

EFFECTS OF AGE AND STOCKING DENSITY ON SPAWNING PERFORMANCE OF NILE TILPIA, *OREOCHROMIS NILOTICUS* (L.) BROODSTOCK REARED IN HAPAS

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Abstract

This experiment was undertaken to investigate the effects of age and stocking density on spawning performance and growth rates of Nile tilapia *Oreochromis niloticus* (L.) broodstock reared in hapas. In a 2×3 factorial design, two different broodstock ages (1-year old and 3-years old) were combined with three different broodstock densities (4, 8 and 12 fish/ m² for lower, intermediate and higher broodstock stocking density, respectively) to obtain 6 experimental treatments. Brood-fish were stocked at a sex ratio of three females to one male (3♀ :1♂). Nile tilapia broodstock age and stocking density significantly (P≤0.05) affected the natural spawning performance. Regardless of broodstock age, the lower stocking density had the highest seed/ female (1213± 184.14 seeds), seed/ g female (6.93± 1.28 seeds) and seed/ day (10.99± 1.53 seeds) followed by intermediate density (1036.25± 129.35 seeds/ female, 6.08± 1.30 seeds/g female and 9.54± 1.21 seeds/ day) and higher density (745.40± 125.75 seeds/ female, 4.33± 0.80 seeds/ g female, 6.93± 1.23 seeds/ day), respectively. Irrespective of broodstock stocking density, the broodstock age significantly (P≤0.05) influenced the female fecundity in terms of seed/ female and seed/ day. The 3-Years old female broodstock had a higher absolute fecundity than 1-years old female tilapia broodstock. At high densities, there is a competition for space which increases social interaction and in turn, causes social stress and possibly thereby affecting reproductive efficiency. The best growth performance and feed utilization was found in fry group spawned by older broodstock group (3- years old broodstock), held at the lowest (4 (3♀ :1♂) fish/ m².) stocking density. The present study suggests that older broodstock (3-years old) at low stocking density 4 (3♀ :1♂) fish/ m² should be used during the propagation season in hatcheries.

Keywords: Nile tilapia, broodstock age, stocking density, reproductive performance, larval quality.

INTRODUCTION

Tilapia is an ideal candidate for warm-water aquaculture. They spawn easily in captivity, use a wide variety of natural foods as well as formulated feeds, tolerate poor water quality, and grow rapidly at warm temperatures. These attributes, along with relatively low input costs, have made tilapia the most widely cultured freshwater fish in tropical and subtropical countries (Biswas *et al.*, 2005; Fasakin *et al.*, 2005, El-Saidy

and Gaber 2005; Peña-Mendoza *et al.* 2005 Borgeson *et al.*, 2006; Tsadik and Bar, 2007 and Tahoun, 2007). For fish culture activities in Egypt as in many parts of the world, the necessity of dependable supply of Nile tilapia, *Oreochromis niloticus* (L.), fry is therefore imperative, but the problem of mass production is still remains. There are many possible reasons for the low production of tilapia fry. These include too low density of broodstock, inappropriate sex ratios, inadequate spawning techniques, broodstock nutrition and high fry mortality (Salama, 1996). Poor broodstock productivity, owing to low fecundity and asynchronous spawning cycles, remains one of the most significant outstanding constraints upon commercial tilapia production and its future expansion. Reproductive success in many fish species has been shown to be influenced by, among other factors, the broodstock, sex ratio, stocking density, age, size, nutrition and feeding regime (Ridha and Cruz, 1989; Smith *et al.*, 1991; Salama, 1996; Izquierdo *et al.*, 2001; Chong *et al.* 2004; Tahoun, 2007; Hammouda *et al.*, 2008 and Ibrahim *et al.* 2008). Broodstock productivity clearly represents the most significant constraint on commercial tilapia production. Increased knowledge of the factors regulating broodstock productivity is therefore of great importance to the further development of tilapia culture (Coward and Bromage, 2000). Maximizing seed productivity in hatcheries is the ultimate aim of broodstock management. Traditional tilapia seed production systems suffer from productivity problems that are associated with tilapia's unique reproductive traits such as early maturity, high frequency spawning, low fecundity and high investment in parental care. Improvements in our understanding of the appropriate culture conditions and management procedure for the brood-fish are essential if we are programming reproductive development to produce reliably the numbers of eggs and fry required by grow-out farms. The aim of the present work therefore was to investigate the effects of broodstock age and stocking density on the reproductive performance of Nile tilapia broodstock and to see whether this identifies possible broodstock management strategies that may be adopted by hatcheries to improve seed production.

MATERIALS AND METHODS

Experimental design

In a 2×3 factorial design, two different Nile tilapia broodstock ages (1-year old and 3-years old) were combined with three different broodstock densities (4, 8 and 12 fish/m²) to obtain 6 experimental treatments. Duplicate groups of brood-fish were stocked in spawning hapas at a ratio of three females to one male (1♀ : 3♂). The experimental design is shown in Table 1.

Table 1. The experimental design and treatments combinations.

Symbol	Broodstock age	Broodstock density
T 1	1-Year old	4 (1♂: 3♀) fish / m ² .
T 2	1-Year old	8 (2♂: 6♀) fish / m ² .
T 3	1-Year old	12 (3♂: 9♀) fish / m ² .
T 4	3-Years old	4 (1♂: 3♀) fish / m ² .
T 5	3-Years old	8 (2♂: 6♀) fish / m ² .
T 6	3-Years old	12 (3♂: 9♀) fish / m ² .

Experimental fish

Over-wintered male and female Nile tilapia *O. niloticus* broodstock were obtained from two commercial fish farms located in both Ismailia and Kafr El-Sheikh Governorates, respectively. Broodstock were netted from earthen ponds, manually selected, sexed and transferred to conditioning hapas (each measuring 6X3X1 m³), and kept separately for 25 days for adaptation to the new environment. Prior to The beginning of the experiment. The broodstock were stocked at a sex ratio of 3 females to 1 male. The average initial weights of the two ages were: 80 g for female and 77.3 g for the 1-year old fish and 307 and 273 g for female and mal, respectively, for the 3-year old fish. A total number of 36 females and 14 males were counted, batch weight and stocked in each hapa at a rate of 4 (3♀:1♂), 8 (6♀:2♂) and 12 (9♀:3♂) fish/ m². At the beginning of experiment, random samples of approximately 10 females and 10 males from each age class were taken, individually weighed and immediately killed and kept frozen at 18 °C until proximate analysis at the end of experiment (lasted for 108 days). Broodstock were fed a diet containing 40 % CP and 3752 Kcal ME/ Kg with a protein to energy ratio of 106 mg protein/ Kcal ME. Broodstock were fed the experimental diet at a feeding rate of 3 % of total biomass in each experimental hapa (six days/ week). Feed was introduced at 9.00 am and 4 pm with amounts adjusted at a bout 15–20 days according to new weights.

Proximate Analytical

At the end of the experiment all broodstock in each hapa were netted, weighed and finally frozen for final body composition analysis. Representative samples of the experimental fish were randomly taken at the beginning and at the end of the experiments. A sample of the experimental fish diet was taken, ground and stored in a deep freezer at -18oC until proximate analysis. All of chemical analyses of diets were determined according to A.O.A.C. (1990).

Growth performance parameters

The growth performance parameters were calculated according to the following equations:-

$$\text{Average Weight Gain (AWG)} = \text{Average final weight (g)} - \text{Average initial weight (g)}$$

Average Daily Gain (ADG) = [Average final weight (g) – Average initial weight (g)] / time (days).

Specific Growth Rate (SGR %/day) = 100 [Ln Wt1 – Ln Wt 0 / T]

Where: - Ln: normal log Wt 0: initial weight (g).

Wt 1: final weight (g) T: time of days.

Feed and protein utilization parameters

Feed and protein utilization parameters were calculated according to the following equations:

Feed Conversion Ratio (FCR) = Total feed consumption/ weight gain.

Protein efficiency ratio (PER) = body weight gain (g)/ protein intake (g).

Protein production value (PPV, %) = 100 [Retained protein (g)/ protein intake].

Energy utilization (EU, %) = 100 [Retained energy (Kcal)]/ energy intake (Kcal).

Spawning performance and seed output

The following reproductive parameters were determined according to Mair *et al.* (2004):

-Absolute fecundity: - the number of seeds per spawning per female.

-Relative fecundity: - the number of seeds per unit weight of female.

-Spawning frequency: - number of spawnings per female throughout the experiment.

Statistical analysis

Statistical analysis of each experiment was done using SAS Version 9 (SAS Institute, 2002) statistical package. Data were statistically analysed in a factorial design procedure. Mean of treatments were compared by Duncan (1955) multiple range test.

RESULTS AND DISCUSSION

Seed production

There were evidences that both Nile tilapia broodstock age and stocking density significantly ($P \leq 0.05$) affected the natural spawning success in mature broodstock in hapa-in-pond hatchery system (Table 2). The results on seed production under the condition of the present work are in accordance with those of Ridha and Cruz (1999) who indicated that, seed production of Nile tilapia reared in re-circulating tank hatchery system was not different from those reported by other worker used aquaria, ponds, hapas and pools. Thus, the present results reconfirmed the earlier results that increasing the broodstock stocking density above 4 fish/ m² led to a reduction in seed production. The use of low stocking densities would maximize production of seeds of the hatchery and lead to efficient utilization of the limited hatchery space.

Table 2. Effect of Nile tilapia broodstock age and stocking density on seed production.

Treatments		Female AIW	Female AFW	Mean weight	Total seed	Seed/ Fish	Seed/ g fish	Seed/ day/m ²
Fish age (year)	Stocking density							
1	4	78.5 b ±0.50	119.0 b ±1.00	98.75 b ±0.25	, c ± ,	, a ± ,	, a ± ,	, c ± ,
1	8	76.5 b ±2.50	121.5 b ±3.50	99.00 b ±0.50	, b ± ,	, a ± ,	, a ± ,	, c d ± ,
1	12	77.0 b ±1.00	112.0b ±2.00	94.50 b ±0.50	, b ± ,	, b ± ,	, b ± ,	, d ± ,
3	4	305.5 a ±0.50	341.0a ± 3.00	323.25a ±1.25 0	, b ± ,	, bc ± ,	, bc ± ,	, a ± ,
3	8	309.0 a ±2.00	345.5 a ±4.50	327.25 a ±3.25	, a ± ,	, cd ± ,	, cd ± ,	, b ± ,
3	12	307.0 a ±0.00	337.0a ±2.00	322.25 a ± 3.25	, a ± ,	, d ± ,	, d ± ,	, c ± ,

Means in the same column having different letters are significantly different ($P \leq 0.05$).

Data on the effect of Nile tilapia broodstock stocking density regardless of age on seed production are shown in Table (3). The results indicated that increasing broodstock density significantly ($P \leq 0.05$) reduced broodstock fecundity (seed per female). The lower stocking density had the highest seed/ female ($12 \ 3 \pm 184.14$ seeds), seed/ g female (6.93 ± 1.28 seeds) and seed/ day (10.99 ± 1.53 seeds) followed by T2 (1036.25 ± 129.35 seeds/ female, 6.08 ± 1.30 seeds/ g female and 9.54 ± 1.21 seeds/ day) and T3 (745.40 ± 125.75 seeds/ female, 4.33 ± 0.80 seeds/ g female, 6.93 ± 1.23 seeds/ day), respectively. Several researchers studied the effects of different stocking densities on the reproductive performance particularly, on Nile tilapia *O. niloticus* have demonstrated that increasing the level of stocking density significantly ($P \leq 0.05$) reduces spawning success and in turn mass production (Little, 1989; Ernst *et al.* 1991; Ridha and Cruz, 1999 and Bhujel, 2000). In this behalf, Brummett (1995) reviewed the environmental factors which influence and regulate maturation and reproduction in tilapia brood-fish and stated that, photoperiod, temperature and population density are predictive cues which affect the onset of sexual maturation and reproduction.

Table 3. Effect of Nile tilapia broodstock stocking density regardless of broodstock age on seed production.

Stocking density	Female AIW	Female AFW	Mean weight	Total seed	S/ F	S/ g F	S/ d/ m ²
4	192.0 a ±65.53	230.0 a b ±64.10ab	211.0 a ±64.81	, a ± ,	1213a ±184.4	, a ± ,	, a ± ,
8	192.8 a ±67.13	233.5 a ±64.71	213.13 a ±65.90	, b ± ,	1036 b ±129.35	, b ± ,	, b ± ,
12	192.3 a ±66.57	224.5 ab ±64.96	208.4 a ±65.76	, c ± ,	745 c ± ,	, c ± ,	, c ± ,

Means in the same column having different letters are significantly different ($P \leq 0.05$).

The effects of Nile tilapia broodstock age regardless of broodstock stocking density on seed production are presented in Table 4. Irrespective of broodstock stocking density, it was observed that, the broodstock age significantly ($P \leq 0.05$) influenced the female fecundity in terms of seed/ female, seed/ g female and seed/ day. The 3-Years old female broodstock had a higher absolute fecundity than 1-years old female tilapia broodstock.

Table 4. Effect of Nile tilapia broodstock age regardless of broodstock stocking density on seed production.

Fish age	Female AIW	Female AFW	Mean weight	Total seed	S/ F	S/ g F	S/ d/ m ²
1	77.3 b ±0.80	117.50 b ±2.09	97.42 b ±0.94	b ± ,	752.7 b ±72.93	7.68 a ±0.68	6.97 b ±0.70
3	307.3a ±1.43	341.17 a ±2.15	324.25 a ±1.56	a ± ,	1243 a ±109.7	, b ± ,	, a ± ,

Means in the same column having different letters are significantly different ($P \leq 0.05$).

The increased seed/ female, seed/ g female and seed/ day/ m² parameters with the lower Nile tilapia broodstock density in our study is confirmed and agreed with the findings of Ridha and Cruz (1999) on Nile tilapia *O. niloticus* in a re-cycling tank system and the work of Behrends and Smitherman (1983) on the inter-specific spawning of *O. mossambicus* females with *O. hornorum* males in happas. The observed higher seed production at the lower stocking density compared to other stocking densities indicated more synchronous spawning activity, and increasing the density beyond 4 (3♀:1♂) fish/ m² was not effective to improve seed production. Comparable conclusion was drawn by Little (1989) who found that a high density such as 4.7 females/ m² (9.5 fish/ m²) produced the lowest seed/ kg female/ day and that the maximum daily seed production was at the lowest density of 8 fish/ m², however higher seed production could be obtained using lower stocking density. The declining seed production per unit of area (1 m³) with the increase of the level of broodstock density in the present work, disagreed with the findings of Obi and Shelton (1988) who found that fry production per unit of area (m²) in tilapia, *O. hornorum* (Trewavas) tended to increase with the increase of broodstock stocking density. Maluwa and Costa-Pierce (1993) reported similar observations for tilapia, *O. shiranus*. Ridha and Cruz (1999) attributed these contrasting results to the differences in stocking densities used and added that, it must be noted that, the maximum stocking densities used by the above authors were 4 and 1.7 fish/ m², respectively and that both two numbers were below the density used by most researchers. Therefore, the conclusion of the above authors that a high number of seed could be produced at a higher stocking density might be true as long as broodstock density did not exceed the optimum density. It can said that, there are great discrepancies among investigators even for

fish of the same species and size and this may be attributed to differences in feeding husbandry, limitations in experimental design and other prevailing culture conditions (Tahoun, 2002 and 2007). Bhujel (2000) reported that, an inverse relationship between stocking density and the percentage of spawning females has been found in production hybrids of tilapia, *O. niloticus* and *O. hornorum*, probably due to some chemical or behavioural factors. High stocking density inhibits reproduction possibly due to the presence of a substance in tilapia mucus, which might cause an auto-allergic response. A stocking density of 5 fish/ m² was found to be more productive as compared to 10 fish/ m² in hapa-in-tanks. Furthermore, a density of 6 fish/ m² of spawning hapa has been more precisely determined as the best stocking density with the help of a well-fitted binomial relationship between the stocking density and the seed output. Recently, Tsadik and Bar (2007) suggested lower stocking density of 3 broodfish/ m³ to improve seed production of hapa -in- pond tilapia hatcheries. The reduced seed production in 1-year old broodstock as compared to 3-years old broodstock disagreed with the findings of Al-Ahmed *et al.* (1988) who found that in both seawater and underground brackish water, the fecundity of yearlings *O. spilurus* (99.7 ±14.6 seed/ kg female/ day) over the entire spawning season was not significantly ($P \leq 0.05$) different from that of 2- to 3-years old broodstock (114.8 ± 13.4 seed/ kg female/ day). The results of the present study were confirmed by those of Ridha and Cruz (1989) who found that, year Class I Nile tilapia broodstock had a higher fecundity than Year Classes II and V. Spawners of Year Class I and possibly Year Class II be used to produce seeds for culturing tilapia were recommended. Older spawners should be discarded as unproductive. Mair *et al.* (2004) confirmed that, the age fecundity relationships are in line with expectations with regard to absolute fecundity although based on findings with other species, admittedly over large age differences, relative fecundity have been expected to decline with age (Siraj *et al.* 1983 and Ridha and Cruz, 1989). Smith *et al.* (1991) compared production of Florid red tilapia seeds (eggs, sac-fry and fry) between year class I (YCI) and year class II (YCII) in brackish-water tanks under commercial scale conditions and found that, that older (YCII) red tilapia females produced more seed per clutch but fewer seed per unit weight than younger (YCI) females. However, despite a large average clutch size, seed production was lower in YCII females due to lower spawning frequency, suggesting fewer reproductively active individuals, or longer inter-spawning periods. Greater proportion of eggs and non-swimming sac-fry in YCII broodstocks also suggested longer inters-pawning periods for older fish. In contrast, Little and Hulata, (2000) stated that, Larger, older fish can perform well in intensive hatchery systems, although frequency of spawning and relative clutch size decline with size and age. Poor handling

efficiency of large fish is also a problem in hapa and tank based hatchery systems, in which broodstocks are individually handled to harvest mouth-brooded seed. In practice fish larger than 300g are difficult to handle quickly and efficiently. Small female produce more eggs per unit body weight. Since adverse environmental conditions stimulate early maturity at smaller size in tilapia, relatively higher fecundity in smaller fish further enhances the chances of species survival under such conditions (Watanabe and Kuo, 1985). Bhujel (2000) cited that, relative size of males and females may be more important as there are often hierarchies in tilapia populations based on the social dominance, which is partially determined by fish size. Male tilapias are aggressive in nature and dominant males control most of the spawning, resulting in many females can not spawn. The hierarchy affects the intensity of spawning and these effects may be greater in clear water systems compared to green water systems (Little, 1989). Provision of artificial nests helps to break hierarchies; thus, more females may have contact with more males and spawn. The hierarchy production can also be minimized by spawning females with smaller and uniformly sized males. In this context, Ridha and Cruz (1999) attributed the low production of tilapia fry to a suboptimal broodstock density (Mire, 1982). On the other hand, under intensive hatchery system, broodstock are often stocked at high densities in small and confined breeding units such as aquaria, tanks and net enclosure hapas), resulting in aggression and fighting among males and thus, affecting seed production (Behrends *et al.* 1993). Therefore, the manipulation of broodstock density is one of several technique applied to improve mass production of tilapia seed production than higher densities (Bautista *et al.* 1988).

Fry nursing trial

Table (4) demonstrates the effects of different broodstock ages and stocking densities on fry growth performance, feed conversion ratio and survival rates. The average initial weight (AIW), AFW, AWG, ADG, feed intake, FCR and survival rates were significantly ($P \leq 0.05$) influenced by the broodstock age and their stocking density. The best AIW, AFW, AWG, ADG, feed intake, FCR and survival rates were recorded for T4 (3-Years old broodstock at a stocking density of 4 (3♀:1♂) fish /m²) as compared to other treatments. Fry specific growth rate did not reflect any significant differences among different treatments. Table (5) demonstrates the effect of broodstock stocking density regardless of broodstock age on fry growth performance. It can be noted that, there were not any significant differences among fry groups in AIW, SGR and feed intake, while AFW, AWG, ADG, FCR and survival rates were significantly ($P \leq 0.05$) affected by broodstock stocking density. Siddiqui *et al.* (1997) found that, fecundity is positively related to the size of fish, the growth of fish decreased with increasing density of fish, it appears that social interaction and social stress were responsible for inefficient food utilization, poor growth and consequently low fecundity at high stocking density. At

high densities, there is a competition for space which increases social interaction and in turn, causes social stress and possibly thereby affecting reproductive efficiency.

Table 5. Effect of Nile tilapia broodstock age and stocking density on fry growth and food conversion ratio.

Treatments		AIW	AFW	AWG	ADG (mg/day)	SGR (%/ day)	Feed intake	FCR	SR (%)
Fish ge (year)	Stocking density								
1	4	0.11bc ±0.01	3.85 bc ±0.05	3.74 bc ±0.06	60.32 c ±0.97	5.74 a ±0.17	6.08 b ±0.19	1.63 b ±0.03	92.5 bc ±0.50
1	8	0.12c ± 0	3.50 c ±0.00	3.39 c ±0.01	54.60 c ±0.08	5.51 a ±0.07	5.70 b ±0.23	1.69 a b ±0.07	94.50 b ±0.50
1	12	0.12c ±0.00	3.75 c ±0.15	3.64 c ±0.16	58.63 c ±2.50	5.62 a ±0.13	6.28 b ±0.54	1.73 a b ±0.08	90.0 d ±1.00
3	4	0.15a ±0	5.45 a ±0.15	5.31 a ±0.15	85.56 a ±2.34	5.85 a ±0.01	8.20 a ±0.20	1.55 b ±0.00	95.0 a ±0.00
3	8	0.14a ±0.00	5.25 a ±0.35	5.12 a ±0.36	82.50a ±5.73	5.90 a ±0.17	8.22 a ±0.37	1.6 b ±0.04	93.5 ac ±0.50
3	12	0.13 b ±0.00	4.45 b ±0.15	4.33 b ±0.16	69.76 b ±2.50	5.76 a ±0.12	8.10 a ±0.03	1.88 a ±0.08	95.50 a ±0.50

Means in the same column having different letters are significantly different ($P \leq 0.05$).

Table 6. Effect of different Nile tilapia broodstock stocking density regardless of age on fry growth food conversion ratio and survival rates.

Stocking density	AIW	AFW	AWG	ADG (mg/ day)	SGR (%/day)	Feed intake	FCR	SR (%)
4	0.13 a ±0.01	4.65 a ±0.47	4.52a ±0.46	72.94a ±7.36	5.80 a ±0.08	7.14 a ±0.62	1.59 b ±0.03	95.a ±0.41
8	0.13 a ±0.01	4.38ab ±0.53	4.25ab ±0.52	68.55ab ±8.39	5.71 a ±0.14	6.96 a ±0.75	1.65 b ±0.04	93.0 b ±0.41
12	0.12 a ±0.00	4.10 b ±0.22	3.98 b ±0.22	64.19b ±3.52	5.69 a ±0.08	7.19 a ±0.57	1.80 a ±0.06	91.0 c ±0.71

Means in the same column having different letters are significantly different ($P \leq 0.05$).

The effects of broodstock age regardless of broodstock stocking density are presented in Table 7 , It is obvious that fry average initial weight, AWG, ADG, feed intake, FCR and survival rates were significantly ($P \leq 0.05$) influenced by the broodstock age. The differences in SGR among different broodstock ages were insignificant.

Table 7. Effect of different Nile tilapia broodstock stocking age regardless of density on fry growth performance and survival rates (Means± SE).

Fish age	AIW	AFW	AWG	ADG (mg/ day)	SGR (%/day)	Feed intake	FCR	SR (%)
1	0.11 b ±0.	3.70b ±0.08	3.59 b ±0.08	57.85b ±1.28	5.62 a ±0.07	6.02 b ±0.19	1.68 a ±0.03	92.33b ±0.88
3	0.14a ±0.00	5.0a ±0.22	4.92 a ±0.22	79.27a ±3.51	5.84 a ±0.06	8.17 a ±0.11	1.62b ±0.07	93.67a ±0.67

Means in the same column having different letters are significantly ($P \leq 0.05$).different.

The superiority in growth performance and feed utilization found in the fry produced by older broodstock group (3- years old broodstock), held at the lowest (4 (3♀:1♂) fish/ m².) stocking density (which had the highest average initial weight) was

confirmed by the results of Ahmed *et al.* (2004) who found that growth performance was significantly ($P \leq 0.05$) affected by fish initial size. Comparable results were obtained by Akbulut *et al.* (2003) who found that, the growth rate and final biomass of rainbow trout *Oncorhynchus mykiss* were significantly ($P \leq 0.05$) affected by initial stocking size. Duston *et al.* (2004) obtained similar results on the growth of juvenile striped bass which significantly ($P \leq 0.05$) affected by the initial stocking size. From previous results, in order to obtain much higher quantity and quality of Nile tilapia seeds, it is recommended to use older broodstock (3-years old broodstock) at low stocking density 4 (3♀:1♂) fish/ m² during the propagation season in hatcheries.

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