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Reproductive performance and the growth of pre-stunted and normal Nile tilapia (*Oreochromis niloticus*) broodfish at varying feeding rates

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Abstract

A 119-day experiment was conducted to investigate the effects of feeding rate and reproductive performance of stunted (S) and non-stunted or normal (N) Nile tilapia (*Oreochromis niloticus*). Both the groups were reared in tanks re-circulated with bio-filtered water and fed with floating pellets (30% crude protein) twice daily. Seed were harvested weekly from the mouths of incubating females. The study showed that early stunting with subsequent high feeding rate can improve both growth and reproductive output in female Nile tilapia. Broodfish type and feeding rate showed significant ($P<0.05$) effects on both the frequency of spawning and the seed output. In general, seed output from normal broodfish increased linearly over the experimental period at all the feeding rates. However, seed output from stunted broodfish showed a linear increment for 3% feeding rate, exponential increment for 2% but quadratic for 1% showing decline after 10th week of the trial period. Results also showed that trends of seed output from stunted broodfish increased linearly with the increase in feeding rate showing that optimum rate could be higher than 3%. While from normal group the relationship was quadratic; increasing from 1%, peaked at 2% and declined at 3% feeding rate. Final GSI of the stunted females was significantly ($P<0.05$) higher than that of normal females. The GSI of stunted fish showed a decreasing trend with the increased feeding rate. Both the broodstock groups fed at 1% biomass grew linearly whereas at 2 and 3%, they grew exponentially. As compared to the normal, stunted broodfish had significantly ($P<0.05$) higher fat content in viscera although similar levels were in carcass and ovary. Carcass fat content was significantly ($P<0.05$) lower in fish fed at 1% biomass but significantly ($P<0.05$) higher in the ovary and viscera of fish fed at 3% biomass. This study shows that tilapia hatchery operators could manipulate the seed production according to the seasonal demand by using appropriate broodstock stunting and feeding strategies.

Keywords: Nile tilapia; Broodfish; Reproduction; Stunting; Seed production; Feeding rate

As a female *Oreochromis* produces small clutches of eggs, commercial hatchery operators have to keep and manage a large number of broodfish to fulfill the demand for seed. For instance, more than 60,000

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working broodfish are required to produce 5–10 million fry per month (Bhujel et al., 2001a,b). Moreover, broodfish grow continuously even when reproducing at a high frequency (Macintosh and Little, 1995). Bigger fish require more feed and space and are difficult to handle while seed harvesting; therefore, broodfish need to be replaced frequently. Tilapia hatchery operators have to make the same number of broodfish ready to replace the working broodstock. Therefore, cost associated with broodstock production and maintenance is one of the major parts of operation cost for commercial tilapia hatcheries. Broodstock management is one of the most important aspects of tilapia seed production (Bhujel, 2000). In the tropics, Nile tilapia (*Oreochromis niloticus*) can reproduce throughout the year. However, lack of spawning synchrony among females (Little et al., 1993) and the failure of induced spawning further intensify the problem of mass seed production on a commercial scale predictably.

Availability of water quite often restricts the market for seed to less than 6 months of a year in various parts of the world. Typically in Thailand, for example, demand for tilapia fry peaks for a period of only 6 months (May–August) in a year when farmers have enough water to stock fish. Appropriate techniques have to be developed to prevent the tilapia broodfish from spending energy to produce fry during low demand and to boost the fry production quickly when high demand starts. One of the suitable ways to prevent tilapia broodfish from spawning might be the stunting which can be achieved using restricted feeding, stocking at high densities and/or holding at low temperatures (Mironova, 1978; Dan and Little, 2000b).

Stunting or growth retardation in tilapia has been reported by several authors in experimental ponds as well as natural water bodies due to over crowding, limited food supply and other environmental stresses (Loya and Fishelson, 1969; Iles, 1973; Bruton and Alllanson, 1974; Eyeson, 1983; Blühdom and Arthington, 1990; Heath and Roff, 1996; Coward et al., 1998; Takagi, 2001). As stunting of any organism to the extent at which the ability of the living organisms is not affected to perform vital functions to survive i.e. below critical level of starvation, is a phenotypic change or reversible process. The stunted fish can compensate the growth including bone growth afterwards when they are exposed to suitable environments and fed sufficiently (Björnsson et al., 1989; Dan and Little, 2000a; Takagi, 2001). Although the phenomenon of compensatory growth is not clearly understood, it is due either to hyper-phagic response by fish, higher metabolic efficiency or the adaptation with low energy requirement for maintenance during stunting phase that allows more energy mobilization for growth in the later phase (Avault, 2000; Gaylord and Gatlin, 2001). Stunting in fish during winter is common natural phenomenon in temperate regions while intentional over-wintering has been a common practice in aquaculture in sub-tropics. It has been found to be profitable in grow-out culture of channel catfish and other species (Hatch et al., 1998). However, limited work has been carried out in reproductive performance. During over-wintering or stunting period, females may loose up to 80% of their body lipids and a substantial reduction may occur in males hampering their sexual maturation (Jobling et al., 1998; Morgan and Metcalfe, 2001). In Baltic herring, egg number, but not the size, was found to be affected by over-wintering just before spawning season. On the other hand, over-wintering of broodstock in prawn has been found to be technically and economically feasible (Canese et al., 1995). More over, increased broods and synchronized reproduction have been achieved from over-wintered female mosquito fish, *Gambusia affinis* (Hynes and Cashner, 1995). Research on over-wintering in tilapia is limited. Studies in Northern Vietnam has reported that over-wintered tilapia fry grew faster than normal fry, with improved economic performance (Dan and Little, 2000a,b). However, whether pre-stunting with restricted feeding of Nile tilapia broodfish had any impacts on the subsequent reproduction, seed output and growth of broodfish were not known. This study was; therefore, carried out to compare the performance of pre-stunted and normal Nile tilapia broodfish at varying feeding rates.

1. Materials and methods

A 119-day experiment was conducted at the Asian Institute of Technology (AIT) near Bangkok, Thailand in a re-circulated, bio-filtered water system using 18 circular tanks (area 1.75 m^2, 50 cm depth) under a roof of galvanized iron sheets. Water flow was maintained at 8–10 L/min in all the tanks which were also aerated. Eight concrete bricks were placed in each tank perpendicularly to the tank wall to provide nesting sites for broodfish (Little et al., 1993).

1.1. Experimental fish and feed

Two groups of broodstock derived from the same *Chitralada* broodstock line of Nile tilapia (*O. niloticus*) maintained at the Asian Institute of Technology (AIT) were used in the experiment. The attributes of the brood fish i.e. normal (N) or non-stunted and stunted (S) group are presented in Table 1. Age of the normal broodfish at which they spawned was 4 months (3 months + 1 week between hatching and swim-up stage + 3 weeks between stocking and spawning). Growth of

Table 1
Attributes of broodfish used in the trial

Attributes	Type of broodfish	
	Normal	Stunted
Age of broodfish		
Post-swim up to stocking	3 months	12 months
Post-hatch to spawning	4 month	13 months
Weight of broodfish at stocking (g)		
Female	43 ± 2^{b}	33 ± 1^{a}
Male	49 ± 2^{c}	35 ± 2^{a}
GSI (%) at stocking		
Female	0.5 ± 0.3^{b}	0.1 ± 0.1^{a}
Male	2.9 ± 1.2^{c}	0.4 ± 0.2^{b}

Values with different superscripts are significantly different at 0.05.

stunted (S) fish was restricted by keeping them in a fine mesh nylon hapa suspended in a pond at high stocking density (>5000 fingerlings.m^{-2}) with limited feeding for 2 months. They were then transferred to two hapas and nursed for 10 additional months at a stocking density of 80 fish m^{-2} feeding with commercial floating pellet (30% CP, Chareon Pokphand Co., Thailand) at 1% biomass daily. During the experiment, the same type of feed was fed to both the groups of stunted and normal broodfish at rates of 1%, 2%, and 3% biomass throughout the whole experimental period.

1.2. Fish stocking and seed collection

Fifteen fish from each treatment and sex group were sampled for individual length and weight at stocking. Ten females and five males (2:1 ratio) were stocked in each experimental replicate tank. Biomass of broodfish (male and female together) from each replicate tank was monitored weekly immediately after each seed collection day in order to adjust the amount of feed for the following week. Broodfish were fed once on seed collection day and twice daily (08.30 and 15.30 h.) on other days. Seed production started from the 4th week of broodfish stocking in tanks. Seed were collected in plastic bowls from the mouths of incubating females as described by Little et al. (1993) every Monday between 08:00 and 10:00 h. Total weights of each stage of eggs (stage I: just spawned eggs, Stage II: eggs with two eye spots, stage III: with protruding eyes and a tail, stage IV: yolk-sac larvae with well developed head and tail) from each replicate tank were measured with an electronic balance (up to two decimal points of g). A towel and a small hand net were used to dry the water from egg mass before weighing.

1.3. Gonado-somatic index (GSI) and proximate composition

Five fish from each sex for each treatment group were sampled at stocking and all the fish at final harvest were weighed individually and killed to remove and weigh the

Table 2
Reproductive performance of stunted and normal (non-stunted) Nile tilapia broodfish subsequently fed at varying rates during the spawning period of 119 days (Mean±standard error)

Feeding rate (% biomass)	Stunted broodfish			Normal broodfish		
	1%	2%	3%	1%	2%	3%
Total spawn	18 ± 6.4^{ax}	25 ± 2.6^{ax}	28 ± 4.9^{bx}	11 ± 2.2^{ax}	21 ± 3.0^{ay}	14 ± 3.1^{axy}
Seed output						
#/spawn	307 ± 12^{ax}	464 ± 39^{ay}	602 ± 45^{by}	372 ± 16^{bx}	492 ± 41^{ay}	465 ± 30^{ay}
# /tank/wk	335 ± 132^{ax}	677 ± 61^{ay}	1029 ± 259^{ay}	259 ± 59^{ax}	594 ± 93^{ay}	375 ± 65^{axy}
# /m2/day	33 ± 13^{ax}	67 ± 6^{ay}	102 ± 26^{ay}	26 ± 6^{ax}	59 ± 9^{ay}	37 ± 6^{axy}
#/g total female / day	11 ± 4^{ax}	15 ± 0^{ax}	15 ± 5^{ax}	9 ± 2^{ax}	11 ± 3^{ax}	7 ± 1^{ax}
% feed conversion to seed	4.3 ± 1.5^{ax}	3.0 ± 0.3^{ax}	2.3 ± 0.7^{ax}	3.1 ± 0.8^{ax}	2.5 ± 0.6^{ax}	0.9 ± 0.2^{ay}
Broodfish survival (%)						
Female	100 ± 0^{ax}	90 ± 10^{ax}	100 ± 0^{bx}	97 ± 3^{ay}	97 ± 3^{a0}	83 ± 3^{ax}
Male	87 ± 13^{ax}	100 ± 0^{ax}	100 ± 0^{ax}	87 ± 7^{ax}	93 ± 7^{ax}	93 ± 7^{ax}
Final weight (g)						
Female	58 ± 4^{ax}	119 ± 4^{ay}	188 ± 14^{az}	64 ± 1^{ax}	136 ± 15^{ay}	169 ± 12^{ay}
Male	75 ± 5^{ax}	144 ± 4^{ay}	212 ± 21^{az}	79 ± 3^{ax}	161 ± 6^{ay}	188 ± 9^{ay}
Relative weight gain (%)						
Female	58 ± 8^{ax}	203 ± 10^{ay}	362 ± 33^{bz}	49 ± 3^{ax}	218 ± 34^{ay}	296 ± 28^{ay}
Male	94 ± 12^{ax}	257 ± 9^{ay}	414 ± 49^{az}	70 ± 8^{ax}	261 ± 14^{ay}	325 ± 20^{ay}
Final GSI*						
Female	4.8 ± 0.7^{ay}	3.8 ± 0.6^{axy}	2.5 ± 0.2^{ax}	3.1 ± 0.2^{ax}	3.6 ± 0.5^{ax}	3.0 ± 0.1^{bx}
Male	1.6 ± 0.3^{ay}	1.5 ± 0.1^{ay}	1.1 ± 0.1^{ax}	1.9 ± 0.2^{ax}	1.4 ± 0.1^{ax}	2.4 ± 1.0^{ax}

GSI* (Gonado–Somatic Index) = gonad weight × 100/body weight.
Mean values with different superscripts are significantly different at 5% level of significance. Superscripts a, b, c are to compare between Normal (N) and Stunted (S) for their corresponding feeding rates but not for within the broodfish group and *x*, *y*, *z* to compare mean values for three feeding rates within the same group of broodfish only.

gonads. Samples of carcass, ovary and viscera were also taken at stocking and final harvest. Pooled samples from each treatment and sex were oven-dried and stored in a deep freezer before analysis. Crude protein and crude fat were analyzed using standard Kjeldahl and Soxhlet methods respectively. All the samples were duplicated while analyzing in the laboratory at AIT.

1.4. Water quality monitoring and analysis

Morning (06:30 h) and afternoon (15:30 h) temperatures and dissolved oxygen concentrations were monitored with a DO meter (YSI model 58) once a week. Ammonia-*N* and nitrite-*N* concentrations were analyzed at the beginning, middle and end of the experiment by collecting and mixing 300 mL of water from each replicate tank of the same treatment in a 1-litre plastic bottle. Samples were duplicated for each treatment and analyzed by using spectrophotometric method for ammonia–nitrogen (standard Phenate method) and nitrite–nitrogen (APHA, 1989).

1.5. Statistical analysis

Two-way ANOVA (2 × 3 factorial) was used to see the effects of two factors; broodfish type (stunted and normal) and the feeding rate (1%, 2% and 3%). Student's *t*-test was used to compare between two means. Regression analysis was used to see the relationship of seed output and growth pattern with the time period. Percentage data (survival, relative weight gain and GSI) were transformed into square root as well as arcsine for statistical analysis.

2. Results

2.1. Reproductive performance

Total spawn, seed output and the gonadosomatic index were compared (Table 2). Seed output over time by week showed a clear pattern (Fig. 1). The trend in seed output from normal broodfish (N) increased linearly over the experimental period while that from stunted broodfish (S), the relationship was found to be linear at 3% and non-linear at other rates. Fig. 1 shows the patterns, and also the equations, of seed production with time for each group at each feeding rate. Two-way ANOVA showed that there were significant ($P<0.05$) overall impacts of both the treatments; broodfish type and subsequent feeding rate on the total seed output. However, no significant ($P>0.05$) interaction effect was found between the two factors.

Two way-ANOVA showed that the average number of spawns by stunted group was significantly ($P<0.05$) higher

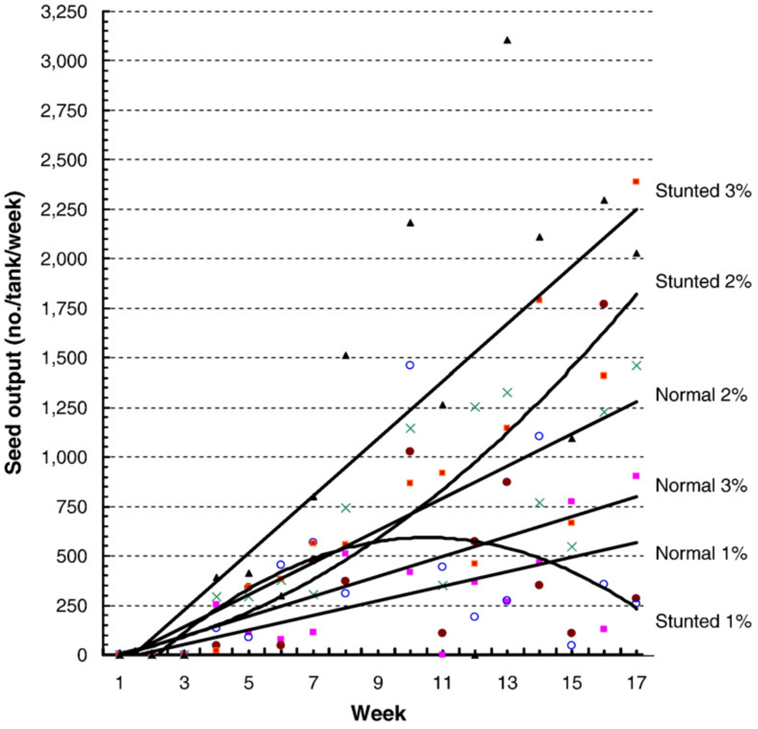

Fig. 1. Seed output (no/tank/week) from stunted and normal/non-stunted Nile tilapia brood fish fed at 1, 2 and 3% biomass over the spawning period of 119 days. Equations of the fitted lines: ■ Normal 1%: $Y=-56.353+36.789^{X}$ ($R^2=0.47$, $P<0.01$) X Normal 2%: $Y=-100.85+81.289X$ ($R^2=0.70$, $P<0.01$) ✷ Normal 3%: $Y=-53.401+50.177X$ ($R^2=0.30$, $P<0.05$)☼ Stunted 1%: $Y=-351.21+179.528X-8.5356X^2$ ($R^2=0.32$, $P<0.1$) ■ Stunted 2%: $Y=-19.540+21.703X+5.0994X^2$ ($R^2=0.77$, $P<0.01$) ▲ Stunted 3%: $Y=-206.16+144.36X$ ($R^2=0.56$, $P<0.01$).

than that of non-stunted broodfish. In normal 2% feeding rate gave higher number of spawn compared to 1% but there was no effect ($P > 0.05$) of feeding rate on the number of spawn in stunted group. Although stunted females were smaller than the normal fish (N) at stocking, more spawns (7) were obtained from the stunted group within the first 3 weeks as compared to the normal group (N), 3 spawns. The spawning in both the groups was regular from the 4th week of the trail.

Similarly, results showed an increasing trend of seed output per spawn (Fig. 2) with the increased feeding rate in the case of stunted broodfish (S). But the trend in normal (N) or non-stunted group was quadratic; increased from 1%, peaked at 2% and declined at 3%. The lowest level (1%) of feeding rate was proved to be too low to support the reproduction in stunted (S) tilapia whereas feeding rate of 3% biomass per day resulted in increasingly higher production. However, there was no significant difference ($P > 0.05$) in the number of eggs per g of female when compared between two broodfish groups and among all the feeding rates. The percentage feed conversion to seed (g of seed/g of feed * 100) decreased with the increase in feeding rate (Fig. 3). However, there was no significant difference between the two fish groups.

Initial average GSIs of both the sexes of the stunted group were significantly ($P < 0.05$) lower than that of the non-stunted broodfish (Table 2). Final GSI of the stunted female group fed at 3% was significantly ($P < 0.05$) lower than that of the normal (N) female group fed at the same level. GSIs of other feeding levels between two groups were not significantly different ($P > 0.05$). The GSI of the male did not differ ($P > 0.05$) between the two groups at any level of feeding. The GSI of the female were significantly ($P < 0.05$) higher than that of males at stocking as well as at harvest for both the age groups. Final GSI of the non-stunted female broodfish remained more or less constant regardless of the feeding rate. In contrast, the final GSI of stunted females was highest at the lowest feeding rate (1%) and showed a decreasing trend with the increasing feeding rate. Final male GSI did not vary with the feeding rate in stunted group while in normal group males fed at 3% rate had significantly lower GSI than of the other two feeding rates.

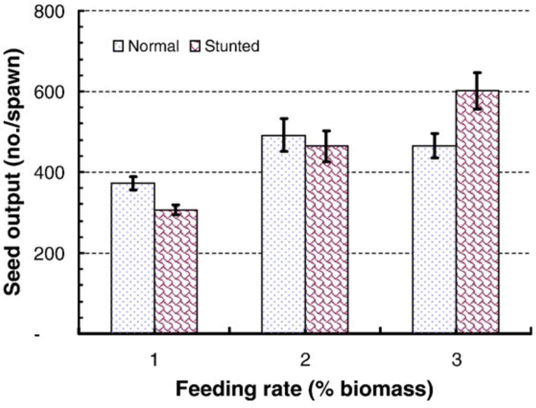

Fig. 2. Relationship between the feeding rate and the seed output (#/spawn) produced by stunted and normal Nile tilapia during the experimental period of 119 days.

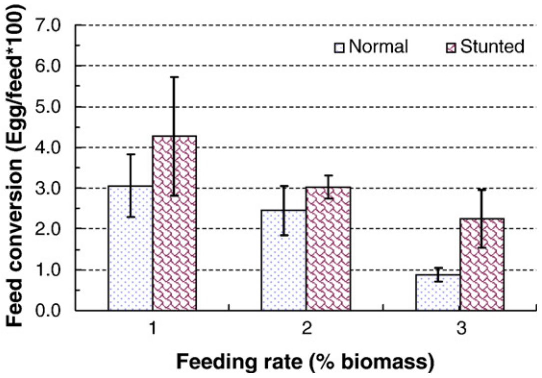

Fig. 3. Percentage of feed conversion to seed (g of seed produced/g of feed * 100) by normal and stunted Nile tilapia fed at 1, 2 and 3% biomass per day during the experimental period of 119 days.

2.2. Broodfish growth and survival

Survival rate, mean weights and gonadosomatic indices of the male and female of both the groups are presented in Table 2. Survival of broodfish ranged from 83 to 100%. Survival of female in normal group fed at 3% was significantly lower ($P < 0.05$) than survivals the other two groups within the same category of broodfish and also lower ($P < 0.05$) than the survival of the stunted females fed at 3% rate. There was no difference ($P > 0.5$) in daily weight gain (DWG, g fish^{-1} day^{-}) between two broodfish types whereas overall effect of the feeding rate on the DWG was highly significant ($P < 0.001$) in both the sexes. On the other hand, stunted group had higher ($P < 0.05$) relative weight gain as compared to the non-stunted group. Males, regardless of the age, had higher relative weight gain than the females. In general, relative weight gain increased with the increase in feeding rate in both the sexes. However, there was no significant difference ($P > 0.05$) in the total length gain between the two age groups of females but significant ($P < 0.05$) difference for male. Feeding rate had a significant ($P < 0.05$) effect on length gain in both the sexes.

Clear distinction in the growth patterns due to feeding rate were observed (Fig. 4) in both age groups. Regression analysis showed significant linear fish growth patterns when fed at 1% biomass ($Y = 32.42 + 1.73X$ where $R^2 = 0.91$, $P < 0.01$ for stunted group and $Y = 35.95 + 1.83X$ where $R^2 = 0.86$, $P < 0.01$) for non-stunted group). But growth patterns were exponential at higher feeding rates such as for stunted group: $Y = 32.68e^{0.08X}$ ($R^2 = 0.98$, $P < 0.01$) at 2% and $Y = 35.76e^{0.11X}$ ($R^2 = 0.96$, $P < 0.01$) at 3% feeding rates and for normal/non-stunted group; $Y = 37.45e^{0.08X}$ ($R^2 = 0.91$, $P < 0.01$ at 2% and $41.17e^{0.091X}$ ($R^2 = 0.98$, $P = 0.00$) at 3% feeding rates. More interestingly, at 3% biomass feeding rate the growth of stunted broodfish surpassed the growth of normal broodfish after 10 weeks.

2.3. Proximate composition

Fat and protein contents of the carcass, ovary and viscera are given in Table 3. Fat content of the viscera of the stunted broodfish was significantly ($P < 0.05$) higher than that of normal

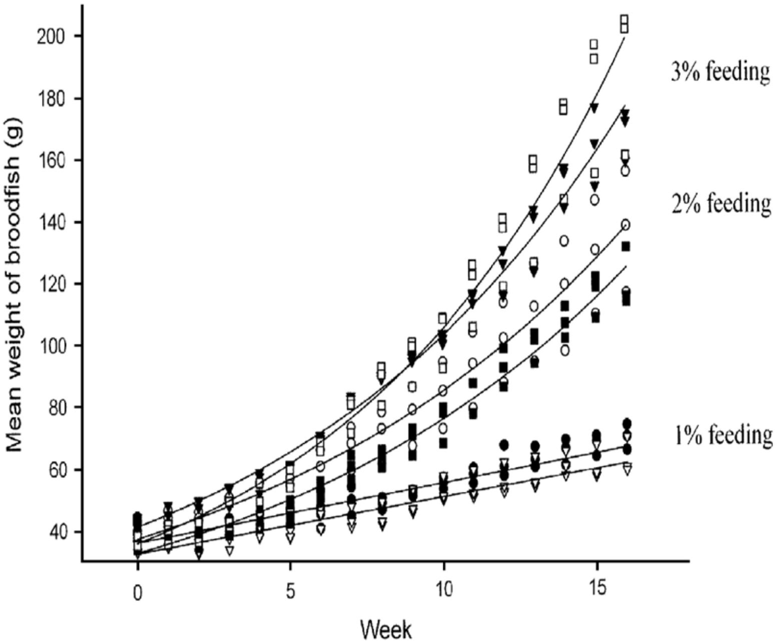

Fig. 4. Growth pattern of previously stunted and normal/non-stunted Nile tilapia broodfish fed at 1, 2 and 3% biomass during 119 days of spawning trial in tanks. Equations of the fitted lines: ▼ Normal 3%: $Y=41.17e^{0.091X}$ ($R^2=0.98$, $P<0.01$) □ Stunted 3%: $Y=35.76e^{0.11X}$ ($R^2=0.96$, $P<0.01$) O Normal 2%: $Y=37.45e^{0.08X}$ ($R^2=0.91$, $P<0.01$) ■ Stunted 2%: $Y=32.68e^{0.08X}$ ($R^2=0.98$, $P<0.01$) ● Normal 1%: $Y=35.95+1.83X$ ($R^2=0.86$, $P<0.01$) ▽ Stunted 1%: $Y=32.42+1.73X$ ($R^2=0.91$, $P<0.01$).

broodfish but there were no significant differences ($P>0.05$) between the two broodfish types for fat content of carcass and the ovary. Fat content of the carcass of stunted group fed at 1% biomass was found to be significantly $P<0.05$) lower than the groups fed at 2% and 3% of biomass but the fat contents of the carcass fed at 2% and 3% were similar ($P>0.05$). Carcass fat content in normal group increased with the feeding rate. Fat contents in the ovary of the groups fed at 3% of biomass was significantly ($P<0.05$) higher than the groups fed at 1% and 2% of biomass in both the broodfish types. However, the groups fed at 1% and 2% of biomass had similar fat contents between them and with the initial fat contents in the ovary. Fat contents in viscera were highest ($P<0.05$) at 3% feeding rate in stunted group while at 2% in normal group. There was a significant ($P<0.05$) interactive effect of broodfish type and the feeding rate on the fat content of viscera. Crude protein content of carcass,

Table 3
Percentage of fat and protein contents in carcass, ovary and viscera of the stunted and normal/non-stunted Nile tilapia broodfish on dry matter basis (mean value ± standard error)

	Stunted broodfish (S)				Normal broodfish (N)			
	Initial	Final			Initial	Final		
Feeding rate →		1%	2%	3%		1%	2%	3%
Carcas								
Protein	$57.7^{axy}\pm2.9$	$59.1^{axy}\pm1.4$	$63.2^{by}\pm0.2$	$59.2^{ax}\pm0.8$	$55.5^{ax}\pm0.8$	$57.5^{axy}\pm1.7$	$61.2^{ay}\pm0.2$	$64.1^{axy}\pm3.0$
Fat	$10.2^{ax}\pm0.0$	$11.9^{ay}\pm0.3$	$18.4^{az}\pm0.6$	$18.8^{ayz}\pm3.4$	$11.3^{ax}\pm2.0$	$13.0^{axyz}\pm6.2$	$19.0^{ay}\pm0.0$	$21.4^{az}\pm0.4$
Ovary								
Protein	NA	$60.5^{ax}\pm0.0$	$58.8^{ax}\pm1.4$	$52.2^{ax}\pm2.7$	NA	NA	$58.4^{ax}\pm0.3$	$57.9^{ax}\pm3.2$
Fat	$24.3^{ax}\pm0.0$	$25.5^{ax}\pm0.0$	$25.9^{ax}\pm0.2$	$29.4^{ay}\pm0.0$	$27^{ax}\pm0.0$	$30.5^{ax}\pm0.0$	$25.1^{ax}\pm0.3$	$33.9^{ay}\pm2.5$
Viscera								
Protein	NA	NA	NA	$37.2^{ax}\pm0.0$	NA	NA	$39.0^{ax}\pm0.3$	$35.6^{ax}\pm2.3$
Fat	$28.1^{ax}\pm0.0$	$35.7^{ax}\pm0.0$	$24.1^{ax}\pm3.5$	$41.2^{ay}\pm0.4$	$24.5^{ax}\pm0.0$	$26.8^{ax}\pm0.0$	$32.2^{ay}\pm0.4$	$28.4^{ax}\pm0.6$

NA — Not available because of inadequate sample for analysis.
Mean values with different superscripts are significantly different at 5% level of significance. Superscripts a, b, c are to compare between Normal (N) and Stunted (S) for their corresponding feeding rates and *x*, *y*, *z* to compare values within the same group of broodfish.

ovary and intestine was significantly ($P < 0.05$) different; highest in the carcass, medium in ovary and the lowest in the viscera. However, there were no significant ($P > 0.05$) differences between the two age groups for the protein content of the carcass, ovary and viscera. Protein contents of ovary and viscera did not differ ($P > 0.05$) with feeding rate.

2.4. Water quality

Water temperature of experimental tanks ranged from 22–29 °C and dissolved oxygen ranged from 4.5–9.5 mg/L. Total ammonia nitrogen (TAN) and nitrite nitrogen levels were found to increase with time but still remained low (<0.4 and 0.1 mg/L respectively). The water quality parameters did not show any specific pattern based on the treatments.

3. Discussion

In this study, stunted females, when fed at higher rate, produced more seed ($P < 0.05$) through an increase in the clutch size (number of eggs per spawn) of the individual female which was due to increase in size of female broodfish. It clearly showed that stunted Nile tilapia females can consume more food, gain higher weight and produce more seed as compared to the non-stunted females. According to Iles (1973), stunting increases the brooding frequency and relative fecundity in tilapia. Similar results were found by Hynes and Cashner (1995) in mosquito fish. But present study showed that seed per spawn can be increased rather than the frequency or spawn and the relative fecundity. However, stunting for more than 12 months can be detrimental as reported in big head carp (*Aristichthyus nobilis*, Richardson) by Santiago et al. (2004).

Present findings showed that seed production from stunted females increased with the increase in feeding rate. Moreover, a higher feeding rate increased the size (weight and length) of fish but did not affect the relative fecundity, which is basically considered to be determined by genetic make-up. Increased seed output was due to the increase in the clutch size. The most possible explanation of this is that increase in feeding rate increased the size (weight) of fish and those bigger fish might have produced more eggs per spawning (Welcomme, 1967; Rana, 1988; Macintosh and Little, 1995).

Another aspect of the study was to determine the optimum feeding rates for the stunted and the normal broodfish. Results with normal brood fish showed an increased seed output when feeding was increased from 1% to 2% but 3% feeding rate appeared to be too high as uneaten feed was observed during the experimental period on the surface of water which might have caused some problems in water quality. At the same time, elevated fat levels in carcass, ovary and the viscera were found in the group fed at 3% rate. This shows that environmental and physiological problems have caused fish death (significantly lower survival, Table 2) when fed high rate that has ultimate consequences of lower seed production compared from the stunted group for the same feeding rate. In contrast, stunted fish could consume more feed (hyperphagic) and utilize nutrients more efficiently to increase seed productivity; the trend was linear. The feeding rate of 3% still gave rise higher seed output indicating that optimum rate could be even higher. This clearly indicated that stunted tilapia consumed more feed (hyper-phagic response) to compensate early growth retardation (Jobling and Koskela, 1996; Takagi, 2001) and the losses from reproduction. Use of feeding rates higher than 3% for stunted broodfish at the beginning (until the peak production is achieved) and then followed by an optimized rate, possibly 2% as it was found to be optimum for normal group, might give the best results.

Interesting relationships were found between feeding rate and the gonadosomatic index (GSI) of females. The non-stunted female did not differ in GSI at stocking and harvesting. The size of the gonad increased proportionately with the increase in the size of fish for all the rates used to feed the normal or non-stunted fish. Therefore, feeding rate did not affect female GSI of this group. The absence of impact of feeding level on final female GSI in non-stunted fish contrasts with a decline with feeding level in stunted females. With higher feeding level (3% biomass), stunted fish grew faster producing more seed per spawning ($P < 0.05$) that resulted in a higher seed yield. The lower GSI of this high fed group indicates that more energy was converted to gonadal cells and released in the form of eggs rather than stored in ovary. Present study focused on female GSIs and their reproductive performance, an in-depth study should be done to evaluate the performance of males as stunting or over-wintering normally affects the sexual maturation of males (Morgan and Metcalfe, 2001; Santiago et al., 2004) and the viability/fertility of sperms.

Various environmental alterations have been identified to control the reproduction in Nile tilapia. For examples, low temperature, high salinity and photoperiod (Koiller and Avtalion, 1985; Watanabe, 1985; Fineman-Kalio, 1988; Bhujel et al., 2001b). However, no suitable system or strategy has been developed so far possibly due to the low efficiency of these factors and the higher costs involved. Present findings showed that suitable combinations of stocking density and restricted feeding strategy might help manipulate timing of seed production according to the fry demand. In this study, stunted (S) broodfish were smaller than the normal (N) group at stocking because of limited feeding and rearing in crowded condition prior to maturation. It was reported that very few stunted females (2–3/week) spawned during the period of first 3 weeks. This showed that onset of maturation and/or spawning in most females was delayed through stunting. Spawning was regular only from the 4th week of stocking indicating that it regained through adequate feeding subsequently. More importantly, egg productivity (per spawn) of stunted Nile tilapia females can be boosted by increasing subsequent feeding. Results of the present study; therefore, supported the concept of stunting as a reversible (phenotypic) process not only for growth (Björnsson et al., 1989) but also true for reproduction. Similar to the compensatory growth (Björnsson et al., 1989; Dan and Little, 2000a; Takagi, 2001), present study revealed that Nile tilapia also showed compensatory reproductive performance. Therefore, in tilapia, delayed sexual maturation together with feeding strategy could be useful for commercial hatcheries to synchronize seed production with the market demand for fry.

In conclusion, stunted Nile tilapia responded increased feed availability to compensate for early growth retardation and produce more seed compared to the normal broodfish. A suitable feeding rate for the normal Nile tilapia broodfish in clear water system was found to be at 2% biomass per day. In contrast, stunted broodfish gave highest seed production at 3% feeding rate. There is an indication (trend) that feeding rate could be possibly further increased to produce more seed. However, the conversion efficiency of feed to seed declines and from a practical standpoint, it might not be advantageous as brood fish grow faster and larger fish are difficult to handle necessitating early replacement of the brood stock which can be costlier. Nevertheless, it can be recommended that hatchery operators keep their broodstock at higher stocking densities under restricted feeding regimes when there is low demand for seed and boost production using stunted broodfish with higher feeding rates when the market demand for seed increases and allow one month of feeding at 3% body weight before spawning.

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