



**AgEcon** SEARCH  
RESEARCH IN AGRICULTURAL & APPLIED ECONOMICS

*The World's Largest Open Access Agricultural & Applied Economics Digital Library*

**This document is discoverable and free to researchers across the globe due to the work of AgEcon Search.**

**Help ensure our sustainability.**

Give to AgEcon Search

AgEcon Search  
<http://ageconsearch.umn.edu>  
[aesearch@umn.edu](mailto:aesearch@umn.edu)

*Papers downloaded from **AgEcon Search** may be used for non-commercial purposes and personal study only. No other use, including posting to another Internet site, is permitted without permission from the copyright owner (not AgEcon Search), or as allowed under the provisions of Fair Use, U.S. Copyright Act, Title 17 U.S.C.*



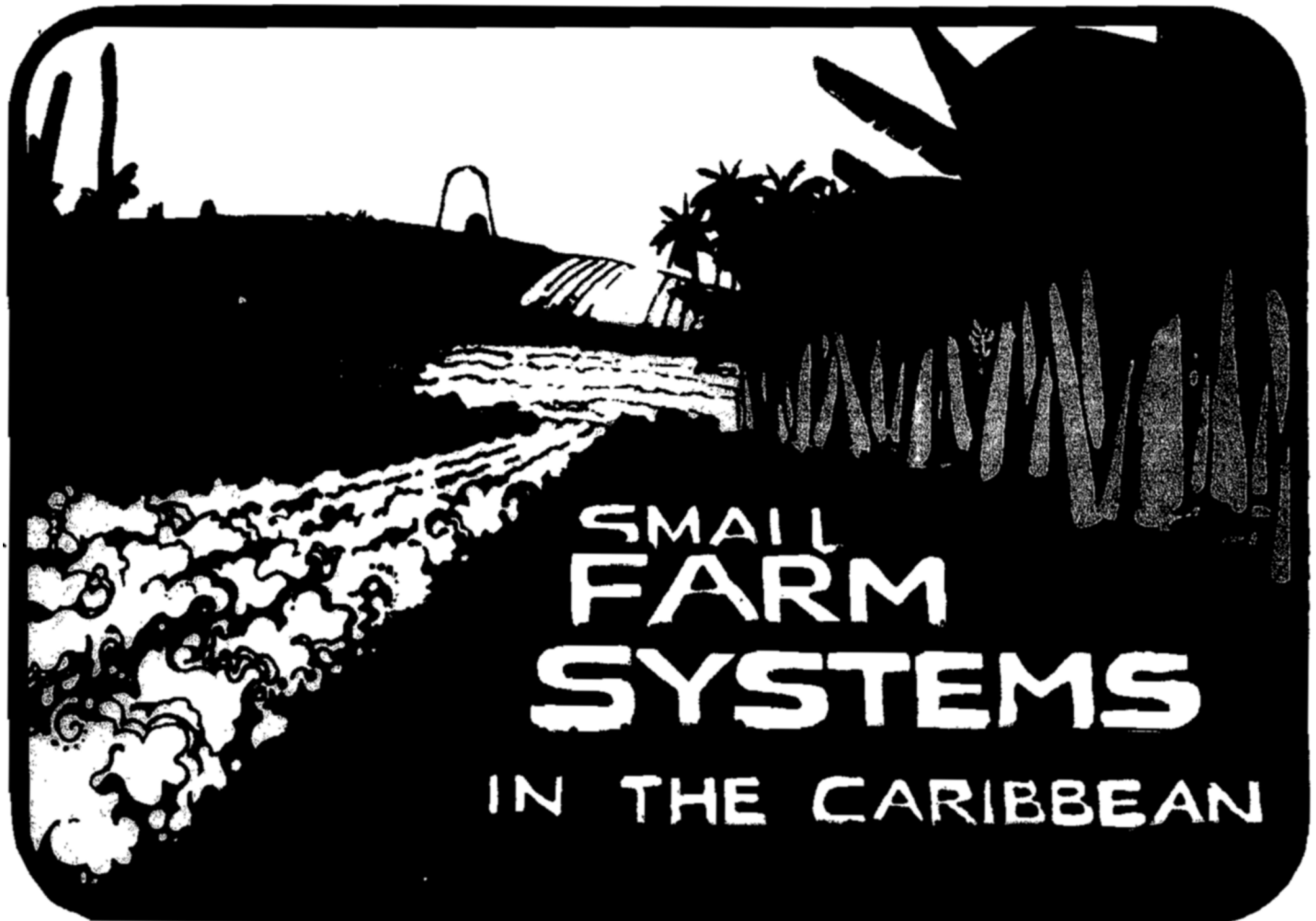
**CARIBBEAN  
FOOD CROPS  
SOCIETY**

Vol. XX

Sociedad Caribeña de Cultivos Alimenticios  
Association Caraïbe des Plantes Alimentaires

# PROCEEDINGS

OF THE 20th ANNUAL MEETING — ST. CROIX, U.S. VIRGIN ISLANDS — OCTOBER 21-26, 1984



*Published by*

THE EASTERN CARIBBEAN CENTER, COLLEGE OF THE VIRGIN ISLANDS *and* THE CARIBBEAN FOOD CROPS SOCIETY



# Tilapia Fry and Fingerling Production in Small Tanks

James E. Rakocy and Ayyappan Nair  
CVI Agricultural Experiment Station  
P.O. Box 920, Kingshill  
St. Croix, U.S. Virgin Islands 00850

Two experiments were conducted to evaluate the use of small tanks as a hatchery for the production of tilapia fry and fingerlings. The effect of stocking density of brood fish on fry production was evaluated using a sex ratio of four females to one male. Brood fish (*Tilapia aurea*) were stocked at rates of 2.7, 5.4 and 8.1 fish/m<sup>2</sup> in nylon spawning nets (hapas) suspended in tanks. Fry were collected seven times at 2-week intervals. Mean fry production was 12.2, 15.1 and 23.8/m<sup>2</sup>/hapa/day or 5.3, 3.9 and 3.8/female/day, respectively. The fry were stocked at rates of 26, 52, 78, 104, 130 and 155/m<sup>2</sup> to determine the optimum rate for fingerling production. The fry were fed four times daily for 63 days. The daily

feeding rate was 15% of initial body weight for three weeks followed by weekly adjustments to 5%. Predation by dragonfly larvae caused wide variation in survival (23-88%). Fry at the 26/m<sup>2</sup> rate grew fastest, averaging 2.3 g with 37% survival, 13.5% actual feeding rate and 2.3 feed conversion ratio. Fry at the 104/m<sup>2</sup> rate weighed 1.2 g with 88% survival, 6% actual feeding rate and 0.75 feed conversion ratio. The data indicates that the daily feeding rate should be higher than 5% of body weight for maximum growth but should not exceed 40 kg/ha/day in small static tanks.

**Keywords:** tilapia, hatchery systems, aquaculture.

In many areas, tilapia producers do not have a commercial source of fingerlings for growout and must therefore produce their own. Their operations may be too small to justify the construction of brood and nursery ponds or the necessary resources may not be available. Small tanks may be the appropriate unit for fry and fingerling production to satisfy their needs.

Several investigators have used tanks in studies involving tilapia fry or fingerling production. Uchida and King (1962) examined the production and growth of *Tilapia mossambica* fry in tanks. Shelton et al. (1978) used tanks for producing *T. aurea* fry for sex reversal experiments. Snow et al. (1983) studied methods of removing *T. aurea* from tanks and raising them to fingerling size. Hughes and Behrends (1983) suspended net enclosures in tanks to study the mass production of *T. nilotica* seed (eggs, sac fry and advanced fry).

The use of net enclosures (hapas) in tanks is a new practice that facilitates fry production. Swim-up fry form schools at the surface and stay close to the tank walls for a few days. At this stage they are easily caught with a dip net and transferred to a nursery unit. However, fry that avoid capture prey upon subsequent spawns and production declines (Uchida and King, 1962; Snow et al., 1983). With hapas, this problem is eliminated as all the fry can be frequently removed by crowding them to one end of the hapa and capturing them with a dip net after the brood fish have been gently removed by hand to the cleared portion of the hapa.

An important factor in the production of fry is the density of brood fish (Hughes and Behrends, 1983). The growth rate of fry to fingerling size is also dependent on density, among other factors (Uchida and King, 1962; and Snow et al., 1983). The objectives of this study were to evaluate the effects of brood fish stocking density on fry production and the stocking level of fry on their growth rates to fingerling size (5g).

## MATERIALS AND METHODS

This study was conducted at the College of the Virgin Islands Agricultural Experiment Station in St. Croix, United States Virgin Islands.

## Fry Production

Fry were produced in nylon hapas suspended in circular tanks. The hapas consisted of 1.6-mm mesh and were 3.05 m long, 1.22 m wide and 1.22 m deep with a surface area of 3.72m<sup>2</sup>. The vinyl-lined tanks were 3.65 m in diameter and 1.22 m deep with a surface area of 10.51 m<sup>2</sup>. The tanks were maintained at a water depth of 1 m and were occasionally aerated when fish exhibited signs of oxygen stress. During the study, water temperature ranged from 22 to 26°C.

Brood fish (*Tilapia aurea*) were stocked in the hapas at three densities (Table 1) with each treatment density replicated twice. The desired sex ratio for each treatment was four females to one male, but five errors in sex identification occurred as a total of 120 brood fish were stocked, greatly altering the sex ratio among treatments.

The brood fish were stocked on 25 November 1981 and fed at a rate of 1% of the initial body weight per day. The feeding rate of the high density treatment was reduced to 0.5% of the initial body weight from day 52 through 91 and increased to 0.75% from day 92 through 117. The experiment was terminated on 22 March 1982.

Fry were collected initially on day 34 and thereafter at 14-day intervals for a total of seven collections. Only advanced, free swimming fry were counted.

## Fingerling Production

As fry were collected and counted, they were stocked in circular tanks to determine the effect of density on growth. The tanks were vinyl-lined steel swimming pools with a surface area of 9.65 m. The water level was maintained at a depth of 0.8 m. Fry were stocked at densities of 26, 52, 78, 104, 130 and 155 fish/m<sup>2</sup>. Each treatment density was replicated three times. Since there were insufficient numbers of fry to stock all the tanks at one time, fry were stocked as they became available during collection from spawning hapas. Fry were stocked four times over a 6-week period (Table 2). The fry were fed Purina Trout Chow (#1), four times daily for 63 consecutive days beginning the day after stocking.

TABLE 1. Experimental design for fry production; 2 replicates per treatment.

Treatment	1	2	3
No. of brood fish/hapa	10	20	30
Brood fish density (#/m <sup>2</sup> hapa)	2.7	5.4	8.1
No. of females/hapa (desired no.)	8.5(8)	14.5(16)	23.5(24)
No. of males/hapa (desired no.)	1.5(2)	5.5(4)	6.5(6)
Sex ratio (female:male)	5.7	2.6	3.6
Initial mean wt. of females(g)	133	138	158
Initial mean wt. of males(g)	170	187	204

TABLE 2. Stocking and harvest dates of replications of 6 stocking densities of tilapia fry fed for 63 days.

Stocking Density (#/m <sup>2</sup> )	Replication	Stocking Date	Harvest Date
26	1	11 Jan	17 Mar
	2	11 Jan	17 Mar
	3	25 Jan	31 Mar
52	1	28 Dec	2 Mar
	2	11 Jan	17 Mar
	3	25 Jan	1 Apr
78	1	28 Dec	2 Mar
	2	11 Jan	18 Mar
	3	8 Feb	13 Apr
104	1	28 Dec	2 Mar
	2	25 Jan	1 Apr
	3	8 Feb	13 Apr
130	1	11 Jan	16 Mar
	2	25 Jan	10 Mar
	3	25 Jan	31 Mar
155	1	11 Jan	17 Mar
	2	25 Jan	30 Mar
	3	25 Jan	31 Mar

The daily feeding rate, which was based on the modification of a rate used by Snow et al. (1983), was 15% of initial body weight for three weeks, followed by weekly adjustments to 5% of body weight based on biweekly sampling. After 63 days, the fingerlings were harvested, sorted into centimeter-length groups, weighed and counted.

All of the tanks were filled with well water. There was no fertilization, aeration or water exchange during the 9-week experimental period. Several water quality variables were measured weekly using standard methods (APHA et al., 1980). Samples were collected early in the morning. Dissolved oxygen (DO) and temperature were measured with a YSI Model 51-A polarographic oxygen meter. A glass electrode was used to measure pH. Total alkalinity was measured by titration with standard acid to the methyl red-bromocresol green end point. Levels of total ammonia-nitrogen and nitrite-nitrogen were determined by the phenate method and diazotization method, respectively. Chlorophyll *a* was measured by using the acetone extraction method (Vollenweider, 1969).

## RESULTS AND DISCUSSION

### Fry Production

Fry production was extremely variable (Table 3). For example, harvests from individual replicates of Treatment 3 (high density) ranged from 0 to 4,947 fry. Hughes and Behrends (1983) obtained similar variability with *T. nilotica* and attribute this to variability in fecundity, differences in spawning frequency, and the relative asynchrony of spawning cycles of individual females.

Fry production increased with an increase in density of brood fish (Table 4). Production in Treatment 3 was 23.8 fry/m<sup>2</sup> of hapa/day, or nearly twice the production of Treatment 1 (low density). It appears that brood fish density of at least 8.1/m<sup>2</sup> would be necessary to maximize fry production of *T. aurea*. Hughes and Behrends (1983) reported that fry production of *T. nilotica* was greater at a brood fish density of 5/m<sup>2</sup> than at 10/m<sup>2</sup>. Uchida and King (1962) found that fry production of *T. mossambica* peaked at a brood fish density of 11.2/m<sup>2</sup>.

As the density of brood fish increased, fry production per female decreased (Table 4). Production of fry/female/day was 5.3 for Treatment 1 compared to 3.8 for Treatment 3. A similar

TABLE 3. Mean number ( $\pm$  standard error) of tilapia fry collected from hapas during 7 harvests at 2-week intervals. Each harvest is the mean of 2 replications.

Harvest	1	2	3
1	498 ( $\pm 498$ )	87 ( $\pm 41$ )	590 ( $\pm 590$ )
2	960 ( $\pm 544$ )	1040 ( $\pm 701$ )	357 ( $\pm 357$ )
3	766 ( $\pm 766$ )	292 ( $\pm 222$ )	2618 ( $\pm 2110$ )
4	565 ( $\pm 556$ )	1421 ( $\pm 345$ )	908 ( $\pm 136$ )
5	1476 ( $\pm 354$ )	2248 ( $\pm 886$ )	2020 ( $\pm 284$ )
6	1050 ( $\pm 422$ )	660 ( $\pm 660$ )	3426 ( $\pm 1248$ )
7	0 ( $\pm 0$ )	810 ( $\pm 310$ )	445 ( $\pm 268$ )
Mean	759 ( $\pm 184$ )	937 ( $\pm 228$ )	1480 ( $\pm 425$ )
Total	5316	6557	10,362

TABLE 4. Tilapia fry production in hapas during a 117-day period. Each value is the mean of 2 replicates.

Treatment	1	2	3
Fry/m <sup>2</sup> hapa/day	12.2	15.1	23.8
Fry/female/day	5.3	3.9	3.8
Fry/g female/day <sup>1</sup>	0.03	0.02	0.02
<sup>1</sup> Based on the average of initial and final weights of females.			

relationship has been demonstrated for *T. nilotica* (Hughes and Behrends, 1983) and *T. mossambica* (Uchida and King, 1962).

Snow et al. (1983) obtained a fry production rate of 17.8/female/day for *T. aurea* by using a fry transfer method in small tanks without hapas. A lower sex ratio (three females to one male) and stocking density (1.6/m<sup>2</sup>) were utilized. Hughes and Behrends (1983) obtained production of seed of 20.4/females/day for *T. nilotica* in hapas. These production rates were substantially higher than the rates obtained in the present study.

At least two factors contributed to low fry production. First, water quality deteriorated as the result of high standing crops of brood fish and high feeding rates. For example, the final standing crop in Treatment 3 was equivalent to 18,600 kg/ha for the hapa and 6,600 kg/ha for the entire tank. The initial feeding rate in Treatment 3 was equivalent to 129 kg/ha/day for the hapa and 46 kg/ha/day for the entire tank. As dense algal blooms developed, algae clogged the mesh, thereby reducing water circulation and exchange between the hapa and the limited tank volume. Batches of dead eggs were occasionally found during fry collection. Poor water quality reduced fry production.

A second reason for low fry production was that the brood fish were fed at a maintenance level and did not receive the nutrition required for maximum fry production. The daily feeding rate never exceeded 1% of the initial body weight, and as the fish grew, they received less than 1% of their actual weight. The feeding rate in Treatment 3 had to be lowered to 0.5% of the initial body weight to limit deterioration of water quality. Hughes and Behrends (1983) and Snow et al. (1983) fed their brood fish at rates of 3% and 2-3% of body weight, respectively. Uchida and King (1962) found that adequate nutrition was very important in obtaining good fry production.

Hapas and small tanks are appropriate fry production units for small operations. To meet production goals, data generated from this and other studies should be utilized to determine production schedules and unit requirements. If fry are needed continuously, daily averages may be adequate for annual projections. However, fry are usually required in large quantities on a given date to coincide with nursery and growout cycles. In this case, mean production figures are less realistic as the result of high variability. The required number of production units, as determined by using mean fry production rates, should probably be doubled to ensure adequate fry production.

### Fingerling Production

The objective of this experiment was to raise 5-g fingerlings, a size that could tolerate restocking at lower rates for additional growth to a larger fingerling size. After 63 days of intensive feeding, the largest group of fingerlings reached a mean weight of 2.3 g. These fingerlings had been stocked at the lowest density—26 fish/m<sup>2</sup> (Table 5). The initial mean weight of fry for all stocking densities was 0.019 g.

A longer growing period would be necessary to obtain 5-g fingerlings under present experimental conditions. Under different conditions a higher growth rate has been obtained. Snow et al. (1983) produced 4.4-g fingerlings (*T. aurea*) in static tanks in a 40-45 day growing period at a stocking density of 62/m<sup>2</sup>. Weight gain averaged 55.5 kg/ha/day. The highest gain in the present study was 16.4 kg/ha/day at a stocking rate of 104/m<sup>2</sup> (Table 5). In both experiments Purina Trout Chow (crumbles) was fed at a daily rate of 15% of body weight for the first three weeks. The feeding rate was then reduced to 2% in the earlier study and 5% in the present study. The difference in growth between the experiments was the result of fertilization. Snow et al. (1983) fertilized the fry rearing tanks with a commercial inorganic fertilizer (20-20-5 for N-P-K) at a rate of 44.8 kg/ha/week until Secchi disc visibility was less than 30 cm. Natural food production that resulted from fertilization was an important component in

the fry diet and promoted rapid early growth. Algal blooms eventually developed in the present study as the feeding rate increased, but the advantage of abundant amounts of natural food for initial growth was lost. If fertilization is not employed, recent findings suggest that the initial feeding rate should be in the range of 40 to 50% (Kubaryk, personal communication). Feed that is not consumed will serve as organic fertilizer and promote the growth of natural foods.

Survival in this study was generally poor, ranging from 32.7 to 87.8% (Table 5). Density did not affect survival since survival of less than 50% occurred at the lowest and highest densities. The fry were the same size and age when they were stocked so that cannibalism was probably minimal. It seems that predation by dragonfly larvae was the major cause of poor and variable survival. Of the 18 tanks utilized in this study, 15 tanks had been full of water for several weeks before fry were stocked and three tanks were drained, cleaned and refilled the day before stocking. These three tanks were stocked at different rates, but survival was 93.9, 97.3 and 97.4%, rates that were uniformly higher than those in any of the other 15 tanks. Large populations of dragonfly larvae had developed in the previously filled tanks but none developed in tanks that were cleaned prior to stocking.

Variable and poor survival greatly affected the results. There was a large difference between the stocking density and the actual density of fish recovered at harvest (Table 5). The density at harvest probably existed throughout most of the experiment since dragonfly larvae prey on fry right after stocking when they are small in size. The feeding rate was calculated on the assumption of 100% survival and therefore the actual feeding rate was much higher than desired (5%) in the treatments with low survival. Table 5 shows the actual feeding rate for the fish surviving at harvest as well as the feed conversion ratio and the final feeding rate in terms of kg/ha/day. Fish at stocking densities of 52 and 104/m<sup>2</sup> had high survival rates, actual feeding rates of less than 6% and feed conversion ratios of less than 0.9. Fish at these densities converted feed well and grew well through week 9 (Figure 1). However, fish at the higher density grew at a much lower rate, possibly because there was less natural food available per fish. Fish at a stocking density of 78/m<sup>2</sup> were fed at an actual rate of 8.0% and exhibited a feed conversion of 1.57. Apparently the quantity of feed was adequate as indicated by the relatively high conversion ratio. The harvest density (48/m<sup>2</sup>) was nearly the same as the harvest density (45/m<sup>2</sup>) of the fish stocked at a rate of 52/m<sup>2</sup>, but the growth rate was slightly lower (Figure 1). The final feeding rate was 41.8 kg/ha/day, which may have caused some deterioration in water quality although no major differences in water quality were detected among any of the stocking densities (Table 6). Fish stocked at densities of 130 and 155/m<sup>2</sup> were fed at actual rates of 15.3 and 10.4%, respectively, and exhibited poor feed conversion (4.39 and 2.29). A sufficient amount of food was available and yet the final mean weights were low (1.4 and 1.3 g) as the result of water quality deterioration. The final feeding rates were 102.7 and 93.6 kg/ha/day, respectively. Tucker and Boyd (1979) found that a maximum feeding rate of 56 kg/ha/day reduced growth and survival of channel catfish in ponds as the result of water quality deterioration. The absence of bottom sediments in tanks and poor water circulation may cause water quality to deteriorate at lower feeding rates than in ponds. Fish stocked at 26/m<sup>2</sup> were fed at an actual rate of 13.6% and exhibited a poor feed conversion (2.61). However, their growth rate was the highest because the final feeding rate was low (25.3 kg/ha/day) and much natural food was available.

Although poor water quality slowed the growth of fish fed at high rates near the end of the experiment (Figure 1), these fish gained a temporary advantage earlier in the experiment when feeding rates (as kg/ha/day) were lower and the fish were at a size where they were able to consume feed at a higher daily percent-

TABLE 5. Fingerling production data for 6 stocking densities of tilapia fry over a 63-day feeding period. Each value is the mean of 3 replicates.<sup>1</sup>

Density (#/m <sup>2</sup> )	Survival	Total Weight	Mean Weight	Feed	Actual	Final	Weight Gain
Stocking Harvest	(%)	(kg/ha)	(g)	Conversion Ratio	Feeding Rate (% body weight)	Feeding Rate (kg/ha/day)	(kg/ha/day)
26	10	36.9 <sup>a</sup>	210 <sup>a</sup>	2.3 <sup>a</sup>	2.61 <sup>ab</sup>	13.6	25.3
52	45	86.3 <sup>b</sup>	769 <sup>bc</sup>	1.7 <sup>ab</sup>	0.87 <sup>b</sup>	5.8	30.1
78	48	62.2 <sup>ab</sup>	671 <sup>bc</sup>	1.5 <sup>b</sup>	1.57 <sup>b</sup>	8.0	41.8
104	91	87.8 <sup>b</sup>	1051 <sup>b</sup>	1.2 <sup>b</sup>	0.75 <sup>b</sup>	5.7	33.9
130	42	32.7 <sup>a</sup>	595 <sup>c</sup>	1.4 <sup>b</sup>	4.37 <sup>a</sup>	15.3	102.7
155	75	48.1 <sup>a</sup>	984 <sup>bc</sup>	1.3 <sup>b</sup>	2.29 <sup>ab</sup>	10.4	93.6

<sup>1</sup> Numbers within columns followed by the same superscript letter are not significantly different (P<0.05), based on Duncan's multiple range test.

TABLE 6. Water quality of tanks stocked with 6 densities of tilapia fry during a 63-day feeding period. The mean and range are expressed in mg/liter unless otherwise specified.

Variable	Stocking Density (#/m <sup>2</sup> )					
	26	52	78	104	130	155
Temperature (°C)	23.8 22.0 - 25.5	24.0 22.0 - 26.0	24.2 23.0 - 26.0	24.2 22.5 - 26.0	24.0 22.0 - 26.0	24.1 22.0 - 26.0
Dissolved Oxygen	8.0 5.2 - 12.5	8.8 4.1 - 13.0	8.8 4.5 - 10.4	9.0 4.4 - 11.7	8.9 2.4 - 14.8	9.6 3.5 - 14.0
pH (units)	9.1 8.8 - 9.5	8.2 7.8 - 9.7	9.4 8.8 - 10.4	9.3 8.8 - 9.6	9.4 8.3 - 9.8	9.3 8.8 - 9.7
Total Alkalinity	866 643 - 1076	839 598 - 1016	848 594 - 1109	875 580 - 1062	850 641 - 1030	891 658 - 1085
Total Ammonia-Nitrogen	0.13 0.01 - 0.80	0.14 0.01 - 0.75	0.16 0.02 - 0.80	0.15 0.01 - 0.60	0.16 0.01 - 0.98	0.14 0.01 - 0.65
Nitrite-Nitrogen	0.84 0.22 - 1.80	0.90 0.20 - 2.40	1.13 0.50 - 2.40	1.16 0.50 - 2.50	0.96 0.25 - 2.58	1.14 0.36 - 2.30
Chlorophyll "a" (ug/liter)	21.9 7.9 - 62.4	22.2 4.5 - 79.3	34.0 4.5 - 71.8	24.1 3.1 - 60.8	20.6 7.9 - 70.3	20.4 7.9 - 44.2

rage of their body weight. For example, fish at an initial density of 130/m<sup>2</sup> and a final feeding rate of 15.3% had the second highest growth rate throughout the first seven weeks (Figure 1).

A length-frequency distribution of harvested fingerlings was calculated for each stocking density and to determine if any of the stocking densities resulted in the production of fingerlings that were more uniform in size. The results illustrated in Figure 2 show that there was considerable variation in length among all stocking densities. Fingerlings generally ranged from 3 to 9 cm in

length at each density. The most frequently occurring length was 4 cm. The mean weight of 4-cm fingerlings ranged from 0.9 to 1.2 g. The distributions were skewed toward the shorter lengths. Fish that were 7 cm long weighed approximately 5 g. The largest fish at harvest was 10-cm long and weighed 16 g.

In summary, the data indicates that as fish approach a mean weight of 2 g in small static tanks, the feeding rate should be greater than 6% of body weight per day but should not exceed 40 kg/ha/day to maintain good growth and feed conversion.

FIGURE 1. Growth curves of tilapia fry stocked at 6 densities and fed for 63 days. Each point is the mean of 3 replications.

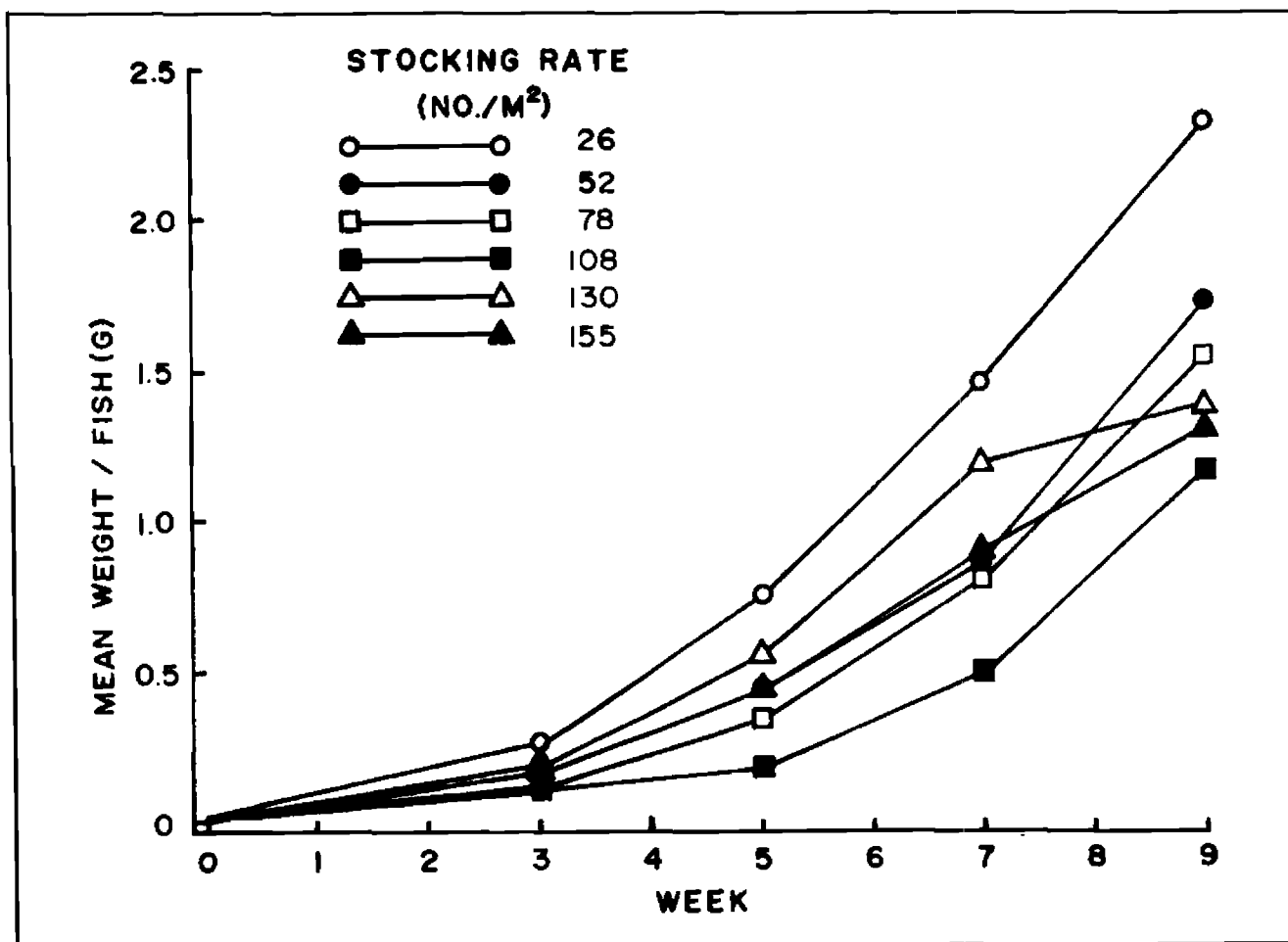
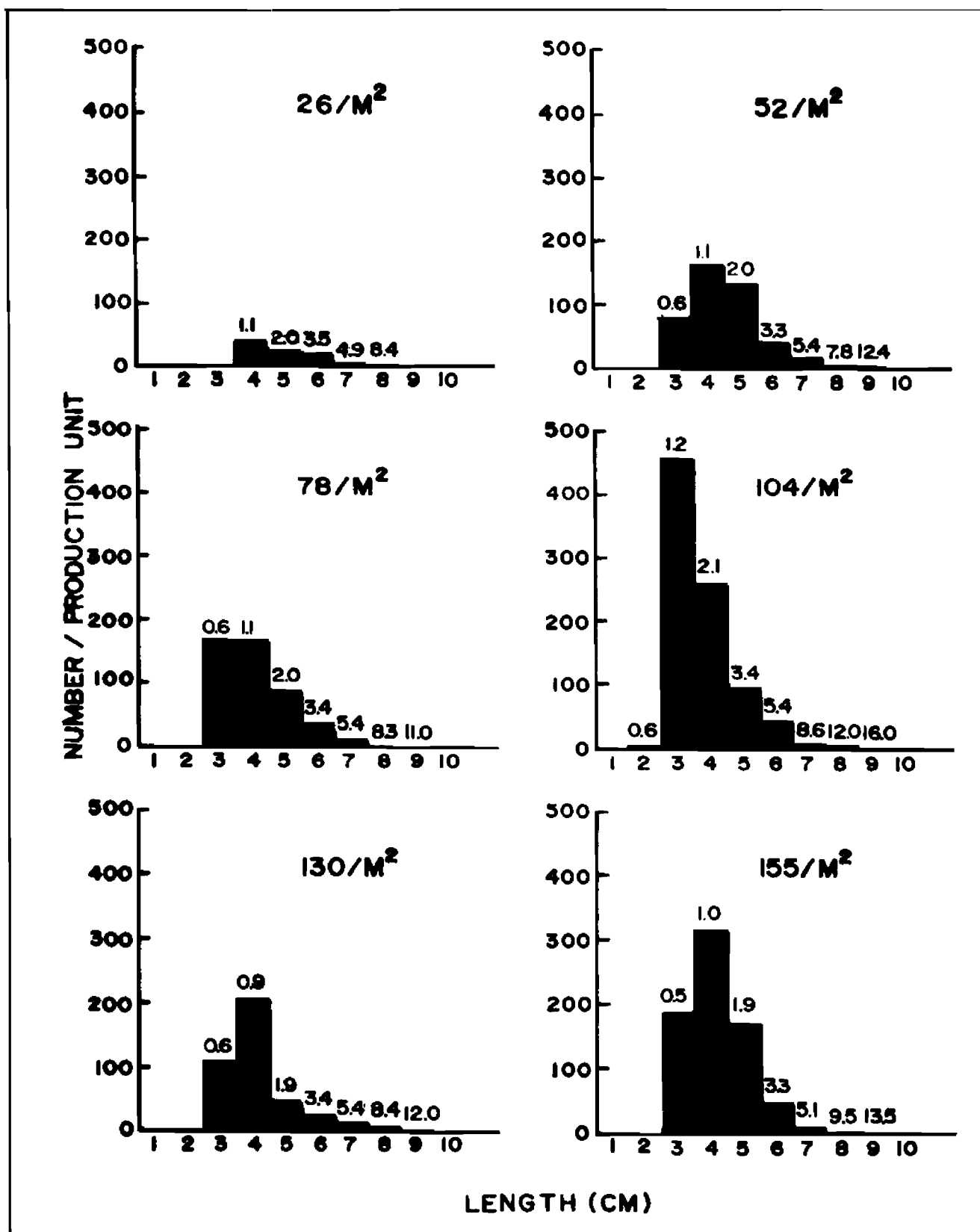


FIGURE 2. Length-frequency distribution at harvest of tilapia fingerlings stocked at 6 densities. The number of fingerlings per production unit is the mean of three replications. The value above each bar is the mean weight of fingerlings in grams of that size group.





## References

1. APHA (American Public Health Association), American Water Works Association, and Water Pollution Control Federation. 1980. Standard methods for the examination of water and wastewater, 15th edition. American Public Health Association, Washington, DC.
2. Hughes, D.G., and L.L. Behrends. 1983. Mass production of *Tilapia nilotica* seed in suspended net enclosures. Pages 394-401 *In*: Proceedings of the International Symposium on Tilapia in Aquaculture, Nazareth, Israel (Eds. L. Fishelson and Z. Yaron).
3. Shelton, W.L., K.D. Hopkins, and G.L. Jensen. 1978. Use of hormones to produce monosex tilapia for aquaculture. Pages 10-27 *In*: Culture of Exotic Fishes Symposium Proceedings. (Eds. R.O. Smitherman, W.L. Shelton, J.H. Grover), Fish Culture Section, American Fisheries Society, Auburn, AL.
4. Snow, J.R., J.M. Berrios-Hernandez, and H.Y. Ye. 1983. A modular system for producing tilapia seed using simple facilities. Pages 402-413 *In*: Proceedings of the International Symposium of Tilapia in Aquaculture, Nazareth, Israel. (Eds. L. Fishelson and Z. Yaron).
5. Tucker, L., and C.E. Boyd. 1979. Effects of feeding rate on water quality, production of channel catfish, and economic returns. Transactions of the American Fisheries Society 108:389-396.
6. Uchida, R.N., and J.E. King. 1962. Tank culture of tilapia. United States Fish and Wildlife Service Bulletin 62:21-152.
7. Vollenweider, R.A. 1969. A manual on methods for measuring primary production in aquatic environments. Blackwell Scientific Publications, Oxford.