Mouthbrooding Efficiency and Spawning Frequency of *Sarotherodon melanotheron* (Rüppel, 1852) in Culture Environments (Ebrié Lagoon, Côte d'Ivoire)

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Abstract

In *Sarotherodon melanotheron*, mouthbrooding efficiency and spawning frequency are two important parameters to consider in the practical management of broodfish reared in captivity. In this species, where males practice mouthbrooding, the number of eggs or fry incubated is positively correlated to male body weight (study made on a population reared in lagoon pens). Mouthbrooding efficiency is discussed in relation to female fecundity, the capacity of the males' mouth, the development stage of the incubated fry and the size ratio between males and females during pairing.

Individual spawning frequency was studied in concrete tanks with isolated pairs and families of different sex ratios. While sex ratios shifted toward the males do not increase spawning frequency significantly, sex ratios shifted toward the females decrease it considerably. The most suitable sex ratio for the production of fry of *S. melanotheron* in captivity is 1:1. Using this sex ratio, mean individual spawning intervals are generally 10-16 days. Annual egg production of this species is estimated, based on long periods of observation (174-587 days) using isolated pairs.

Introduction

Contrary to what has been observed for most cultured fish species, tilapias reproduce spontaneously and rapidly in captivity. Improved reproduction management and planning of fry production for fish culture rely on the assessment of egg production of each species. In sexually mature fish, egg production is measured using the number of fry produced per spawning episode and the spawning intervals.

In mouthbrooders (genera *Oreochromis* and *Sarotherodon*), the number of fry produced in each spawning depends, in turn, on two elements, namely, female fecundity and successful mouthbrooding (Welcomme 1967; Marshall 1979). The latter point is very important when mouthbrooding is practiced by the male as is the case in *Sarotherodon melanotheron*. Here, the mouth capacity can be a limiting factor for the incorporation of the brood in the mouth and for the development of the offspring after hatching (Aronson 1949).

In the present study, efficiency of mouthbrooding was studied in *S. melanotheron* in relation to the fecundity of females, the mouth capacity of the males, the stage

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of development of the incubated fry and the size ratio between males and females during pairing. Spawning frequency was observed in concrete tanks using isolated pairs of fish and families of different sex ratios. Based on these observations, the annual egg production of *S. melanotheron* was estimated.

In this species, contrary to other mouthbrooding tilapias, protective parental behavior is abruptly interrupted upon release of the swim-up fry, which then becomes totally independent (Aronson 1949; Lowe-McConnell 1955).

Materials and Methods

The study was conducted at the Layo experimental fish culture station, 40 km west of Abidjan, in an oligomesohaline part of Ebrié Lagoon (Côte d'Ivoire). In Layo, seasonal salinity ranges between 0 and 10 ppt with a mean monthly water temperature of 27-32°C and pH values ranging between 6.5 and 7.5.

Mouthbrooding

Female fecundity and the number of eggs or fry incubated by the males were studied in a population of *S. melanotheron* of different sizes reared in a 625-m^2 lagoon pen with an initial stocking density of 5 individuals·m^{-2}. The fish were fed with pelleted feed containing 31% crude proteins, distributed at a daily rate of 5% of fish biomass.

Fish fecundity was studied as described in Legendre and Ecoutin (this vol.). Male brooders (n=127), identified underwater—using diving equipment—by the characteristic deformation of their mouth, were captured individually with a handnet and immediately placed in a basin where the offspring was generally spat out right away.

These males were killed soon afterwards, weighed to the nearest 1 g and dissected to count the number of fry swallowed during capture. In some, the mouth capacity was determined by filling the mouth with a silicone paste using a method similar to that described by Drenner (1972). The dry casts were then removed and cleaned while their volume was measured by the displacement of water in a graded test tube.

Eggs and fry were preserved in 4% formalin and counted individually. Six arbitrary stages, visible to the naked eye, were considered to characterize the development stage of each clutch (Table 1). The mean volume of eggs or fry was determined using batches of 50 individuals in a graded test tube and the total volume of the clutch was estimated using the product: number of eggs or fry incubated x mean volume of the fry.

Spawning Frequency

ISOLATED PAIRS

Spawning frequency or the time interval between two successive spawning episodes was first studied in four pairs of fish placed in four different concrete tanks (4 m^2; water depth = 0.5 m) using lagoon water. These pairs, composed of broodfish of different sizes (120-270 g) and given feed containing 31% crude proteins at a daily rate of 3% of the fish biomass, were observed over a period of 174-587 days. Each week, the tanks were drained and spawnings were recorded. Eggs or swim-up fry were removed from the mouth of the males and counted individually. The actual spawning date was estimated based on the development stage of the offspring collected. In all cases, the offspring were removed from the tanks.

FAMILIES OF BROODFISH

In a second experiment conducted in similar conditions over a period of 76 days,

Table 1. Definition of arbitrary stages used for the characterization of ontogenic development of eggs and fry incubated by the males of *Sarotherodon melanotheron*, details of with the mean age, size and volume of eggs and fry: figure in parentheses are ranges of mean values.

Stage	Description	Age (days)[a]	Size (mm)[b]	Volume (ml)
1	From fertilization to formation of melanophores	0-2	3.4 (3.3-3.5)	17.4 (13.9-21.3)
2	From first melanophores to pigmentation of the eyes	2-4	3.3 (3.2-3.4)	
3	From pigmentation of the eyes to hatching	4-6	3.5 (3.1-3.7)	
4	From hatching to first phase of yolksac absorption	-	7.5 (5.5-8.8)	18.4 (15.2-22.7)
5	Second phase of yolksac absorption	-	10.1 (9.0-10.8)	22.7 (18.8-25.0)
6	Swim-up stage	14-15	11.4 (10.7-13.0)	26.0 (19.5-40.5)

[a]Age post-fertilization; based on Shaw and Aronson (1954) and Shaw (1956).
[b]Mean diameters for eggs; total length for fry.

spawning frequency was compared in families composed of 10 individuals of similar weight (200-230 g) with different sex ratios (F:M): 5:5; 9:1; and 1:9 (two replicates per treatment). Two additional pairs were placed in two concrete tanks and observed during the same period. Each week, all tanks were drained and the fish with eggs in their mouth were counted. Several times during draining, some fish spat out the eggs which were immediately cannibalized by the other fish in the tank. Because of this, the number of eggs produced by the families could not be determined. This problem did not occur with the isolated pairs as capture was easier and faster. At the end of the experiment, all individuals were killed for macroscopic examination of the gonads.

Results and Discussion

Mouthbrooding Efficiency

Of the 127 males sampled from the pen population, 30% swallowed part of their brood during capture. This indicates that the stomach of the fish should be routinely examined to obtain an accurate estimate of the number of incubated eggs or fry. One male swallowed nearly half of its brood (207 newly hatched individuals). However, in most cases, the number of eggs found in the stomachs did not exceed 5% of the total offspring.

A positive linear relationship (r = 0.793) was found between the number of incubated eggs or fry and the weight of the male brooders (Fig. 1). Covariance analysis was used to compare the regression lines between incubated stock and weight of the males, on the one hand, and fecundity and weight of the females, on the other hand. No difference was found between slopes; in contrast, the Y intercepts differed significantly. The two regression lines can therefore be considered parallel (Fig. 1). This result suggests a preferential size ratio between males and females during pairing, this size ratio being close to parity. The high increase in the number of incubated eggs with male weight shows that the largest males do

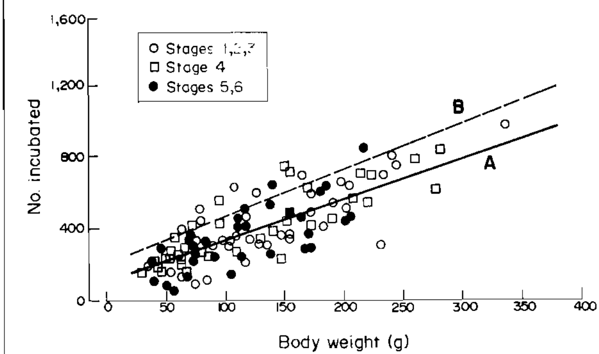

Fig. 1. (A) Relationship between number of eggs or fry incubated (N) and body weight of males (Wm) in *Sarotherodon melanotheron* reared in pens; N = 2.29 Wm + 107.15 (r = 0.793). The development stage of the clutch is indicated for each individual. (B) Relationship between fecundity (F) and body weight of females (Wf) in *S. melanotheron* reared in pens; F = 2.61 Wf + 203.91 (r = 0.777).

not mate spontaneously with the smallest females.

When the incubated stocks are examined with regard to their development stage (see Table 1), the scattergrams appear to be similar for eggs and for swim-up fry (Fig. 1), suggesting a very limited loss in eggs and fry during incubation. This was confirmed by estimating, for each individual, the ratio (R) between actual incubated stock and stock estimated by the general model describing the increase in average size of clutch with male weight (Fig. 1): R = observed stock/(2.29 Wm + 107.15). Results showed that "R" remains close to 1 (Table 2) regardless of the development stage of eggs and fry. This confirms that embryonic mortality is very low during the mouthbrooding period in *S. melanotheron*.

In *Oreochromis leucostictus*, where the females incubate the eggs, Welcomme (1967) defined mouthbrooding efficiency as the ratio of incubated stock (fertility) and number of eggs initially produced (fecundity).

In *S. melanotheron*, as incubation is practiced by the male, the estimation of mouthbrooding efficiency must be based on hypothetical size ratios between males and females during pairing. Since we have already observed that the preferential size ratio is close to parity, three hypothetical ratios were considered: (1) males and females of equal body weight; (2) males with a body weight 25% higher than that of the females; and (3) males with body weight 25% lower than that of the females.

In case no. 1 (equal weights), mouthbrooding efficiency is minimal (60%) when the male is small (25 g). Efficiency gradually increases with male weights of about 150 g, but does not exceed 80% in males of 400 g (Fig. 2).

When the male is slightly larger than the female (case no. 2), mouthbrooding efficiency improves significantly, reaching a value of 100% for males with body weight > 300 g. In contrast, when male weight is lower than female weight (case no. 3), mouthbrooding efficiency decreases significantly, never exceeding 65% (Fig. 2).

In *S. melanotheron*, mouthbrooding efficiency is similar to that observed in *Oreochromis macrochir* (60-100% depending on female sizes; Marshall 1979) and significantly higher than that reported for *O. leucostictus* (where it is never > 50%; Welcomme 1967). It should, however, be noted that both studies were conducted on mouthbrooding females captured in the wild with a seine net, and that the eggs and the fry that may have been

Table 2. Values of "R" (observed incubated stock/ estimated incubated stock [see text]) in relation to the development stage of eggs and fry incubated.

Development stage	R	No. of clutches observed
1	0.99	16
2	1.01	15
3	1.01	18
4	1.06	38
5	0.87	11
6	0.98	26

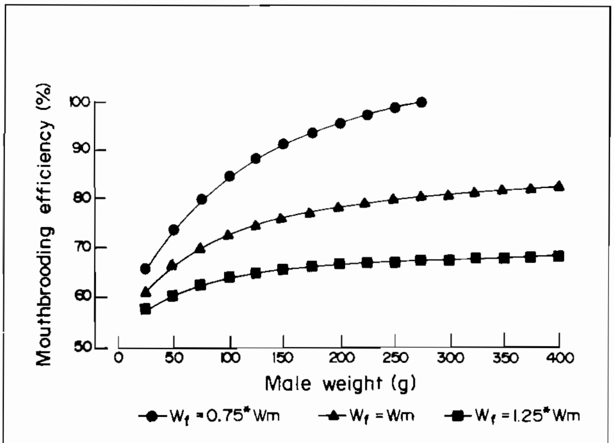

Fig. 2. Mouthbrooding efficiency in *S. melanotheron* based on different hypothetical ratios between the weight of males (Wm) and the weight of females (Wf) during pairing.

swallowed were not counted. Therefore, it is possible that the broods incubated by these species were underestimated.

In *S. melanotheron*, mouth capacity is related to male weight by a positive linear relationship ($r = 0.927$; Fig. 3). The comparison of this relationship with the increase in mean volume of eggs produced in relation to female weight (Fig. 3) shows that mouth capacity increases faster with male weight than the spawn volume increases with female weight. The spawn volume of females with body weight < 100 g does not differ noticeably from the mouth capacity of males of similar weight. The mean buccal volume of males with body weight < 50 g is too small to allow the complete development of the average clutch produced by a female of similar weight. Only males with body weight > 150 g have a buccal volume always higher than the mean clutch volume at the end of its development (Fig. 3). Therefore, when pairing is between males and females of equal weight, mouth capacity constitutes a limiting factor for mouthbrooding only in males of body weight < 150 g.

The percentage of the male mouth capacity occupied by the clutch (clutch volume x 100/mouth capacity) was determined for 30 male brooders of different sizes (Fig. 4). This proportion is higher (about 40-90%) in males of body weight < 150 g than in larger males, in which it never exceeds 60%. These observations provide a reasonable explanation of the fact that mouthbrooding is less efficient in males with body weight < 150 g than in males with higher body weight (Fig. 2). These observations also tend to confirm that, in a population of individuals of different sizes, pairing preferentially takes place between males and females of similar size. As mentioned previously (Fig. 1), the largest males do not mate spontaneously with the smallest females. The fact that the proportion of the mouth occupied by the clutch does not exceed 60% in males with body weight > 150 g (Fig. 4) confirms that males neither mate spontaneously with females that are much bigger than they are.

In the wild (Ebrié Lagoon), where the size at first sexual maturity is higher than in culture conditions (Legendre and Ecoutin, this vol.), mouthbrooding efficiency is likely to be higher. The fork length of the smallest mature male observed in the lagoon environment reached 148 mm (80 g) against 105 mm (22 g) in pen culture. Because of the limited mouth capacity of the small males, the stunting (or sexual precocity) observed in culture conditions should result in lower yields of fry per single spawn.

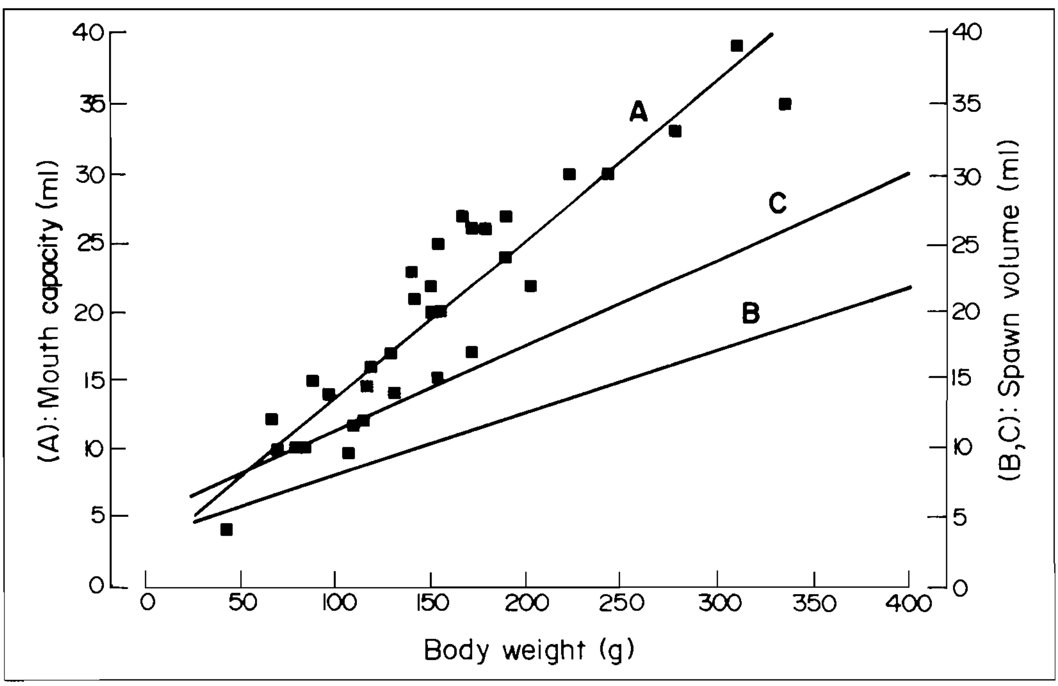

Fig. 3. (A) Relationship between the mouth capacity (Vm) and the body weight of males (Wm) in *Sarotherodon melanotheron*. Vm = 0.114 Wm + 2.21 (r = 0.927). (B) Eggs: mean increase in spawn volume with weight of female. Spawn volume = fecundity x mean volume of one egg (17.4 µl). (C) Swim-up fry: mean increase in spawn volume with weight of female. Spawn volume = fecundity x mean volume of one fry (26.0 µl). In B and C, fecundity is estimated by the relationship F = 2.61 Wf + 203.91, where Wf = female body weight (Fig. 1).

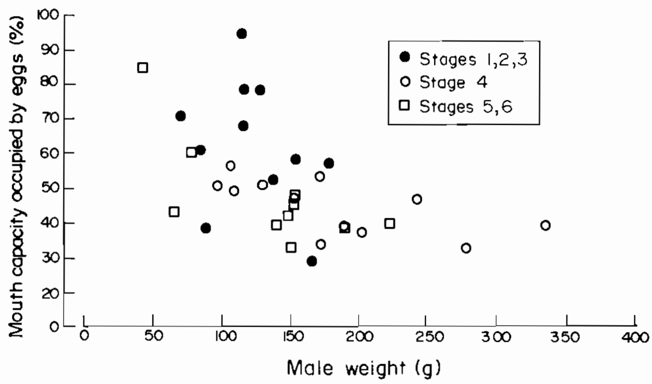

Fig. 4. Percentage of the mouth capacity occupied by eggs or fry incubated in relation to male body weight in *S. melanotheron*. The development stage of the clutch is indicated for each individual.

Spawning Frequency and Number of Eggs Collected

In isolated pairs, the mean spawning interval is generally 10-16 days (Tables 3 and 4). Only one pair composed of a large female and a small male showed higher mean intervals (25 days; Table 3). For all pairs combined, 6 and 39 days were the extreme values in the range. Therefore, the spawning frequency of *S. melanotheron* reared in 2-m^3 tanks is very regular compared to the values observed in other species of tilapias such as *O. niloticus* or *O. vulcani* (Mires 1982). Aronson (1945) reported that the spawning intervals of *S. melanotheron* reared in aquarium varied between 8 days and one year with a mode of 15 days, the latter value being in agreement with our observations.

The routine counting of clutches from each pair of the experiment showed that compared to the number of eggs or fry produced at longer spawning intervals, shorter cycles (six to eight days) never imply a significant reduction in eggs or fry production, therefore reflecting a faster vitellogenesis which involves total spawn rather than partial spawning occurrence. In general, the mean spawning interval is shorter in *S. melanotheron* (two weeks approximately) than in the species of *Oreochromis* (generally, four to six weeks; Baroiller and Jalabert 1989). In *Oreochromis*, it is established that the presence of eggs or fry in the mouth of the females has an inhibiting effect on the development of oocytes (Smith and Haley 1988). In *O. niloticus*, the frequent removal of incubating eggs is one of the methods used to increase spawning frequency and fry production (Verdegem and McGinty 1987).

The average number of eggs collected per spawning episode for the different pairs observed varied between 368 and 718 (Table 3). This quantity is closely related to the size of the males used in this experiment and does not seem to be much affected by female fecundity. Indeed, the relationship (Fig. 1) between the incubated stock and the weight of males appears highly suitable for use as a model for estimating the production of eggs by the broodfish of *S. melanotheron* reared in culture conditions (Table 3). When the weight of the males (about 200 g) is higher than the weight of females (about 150 g), the annual production of eggs for a pair

Table 3. Spawning frequency and number of eggs collected in isolated pairs of *S. melanotheron* in concrete tanks. Comparison between observed and estimated productions of eggs.

Pair no.	Observation period (day)	Mean body weight of broodfish (g)		No. of spawns observed	Mean spawning interval (day)	Total number of eggs collected	Number of eggs collected per year	Average number of eggs per spawn	Estimate of egg no.	
		Female	Male						incubated per male[a]	produced per female[b]
1	587	172	194	43	14.0±1.7	24,754	15,392	576	551	653
2	475	164	130	31	15.8±3.5	15,473	11,889	499	405	632
3	398	152	269	34	12.1±0.9	24,425	22,400	718	723	601
4	174	243	118	8	24.8±7.5	2,942	6,171	368	377	838

[a]Average number estimated using the relation between the number of eggs or fry incubated (N) and the weight of males (Wm): N=2.29 Wm + 107.15 (r=0.793).

[b]Average number estimated using the relation between fecundity (F) and weight of females (Wf): F=2.61 Wf + 203.91 (r=0.777).

Table 4. Spawning frequency in *S. melanotheron* for families of different sex ratios over a period of 76 days in concrete tanks. Values are the means of two replicates.

Composition of the families (No. females/no. males)	Average no. of spawns observed	Mean no. of spawns per female	Mean spawning interval (day)
1/1	6	6[a]	13.1[a]
5/5	29	5.8[a]	13.2[a]
1/9	7.5	7.5[a]	10.6[a]
9/1	14	1.6[b]	49.5[b]

Values with the same letter in a same column are not significantly different at the 5% significance level.

varies between 15,000 and 23,000 (Table 3). However, it should be noted that in the same culture conditions, the spawning frequency of *S. melanotheron* is higher in the dry season (two to three spawns per month) than during the rainy season (1.5 spawns per month; Legendre and Ecoutin 1989).

In 2-m^3 tanks, the spawning frequency per female in an isolated pair or in a family of 10 broodfish with equal sex ratios is identical (Table 4). Annual production of eggs in such a family can be directly estimated using the model linking the number of eggs or fry incubated to male weights. When the sex ratio is strongly in favor of males (9:1), the mean spawning interval, although slightly lower, does not differ significantly from that observed in families with equal sex ratios (Table 4). In contrast, when the sex ratio is in favor of the females (1:9), the spawning interval is considerably increased (50 days on average). The macroscopic examination of the gonads of these females at the end of the experiment showed that in 25% of the cases, post-vitellogenesis oocytes present in the ovaries showed high levels of atresia. This suggests that females are capable of completing normal cycles of vitellogenesis, but that lack of males in sufficient number regularly causes the total reabsorption of the oocytes ready for spawning. It is also possible that in this particular situation, the spawning frequency was underestimated: 29% of the observed incubations were done by females (with nonfertilized eggs); however, females have a strong tendency to swallow the eggs that they incubate (Aronson 1949).

Taken together, these results indicate that the most suitable sex ratio for the production of eggs and fry in *S. melanotheron* reared in captivity is 1:1. A higher male sex ratio does not significantly increase individual spawning frequency while a higher female sex ratio decreases it considerably.

From a practical point of view, the abovementioned problem of cannibalism on eggs and fry spat out by the mouthbrooders during draining indicates that this particular system, with weekly collection of the offspring, is poorly adapted for the efficient management of broodfish. In the future, this problem should be solved by maintaining fish in hapa-like structures which are easier to handle (Hugues and Behrends 1983) and allow rapid and simultaneous capture of all broodfish.

Conclusion

In *S. melanotheron*, mouthbrooding efficiency is reduced in males with body weight < 150 g compared to larger individuals. Smaller males have a limited mouth capacity which can hardly take in all the eggs produced by the smallest females. Due to this physical constraint, mouthbrooding efficiency is significantly improved when a female mates with a larger male. Egg and fry mortalities appear to be low during the mouthbrooding phase. When creating broodfish families, it is recommended not to use males with body weight < 150 g and to always choose males larger than females.

In captive *S. melanotheron*, spawning intervals are about two weeks. The most suitable sex ratio for the constitution of families of broodfish for egg and fry production in culture conditions is 1:1. Observations on egg production by isolated pairs over a long period of time indicate that the relationship between the number of eggs and fry incubated, and the weight of the males can be used to predict and plan the production of fry in a fish farm.

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