the hatchery of the Department of Fish Culture and Fisheries of the Agricultural University at Wageningen, The Netherlands. These fish were the ancestors of subsequent generations of broodfish, raised in Wageningen since that time. In 1982 and 1983, females from the *Clarias* population at Wageningen were crossed with males from the *Clarias* population in the Central African Republic in order to increase the genetic variance. Preliminary results of Richter and Van Den Hurk (1982) indicated that these fish can be spawned regularly for 3 months after reaching maturity.

The aims of the present experiments are:

(1) to evaluate the hypothesis that photoperiodicity and water temperature regulate the reproductive cycle of female *Clarias gariepinus*, by studying

the effects of these environmental factors on female African catfish under pond and hatchery conditions;

(2) to compare the annual changes in ovarian recrudescence, regression and sensitivity to spawning-inducing hormones in African catfish from the hatchery-reared population kept in indoor tanks at Wageningen, The Netherlands, with such annual changes in conspecifics from the Hula Nature Reserve in Northern Israel that were kept in outdoor fish ponds at the Intensive Fish Culture Station, Ginosar, Israel, and in indoor tanks at the Kinneret Limnological Laboratory, Tabgha, Israel.

MATERIALS AND METHODS

Experiment 1

Pond experiments were carried out at the Intensive Fish Culture Station at Ginosar, Israel.

Husbandry of broodstock

Mature male and female *Clarias gariepinus* of unknown age and weighing about 1 kg were collected in the Hula Nature Reserve and Lake Kinneret from August until October 1981. They were transferred to two ponds of $20 \times 10 \times 1$ m at the Ginosar Intensive Fish Culture Station. One of the ponds was stocked with a mixed-sex group of 130 males and 130 females, the other with a mono-sex population of 256 females. The initial biomass in the ponds was 260 kg and 242 kg respectively. The ponds were surrounded by a fence to prevent fish escaping. The animals were fed daily between 5 and 6 a.m. with a channel catfish pellet (crude protein 30%, Zemach, Israel) at a daily rate of 1% of their wet body weight. In winter the water inflow in the ponds was 1 l/s, and the O_2 concentration of the water, measured at the outlet at 5 a.m., was 6 ppm. During summer the water inflow was gradually increased in order to maintain the original O_2 concentration.

Experimental design

The experiments were carried out to study annual changes in ovarian development and sensitivity to the oocyte maturation-inducing corticosteroid deoxycorticosterone-acetate (DOCA; Richter and Van Den Hurk, 1982) in broodfish taken from a natural population and maintained under sub-tropical conditions of light and temperature.

The experiments lasted from May 1982 to August 1983. During that period the daylength was measured at the water surface, and the daily maximal and minimal temperatures at the bottom of the ponds. The data are given in Fig. 1.

At intervals of about 6 weeks, samples were collected at random from the

two ponds. Each sample consisted of four fish from the mono-sex group and two from the mixed-sex group for the determination of the stage of ovarian development, and ten fish from the mono-sex group and five fish from the mixed-sex group for measuring the ovarian sensitivity to DOCA.

The gonadosomatic index [GSI = (ovary weight × 100) / (ovary weight + body weight)] was used as a parameter for ovarian development. The pseudogonadosomatic index [PGSI = (weight of egg mass collected by stripping × 100) / (body weight before injection − weight of stripped eggs)] was used as a parameter of the sensitivity to DOCA. For the DOCA-injection experiments, the fish were transferred to containers of ± 45 l. They were kept individually at 25 °C. After one day of starvation, they were injected with a single dose of 0.05 mg DOCA per gram body weight. The animals were stripped 14 h after injection. Shortly after stripping the fish were killed and disposed of.

Experiment 2

Hatchery experiments were carried out at the Kinneret Limnological Laboratory at Tabgha, Israel.

Husbandry of broodstock

Mature male and female *C. gariepinus* of unknown age and weighing about 1 kg were collected in the Hula Nature Reserve during August 1982. A total of 35 males and 85 females was transferred to the hatchery of the Kinneret Limnological Laboratory and kept in a flow-through tank of 800 l at ± 25 °C. The water flow was 40 l/min, maintaining the O^2 concentration above 6 ppm. The fish were fed a channel catfish pellet (crude protein 30%, Zemach, Israel) at a daily rate of 0.5% of their wet body weight.

Experimental design

The experiments were carried out to study annual changes in ovarian development, in sensitivity to the oocyte maturation and ovulation-inducing cPS (Richter and Van Den Hurk, 1982), and in fecundity, of broodfish, collected from a natural population and kept under sub-tropical light periodicity (Fig. 2) and constant high temperatures. To that end, ten fish of the stock were randomly sampled and marked individually at the beginning of the experiments. These fish were used for measurements every 6–8 weeks, starting on 25 November 1982. Due to accidental death of the experimental animals, the series of experiments was interrupted during summer 1983, and resumed with a new group of fish of the same tank stock on 5 October 1983. The second part of the series of experiments continued until 26 April 1984.

Ovarian development was estimated by trying to collect eggs via a cannula, inserted into the oviduct, and by measuring for each fish the diameter of about

20 oocytes, collected in this way (Viveen et al., 1985). Eggs could only be collected from ovaries with abundant postvitellogenic oocytes.

The number of fish ovulating after cPS administration and the PGSI were taken as parameters of the ovarian sensitivity to cPS. Each fish was injected with 4 mg cPS per gram wet body weight, and stripped 12 h later. Fecundity was expressed as the percentage of normal larvae hatching from the eggs. This percentage was calculated from the total number of eggs per gram and the number of normal larvae hatching from these eggs.

Experiments 3 and 4

Hatchery experiments were carried out at the Department of Fish Culture and Fisheries of the Agricultural University of Wageningen, The Netherlands.

Husbandry of broodstock

The broodfish of the experimental series 3 and 4 originated from eggs which hatched in November 1981 and May 1982, respectively. Techniques for egg incubation, and larval and fingerling rearing were used as described by Hogendoorn (1980, 1981), and Viveen et al. (1985). Larvae and immature fish were kept under a light regime of the local daylight period, supplemented by artificial light to a daily photoperiod of 12 h or more (Fig. 2). In these fish gametogenesis was completed when the animals had reached the age of 7 months.

The broodfish were kept in flow-through tanks, containing 800 l water at 25 °C. The water flow was 15 l/min, maintaining the O_2 concentration above 3 ppm. In experiment 3 the animals were kept under the semi-natural Dutch light periodicity, also used for larvae and immature fish (Fig. 2), and in experiment 4 under an artificial light periodicity, comparable to the normal light periodicity in Israel (Fig. 2). The fish were stocked in a mixed-sex group of 35 males and 85 females. The average wet body weight of the fish in experiments 3 and 4 was 600 g and 450 g, respectively. Those of experiment 3 were fed Trouvit no. 4 commercial trout pellets (crude protein 50%), and those of experiment 4 a channel catfish pellet (crude protein 30%) at a daily rate of 0.5% of their wet body weight. Both types of pellets were compounded by Trouw International, The Netherlands.

Experimental design

Experiment 3 was carried out to study annual changes in ovarian development, in sensitivity to cPS and in induced egg production, in broodfish raised and kept in an indoor hatchery under semi-natural Dutch light periodicity and a constant high temperature. Experiment 4 ran parallel to experiment 2, and served to compare the effects of the experimental conditions in African catfish reared in the laboratory with those in conspecifics originating from the catfish population in the Hula Nature Reserve. Experiments 3 and 4 were carried out

with nine and eleven randomly sampled and marked females, respectively. The experimental procedure and parameters were the same as in experiment 2. Experiment 3 lasted from 2 December 1983 until 14 March 1984, and experiment 4 from 13 March 1983 until 28 March 1984.

Statistics

Correlations of light periodicity with both the mean diameter of the oocytes, collected before injection of the spawning-inducing hormone preparation, and the mean percentage of larvae hatching from the eggs, were analyzed with SPSS (Nie et al., 175), using the rank correlation test of Spearman. Correlation coefficients of the statistical analyses, with light periodicity as independent variable, and the diameter of the oocytes and the percentage of normal larvae as dependent variables, were calculated for the results of experiments 2, 3 and 4 (Table 2).

RESULTS

Experiment 1

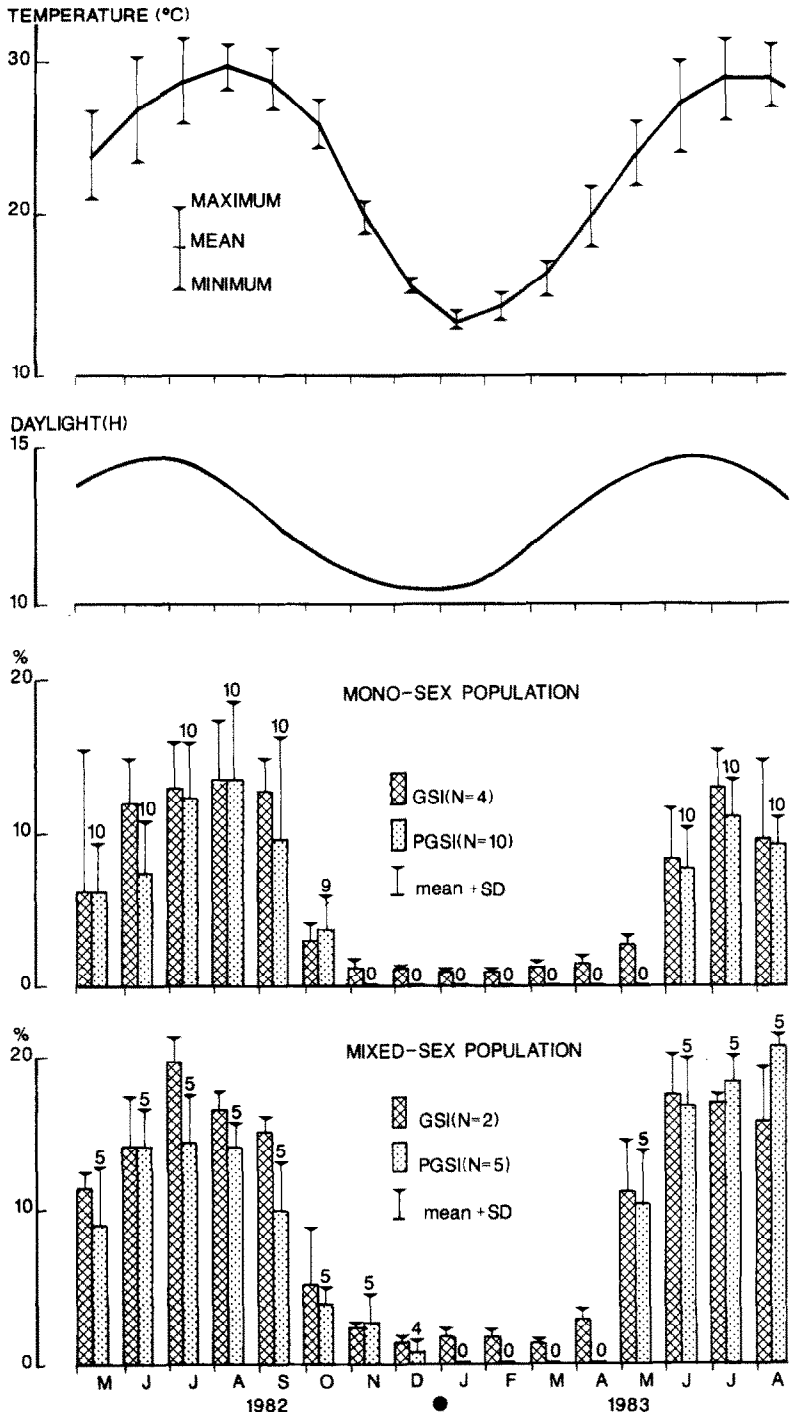
As follows from Fig. 1, in female African catfish collected in the Hula Nature Reserve, and kept in nearby outdoor fish ponds for more than half a year, the GSI rapidly increased in April and May, remained high from June until September, decreased in September and October, and remained low from November until March.

The PGSI followed the same pattern, being maximal during the summer months. Eggs could not be obtained, however, by DOCA injections and stripping during the period January to April in the mixed-sex group and during the period November to May in the mono-sex group. This difference between the two groups coincided with a tendency towards a higher GSI and PGSI from May to August in the mixed-sex group. In both groups the changes in the GSI and PGSI followed the annual changes in daily photoperiod and water temperature. This indicates that ovarian recrudescence became apparent some time after the onset of the yearly increase in daylength and temperature, and ovarian regression some time after the beginning of the annual decrease in these two ambiental factors.

Experiments 2–4

In experiments 3 and 4, carried out in the hatchery at Wageningen, the laboratory-reared animals never failed to have oocytes that could be extracted by inserting a cannula into the oviduct, before administering cPS. In experiment 2, oocytes could be obtained from eight or more out of ten catfish from the

EXPERIMENT 1



Hula Nature Reserve, kept in the hatchery at Tabgha, throughout the year, except in late autumn. Indeed, in the November samples, only four out of ten animals could be used for measuring the diameter of the oocytes.

In all three experiments the diameter of the oocytes ranged between 1.1 and 1.5 mm (Fig. 2) without showing a clear annual cycle and a significant correlation with light periodicity. A significant positive correlation ($P<0.01$) was observed, however, in the second half of experiment 2, but not in the first half of that experiment (Table 2).

In the fish reared at Wageningen, the sensitivity to cPS, as reflected by the PGSI, ranged between 9.0 and 15.1% in experiment 3, and between 4.8 and 13.0% in experiment 4 (Fig. 2).

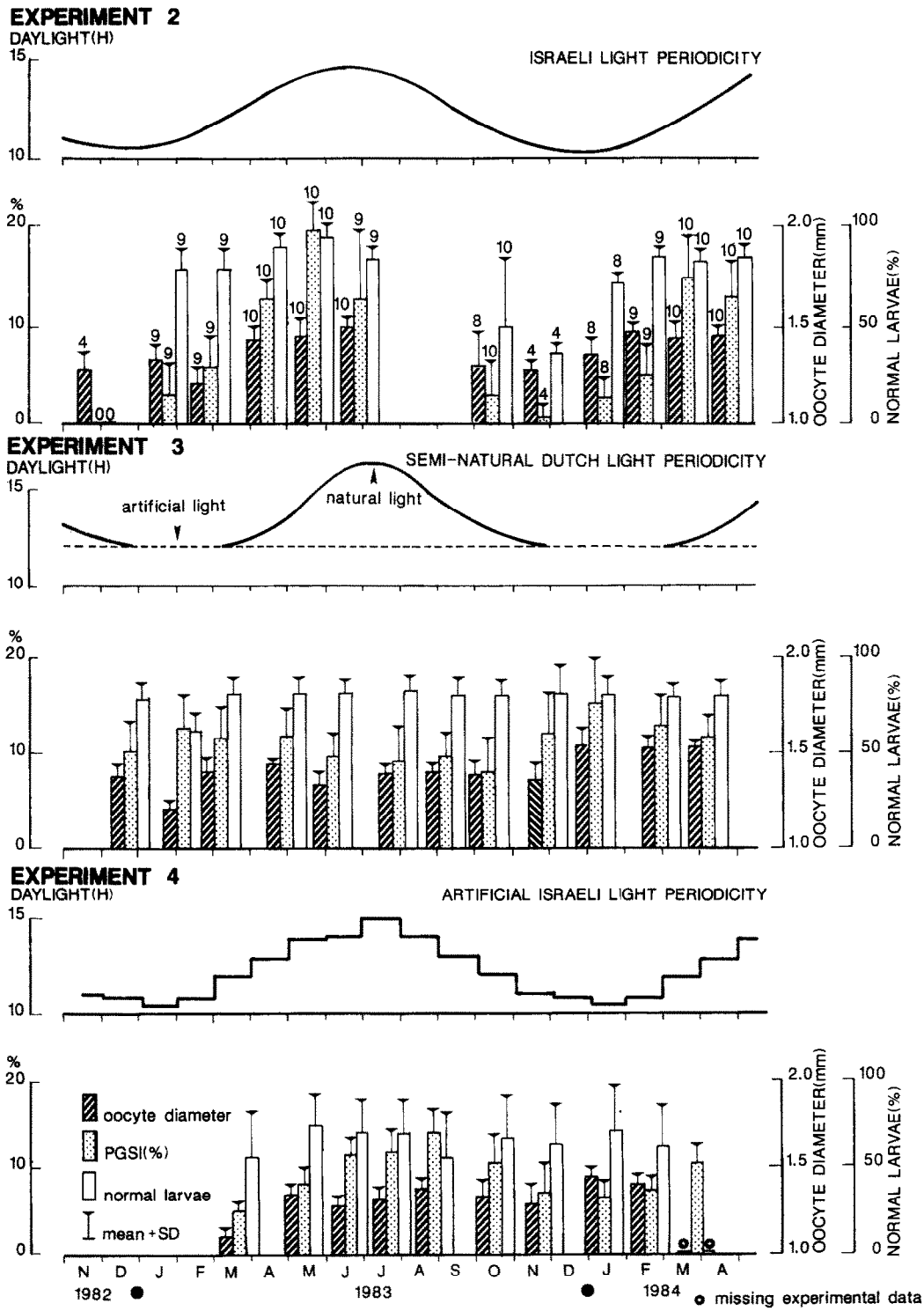
Under conditions comparable to those of experiment 4, the fish from the Hula Nature Reserve showed a low PGSI, ranging between 0.7 and 6.0 under natural short-day conditions from October to February, and a considerably higher PGSI of 13.0 to 22.6 under natural long-day conditions from April to June (Fig. 2). A similar simultaneous trend was not found in experiments 3 and 4.

The percentage of normal larvae hatching from the eggs obtained by injecting female catfish with cPS, ranged between 75.5 and 85.9% in experiment 3, and between 50.9 and 67.2% in experimennt 4. It did not show any significant correlation with light periodicity (Table 2). In experiment 2 the percentage of normal larvae was relatively high, i.e. between 73.9 and 90.8% from January to June, and much lower, i.e. 54.7 and 35.7% in October and November, respectively (Fig. 2). The percentage of normal larvae showed a positive correlation ($P<0.05$) with light periodicity in the first half of experiment 2 (Table 2).

DISCUSSION

Females from the natural population of African catfish, *Clarias gariepinus*, in the Hula Nature Reserve (Northern Israel) show a reproductive cycle consisting of three successive period (Van Den Hurk et al., 1986; Van Oordt et al., 1987). As follows from the annual changes in GSI and PGSI, these periods can also be recognized in females from the same population, kept in a nearby outdoor fish pond, together with male conspecifics. There are some differences, probably connected with the absence of spontaneous breeding behaviour and spawning in the pond animals. Confinement does not seem to affect the relative weight of the ovaries, but has some influence on cyclical changes, both the

Fig. 1. Seasonal changes in gonadosomatic index (GSI) and in pseudogonadosomatic index (PGSI), resulting from the injection of deoxycorticosterone-acetate (DOCA) and stripping, in female African catfish, kept in fish ponds. N = number of broodfish per sample. For each sample the number of fish that produced eggs after DOCA administration and stripping is given above the standard deviation (SD) of its PGSI bar.


EXPERIMENT 2
DAYLIGHT(H)
ISRAELI LIGHT PERIODICITY
EXPERIMENT 3
DAYLIGHT(H)
SEMI-NATURAL DUTCH LIGHT PERIODICITY
artificial light
natural light
EXPERIMENT 4
DAYLIGHT(H)
ARTIFICIAL ISRAELI LIGHT PERIODICITY
oocyte diameter
PGSI(%)
normal larvae
mean + SD
OOCYTE DIAMETER(mm)
NORMAL LARVAE(%)
N D J F M A M J J A S O N D J F M A
1982
1983
1984
missing experimental data

increase and decrease in GSI beginning about one month later than in nature. The main increase in GSI and PGSI was found in April–May, indicating that ovarian recrudescence took place between March and June, and not between February and May, as in the Hula Nature Reserve. Likewise, the major decrease in GSI and PGSI was observed in September and October, and not in July and August, as described for African catfish of the Hula Nature Reserve. It may be that the relatively early recrudescence of the ovary in the Hula Nature Reserve is caused by the high water temperature of shallow parts of the pools in which catfish were observed sun-bathing during day-time (Viveen, unpublished). Regression of the ovaries in the Hula Nature Reserve might be enhanced by unsatisfactory feeding conditions when the pools dried up in August (Van Den Hurk et al., 1986), and – probably more important – by the evacuation of most postvitellogenic oocytes during the preceding spawning period. At any rate, the difference in ovarian cycle between the natural population and the mixed-sex group cannot be asribed to an influence of daylength.

The mixed-sex and the mono-sex pond groups differed in GSI and PGSI from May to August, with somewhat higher values in the former. A more dis-

TABLE 2

Correlation coefficients of the rank correlation test of Spearman with light periodicity as independent variable, and mean oocyte diameter before induced spawning, and percentage of normal larvae after hatching, as dependent variables (In brackets the number of separate measurements per experiment)

	Mean oocyte diameter	Mean percentage of normal larvae
Experiment 2		
first half	0.1354	0.2554*
	(60)	(60)
second half	0.3321**	−0.1242
	(60)	(60)
Experiment 3	−0.0432	0.1390
	(105)	(106)
Experiment 4	−0.1396	0.0293
	(110)	(100)

*$P < 0.05$; **$P < 0.01$.

Fig. 2. Seasonal changes in the diameter of oocytes, in pseudogonadosomatic index (PGSI) resulting from the injection of carp pituitary suspension (cPS), and in percentage of healthy larvae hatching from the ovulated eggs. For each sample (experiment 2) the number of fish from which oocytes could be extracted is indicated above the standard deviation (SD) of its oocytes diameter bar, and the number of fish responding to cPS is indicated above the SD of its PGSI bar. In experiment 3 and 4 all fish could be used for measuring the diameter of the oocytes before induced ovulation, and all fish responded to cPS.

tinct difference between the two groups, however, was observed in the length of the resting period, which in the mono-sex group lasted for 7 months, and in the mixed-sex group only 4 months. The presence of males seems to enhance ovarian recrudescence and to delay its regression. Under laboratory conditions at Wageningen, Henken et al. (1987) could confirm the positive influence of males on the GSI of female *C. gariepinus*. This may indicate a role of male sex pheromones on follicle development and maintenance in the ovary. The steroid glucuronides produced by testes and seminal vesicle (Lambert et al., 1986; Schoonen and Lambert, 1986a,b; Schoonen et al., 1987a,b,c; Resink et al., 1987b) could have such a pheromonal function.

Thus, it seems that husbandry conditions and the presence of males may influence the ovarian cycle of *C. gariepinus*, but this cycle continues to follow the annual changes in daily photoperiod and water temperature, and remains discontinuous, even though in fish ponds oocyte maturation and ovulation remain absent.

An important change could be realized by bringing the animals from the Hula Nature Reserve, not to outdoor ponds but to an indoor hatchery tank with a constant water temperature of 25 °C and a normal local photoperiodicity. The period during which oocytes could be obtained by inserting a cannula into the oviduct, and ovulation could be induced in almost all experimental animals by administering cPS, lasted from January until October. Even in November some animals appeared to have postvitellogenic oocytes in the ovaries, although the viability of these oocytes was subnormal. This means that under conditions of constant high water temperatures, proper feeding, the presence of male conspecifics, and a normal photoperiodicity, large quantities of normal larvae can be obtained during at least 10 months of the year. It also implies that water temperature is a more important factor in regulating the ovarian cycle than daylength, although the close correlation between the annual changes in daylength and the percentage of normal larvae during the first half of the hatchery experiment at Tabgha could point to possible influences of the photoperiodicity on ovarian processes.

The results of the experiments carried out in the hatchery at Wageningen under conditions of high water temperatures and a semi-natural Dutch light periodicity as well as an artificial Israeli light periodicity, however, did not confirm the hypothesis of an influence of daylength on processes leading to the production of postvitellogenic oocytes. The African catfish, reared at the Wageningen hatchery, showed a continuous ovarian cycle with fully grown oocytes that can be extracted by inserting a cannula into the oviduct, at all seasons. Likewise, eggs could be obtained by cPS administration and stripping throughout the experiments, and the percentage of healthy larvae showed very little fluctuation. Various parameters remained somewhat lower in the animals kept under an Israeli light regime than in those kept under a semi-natural Dutch light periodicity, but those differences are probably attributable to the

lower initial body weight of the former group and the difference in protein content of the food. The overall conclusion from the experiments carried out at Wageningen seems to be that light periodicity does not influence the formation of numerous healthy postvitellogenic oocytes in *C. gariepinus* reared in indoor hatcheries. An independence from light periodicity with respect to ovarian recrudescence has also been described by Sudararaj and Sehgal (1970) and by Sundararaj and Vasal (1976) for the Indian catfish, *Heteropneustes fossilis*.

In comparing the results of all four experiments, it appears that in *C. gariepinus* constant high temperatures enhance the production of postvitellogenic oocytes and the PGSI, but do not entirely prevent the discontinuity of the ovarian cycle. In addition, changes in daylength do not seem to prevent a fading of the cyclic character of ovarian processes. Continuity and discontinuity of the ovarian cycle seem to be determined by environmental factors prevailing during early stages of development. The fish used for the experiments in Israel and those studied in ecological field research (Table 1) had developed under natural circumstances of seasonal changes in climatic conditions and availability of food; and they preserved an annual rhythmicity of ovarian processes. On the other hand, the fish used in The Netherlands had been raised in a hatchery at constant high water temperatures and ample food supply, and only the daylength changed with the seasons; and they showed a continuous ovarian cycle. Thus, it seems that in adult females from natural populations the ovarian cycle results primarily from an inherent circannual rhythm in the activity of internal factors, regulating ovarian processes. Such an endogenous rhythm can possibly be imprinted (e.g. by a periodic shortage of food) at an early stage of the ecological life cycle.

As in almost all vertebrates, gonadal processes in catfish depend on gonadotropic hormone (GTH), secreted by the pituitary gland. Resink et al. (1987a,c), however, observed that in feral African catfish a more or less constant low plasma level of GTH suffices for gametogenesis and the production of gonadal hormones. Sundararaj (1959, 1960) and Rizkalla and Yoakim (1975) arrived at similar conclusions for the Indian catfish and the Nile catfish, *Synodontis schall*, respectively. It is only during the breeding period, immediately preceding oocyte maturation and ovulation, that in female African catfish the pituitary shows a brief but considerable secretion of GTH (Resink et al., 1987c). At the end of the breeding period, the gonadotropic cells enter a period of gradual regression (Peute et al., 1986; Vam Oordt et al., 1987), but continue to secrete small amounts of GTH (Resink et al., 1987a). In laboratory-reared African catfish the GTH concentration is always low (De Leeuw et al., 1985a,b, 1986, 1987; Richter et al., 1987); sufficient for complete gametogenesis, including the formation of postvitellogenic oocytes, and the production of gonadal steroids, but not high enough for oocyte maturation and ovulation (Lambert and Van Den Hurk, 1982).

The results of the present experiments demonstrate that under conditions

of high water temperatures, adequate feeding, the presence of male conspecifics and different light regimes, the ovaries of *G. gariepinus* contain large quantities of normal postvitellogenic oocytes all the year round, especially when the animals have been reared in indoor hatcheries. It seems that the relatively low gonadotropic activity, necessary for the development and maintenance of ovaries filled with postvitellogenic oocytes, is not influenced by seasonal changes in daylength. The absence of spontaneous breeding in African catfish transferred from the Hula Nature Reserve to nearby fish ponds indicates that daylength is not the primary factor determining the prespawning GTH surge. Indeed, other environmental factors, such as a rise in the water level, leading to flooding of the shores of shallow lakes and pools in which African catfish live (Micha, 1974; Bruton, 1979; Van Den Hurk et al., 1986) seem to trigger a rise in GTH secretion by the pituitary. At the same time, sex pheromones may induce a GTH surge (Resink et al., 1987b).

Since a proper rise in water level is difficult to realize under husbandry conditions, and catfish sex pheromones are not yet available, the GTH surge, necessary for oocyte maturation and ovulation, has to be induced artificially. To that end GTH preparations can be administered, such as pituitary suspensions (Hogendoorn and Vismans, 1980; Richter and Van Den Hurk, 1982; Viveen et al., 1985) and human chorionic gonadotropin (HCG; Eding et al., 1982). As the pituitary of *C. gariepinus*, reared in the laboratory, contains large amounts of GTH (Peute et al., 1986), induction of the release of endogenous GTH by the administration of pimozide or other anti-dopamine drugs in combination with an analogue of luteinizing hormone-releasing hormone (LHRHa) can also be used to induce oocyte maturation and ovulation (De Leeuw et al., 1985a,b, 1987; Goos et al., 1987; Richter et al., 1987).

In conclusion, for culturing *C. gariepinus*, and especially for propagation throughout the year independent of the seasons, the broodfish should preferably be raised in a hatchery with high water temperatures (25°C or higher), in the presence of male conspecifics, and with ample feeding, in order to ensure a continuous production of viable eggs. The husbandry of broodfish and the methods used for artificial spawning are relatively simple (Viveen et al., 1985) and could be applied for increasing the production of *C. gariepinus* in Africa (Richter, 1976).

ACKNOWLEDGEMENTS

The experiments carried out in Israel formed part of the Dutch–Israeli *Clarias* Project, commissioned by The Netherlands Ministry for Development Cooperation to Prof. Dr. P.G.W.J. Van Oordt. The authors thank Mr. U. Rapaport, director of the Ginosar Intensive Fish Culture Station and Dr. M. Gophen, director of the Kinneret Limnological Laboratory, for their hospitality, and Mr. E. Glusman, director of the Hula Nature Reserve Authorities for providing

the possibility of collecting feral African catfish. Our thanks are also due to the Israeli members of the Project, Mrs. R. Pinkas, M.Sc., O. Netzer and M. Sternbach for assisting in collecting and looking after the animals and in the experimental work; as well as to Prof. Dr. E.A. Huisman, chairman of the Department of Fish Culture and Fisheries, Agricultural University of Wageningen, and to Dr. F. Meyndert, Netherlands Ministry of Development Cooperation, for their continuous interest in the project. Trouw International, Putten, The Netherlands, is acknowledged for compounding the pellets; Intervet International, Boxmeer, The Netherlands, for supplying the hormones.

REFERENCES

Babiker, M.M., 1984. Aspects of the biology of the catfish *Clarias lazera* (Cuv. & Val.) related to its economic cultivation. Hydrobiologica, 110: 295–304.

Bruton, M.N., 1979. The breeding biology and early development of *Clarias gariepinus* (Pisces; Clariidae) in Lake Sibaya, South Africa, with a review of breeding in species of the subgenus *Clarias* (*Clarias*). Trans. Zool. Soc. Lond., 35: 1–45.

De Leeuw, R., Goos, H.J.Th., Richter, C.J.J. and Eding, E.H., 1985a. Pimozide-LHRHa-induced breeding of the African catfish, *Clarias gariepinus* (Burchell). Aquaculture, 44: 295–302.

De Leeuw, R., Resink, J.W., Rooyakkers, E.J.M. and Goos, H.J.Th., 1985b. Pimozide modulates the luteinizing hormone-releasing hormone effect on gonadotrophin release in the African catfish, *Clarias lazera*. Gen. Comp. Endocrinol., 58: 120–127.

De Leeuw, R., Wurth, Y.A., Zandbergen, M.A., Peute, J. and Goos, H.J.Th., 1986. The effect of aromatizable androgens, non-aromatizable androgens, and estrogens on gonadotropin release in castrated African catfish, *Clarias gariepinus* (Burchell). Cell Tissue Res., 243: 587–594.

De Leeuw, R., Van Asselt, L.A.C., Goos, H.J.Th., Peute, J., Lambert, J.G.D. and Van Oordt, P.G.W.J., 1987. The regulation of gonadotropin release by neurohormones and gonadal steroids in the African catfish, *Clarias gariepinus* (Burchell). Aquaculture, 63: 43–58.

Eding, E.H., Janssen, J.A.L., Kleine Staarman, G.H.L. and Richter, C.J.J., 1982. Effects of human chorionic gonadotropin (HCG) on maturation and ovulation of oocytes in the catfish *Clarias lazera* (C. & V.). In: C.J.J. Richter and H.J.Th. Goos (Editors), Proc. Int. Symp. Reproductive Physiology of Fish, Wageningen, The Netherlands, 2–6 August 1982. PUDOC, Wageningen, p. 195.

Goos, H.J.Th., Joy, P.K., de Leeuw, R., Van Oordt, P.G.W.J., Van Delft, A.M.L. and Gielen, J.Th., 1987. The effect of luteinizing hormone releasing hormone analogue (LHRHa) in combination with different drugs with anti-dopamine and anti-serotonin properties on gonadotropin release and ovulation in the African catfish, *Clarias gariepinus*. Aquaculture, 63: 143–156.

Henken, A.M., Boon, J.B., Cattel, B.C. and Lobée, H.W.J., 1987. Differences in growth rate and feed utilization between male and female African catfish, *Clarias gariepinus* (Burchell 1822). Aquaculture, 63: 221–232.

Hogendoorn, H., 1980. Controlled propagation of the African catfish, *Clarias lazera* (C. & V.). III. Feeding and growth of fry. Aquaculture, 21: 233–241.

Hogendoorn, H., 1981. Controlled propagation of the African catfish, *Clarias lazera* (C. & V.). IV. Effect of feeding regime in fingerling culture. Aquaculture, 24: 123–131.

Hogendoorn, H. and Vismans, M.M., 1980. Controlled propagation of the African catfish, *Clarias lazera* (C. & V.). II. Artificial reproduction. Aquaculture, 21: 39–53.

Hogendoorn, H. and Wieme, R., 1975. Preliminary results concerning the culture of *Clarias lazera* in Cameroon. CIFA/75/SE10 (FAO/CIFA Symposium on Aquaculture in Africa).

Holl, E.A., 1966. Some notes on the breeding of the barbel *Clarias gariepinus* (Burchell) in Rhodesia. Newsl. Limnol. Soc. S. Africa, 7: 38–41.

Holl, E.A., 1968. Notes of spawning behaviour of the barbel *Clarias gariepinus* (Burchell) in Rhodesia. Zool. Afr., 3: 185–188.

Lambert, J.G.D. and Van Den Hurk, R., 1982. Steroidogenesis in the ovaries of the African catfish, *Clarias lazera*, before and after an HCG-induced ovulation. In: C.J.J. Richter and H.J.Th. Goos (Editors), Proc. Int. Symp. Reproductive Physiology of Fish, Wageningen, The Netherlands, 2–6 August 1982. PUDOC, Wageningen, pp. 99–102.

Lambert, J.G.D., Van Den Hurk, R., Schoonen, W.G.E.J., Resink, J.W. and Van Oordt, P.G.W.J., 1986. Gonadal steroidogenesis and the possible role of steroid glucuronides as sex pheromones in two species of teleosts. Fish Physiol. Biochem., 2: 101–107.

Micha, J.C., 1974. Fish populations study of Ubangui River: trying local wild species for fish culture. Aquaculture, 4: 85–87.

Micha, J.C., 1975. Synthèse des essais de reproduction, d'alevinage et de production chez un silure Africain: *Clarias lazera*. CIFA/75/SE5 (FAO/CIFA Symposium on Aquaculture in Africa), p. 23.

Nie, N.N., Hull, C.H, Jenkins, J.G., Steinbrenner, K. and Bent, D.H., 1975. Statistical Package for the Social Sciences, 2nd edn. McGraw Hill, New York, NY, 675 pp.

Peute, J., Zandbergen, M.A., Goos, H.J.Th., De Leeuw, R., Pinkas, R., Viveen, W.J.A.R. and Van Oordt, P.G.W.J. 1986. Pituitary gonadotropin contents and ultrastructure of the gonadotrops in the African catfish, *Clarias gariepinus*, during the annual cycle in a natural habitat. Can. J. Zool., 64: 1718–1726.

Resink, J.W., Schoonen, W.G.E.J., Van Den Hurk, R., Viveen, W.J.A.R. and Lambert, J.G.D., 1987a. Seasonal changes in steroid metabolism in the male reproductive organ-system of the African catfish, *Clarias gariepinus*. Aquaculture, 63: 59–76.

Resink, J.W., Van Den Hurk, R. and Groeninx-Van Zoelen, R.F.O., 1987b. The seminal vesicle as source of sex attracting substances in the African catfish, *Clarias gariepinus*. Aquaculture, 63: 115–127.

Resink, J.W., Van Den Hurk, R., Voorthuis, P.K., Terlou, M., De Leeuw, R. and Viveen, W.J.A.R., 1987c. Quantitative enzyme histochemistry of steroid and glucuronide synthesis in testes and seminal vesicle, and its correlation to plasma gonadotropin level in *Clarias gariepinus*. Aquaculure, 63: 97–114.

Richter, C.J.J., 1976. The African catfish, *Clarias lazera* (C. & V.), a new possibility for fish culture in tropical regions? In: E.A. Huisman (Editor), Aspects of Fish Culture and Fish Breeding. Misc. Pap. 13, Agricultural University, Wageningen, pp. 51–71.

Richter, C.J.J. and Van Den Hurk, R., 1982. Effects of 11-desoxycorticosterone-acetate and carp pituitary suspension on follicle maturation in the ovaries of the African catfish, *Clarias lazera* (C. & V.). Aquaculture, 29: 53–66.

Richter, C.J.J., Eding, E.H., Goos, H.J.Th., De Leeuw, R., Scott, A.P. and Van Oordt, P.G.W.J., 1987. The effect of pimozide-LHRHa and 17α-hydroxyprogesterone on plasma steroid levels and ovulation in the African catfish, *Clarias gariepinus*. Aquaculture, 63: 157–168.

Rizkalla, W. and Yoakim, E., 1975. Seasonal changes in the pituitary gland of the Nile catfish. *Synodontis schall* (Block-Schneider). Libyan J. Sci., 5: 15–29.

Schoonen, W.G.E.J. and Lambert, J.G.D., 1986a. Steroid metabolism in the testes of the African catfish, *Clarias gariepinus* (Burchell), during the spawning season, under natural conditions and kept in ponds. Gen. Comp. Endocrinol., 61: 40–52.

Schoonen, W.G.E.J. and Lambert, J.G.D., 1986b. Steroid metabolism in the seminal vesicles of the African catfish, *Clarias gariepinus* (Burchell), during the spawning season, under natural conditions and kept in ponds. Gen. Comp. Endocrinol., 61: 355–367.

Schoonen, W.G.E.J., Granneman, J.C.M., Lambert, J.G.D. and Van Oordt, P.G.W.J., 1987a. Ste-

roidogenesis in the testes and seminal vesicles of spawning and non-spawning African catfish, *Clarias gariepinus*. Aquaculture, 63: 77–88.

Schoonen, W.G.E.J., Granneman, J.C.M., Lambert, J.G.D., Viveen, W.J.A.R. and Van Oordt, P.G.W.J., 1987b. A quantitative study of steroid bioconversions in the seminal vesicles of the African catfish, *Clarias gariepinus* (Burchell), under natural spawning and non-spawning conditions and under fish farm conditions. Comp. Biochem. Physiol., in press.

Schoonen, W.G.E.J., Lambert, J.G.D., Resink, J.W., Viveen, W.J.A.R. and Van Oordt, P.G.W.J., 1987c. A quantitative study of steroid bioconversions in the testes of the African catfish, *Clarias gariepinus* (Burchell), under natural spawning and natural and cultural non-spawning conditions. J. Endocrinol., 112: in press.

Sundararaj, B.I., 1959. A study on the correlation between the structure of the pituitary gland of the Indian catfish *Heteropneustes* and the seasonal changes in the ovary. Acta Anat., 37: 47–80.

Sundararaj, B.I., 1960. Correlation between the structure of the pituitary and the changes in the testes of the Indian catfish *Heteropneustes*, Acta Anat., 40: 305–322.

Sundararaj, B.I. and Sehgal, A., 1970. Short and long-term effects of imposition of total darkness on the annual ovarian cycle of the catfish *Heteropneustes fossilis* (Bloch). J. Interdiscipl. Cycle Res., 1: 291–301.

Sundararaj. B.I. and Vasal, S., 1976. Photoperiod and temperature control in the regulation of reproduction in the female catfish, *Heteropneustes fossilis*. J. Fish. Res. Board Can., 33: 959–973.

Teugels, G.G., 1984. The nomenclature of African *Clarias* species used in aquaculture. Aquaculture, 38: 373–374.

Thomas, J.D., 1966. On the biology of the catfish, *Clarias senegalis*, in a man-made lake in the Ghanaian savanna with particular reference to its feeding habits. J. Zool. Lond., 148: 476–514.

Van Den Hurk, R., Viveen, W.J.A.R., Pinkas, R. and Van Oordt, P.G.W.J., 1986. The natural gonadal cycle in the African catfish, *Clarias gariepinus*; a basis for applied studies on its reproduction in fish farms. Isr. J. Zool., in press.

Van Oordt, P.G.W.J., Peute, J., Van Den Hurk, R. and Viveen, W.J.A.R., 1987. Annual correlative changes in gonads and pituitary gonadotropes of feral African catfish, *Clarias gariepinus*. Aquaculture, 63: 27–41.

Viveen, W.J.A.R., Richter, C.J.J., Van Oordt, P.G.W.J., Janssen, J.A.L. and Huisman, E.A., 1985. Pratical manual for the culture of the Afrian catfish (*Clarias gariepinus*). The Netherlands Ministry for Development Cooperation, Section for Research and Technology, P.O. Box 20061, 2500 EB The Hague, The Netherlands, 128 pp.

Willoughy, N.G. and Tweddle, D., 1976. The ecology of the catfish, *Clarias gariepinus* and *Clarias ngamensis*, in the Shire Valley, Malawi. J. Zool. Lond., 186: 507–514.