By E. L. HAMBLYN

INTRODUCTION

During the course of work on the growth and breeding of the Nile Perch at Sagana in Kenya a number of observations were made on populations of *Tilapia* subject to predation by Nile Perch. This work touches upon a central problem in fish culture, viz., the control of rapidly expanding fish populations by predation where monosex culture or culture of non-breeding species is impractical. *Tilapia* ponds often present this problem which may be approached by considering stock-reduction methods. The use of the Nile Perch in this stock-controlling role is further enhanced by virtue of its qualities as a high-priced table fish. The work on the Luwala Sugar Estate Dam near Jinja, and on the experimental dams at Sagana, suggest two distinct courses of events during stock-control experiments, depending on whether the Nile Perch breeds or not. In further experiments the impact of predation by Nile Perch, and also by Black Bass *(Micropterus salmoides)* over a short period, is detailed for a limited population of *Tilapia nigra,* and the sequence by which a suitable prey population is established and utilized is discussed.

THE FOUR-ACRE DAM AT SAGANA

This dam is an example of a pond where the *Tilapia,* principally *T. melanopleura* and *T. nigra.* were small in size, present in very high numbers and were observed to be breeding at a small size (12.0-16.0 cm. total length). Length frequency distributions for *T. melanopleura* and *T. nigra* at the beginning and end of a fourteen-month period appear in Table AI.

At the beginning *T. nigra* outnumbered *T. melanopleura* by nearly four to one and on average were larger in size. Both species showed unimodal distributions but the mode for *T. melanopleura* was spread over two consecutive length groups (4.0 to 5.9 cm.) at the low end of the range while the modal length of *T. nigra* (7.0 to 7.9 cm.) was clearly defined and was near the centre of the distribution.

At the end of the experiment three well marked modes were evident in the *T. nigra* distribution whereas the *T. melanopleura* distribution was still unimodal, had a well defined modal class and approximated a typical net-selection curve. However, these final samples were obtained by draining the dam and sampling the whole fish population whilst the earlier samples were obtained from seine-net hauls only. Size selection by the seine-net (mesh 16 mm.) would have tended to exclude the smaller fish and would have entirely missed the smallest individuals below the first mode of the *T. nigra* distribution (3.0 to 3.9 cm.). The shape of the original *T. melanopleura* distribution may also have its origin here.

Over the fourteen-month period an increase in the number of *T. melanopleura* relative to the number of *T. nigra* had taken place but the latter species was still larger on average than the *T. melanopleura.* The stock of *T. nigra* were now characterized by relatively strong numbers. The final biomass of *T. nigra* represented nearly three times the biomass of *T. melanopleura* and comprised a small number of large individuals compared to a large number of small individual *T. melanopleura* (Table A.2).

The whole fish population recorded on 22nd March 1962 (with the exception of a negligible number of *Gambusia, Barbus, T. mossambica* and *T. zillii)* is shown in Table A3. The dam had supported 95,100 fish weighing 624.7 kg. But for nine

Nile Perch and the four exceptions noted above all these fish were *Tilapia* which together outnumbered the Nile Perch by 10,566: 1. The ratio by weight, however, was only 20: 1. The Nile Perch had grown from a total weight of 6.5 kg. at the start to 30.4 kg., a gain of 23.9 kg.

In the absence of any numerical estimate for the numbers of *Tilapia* present at the beginning, no numerical changes wrought by the predator can be detected. The emergence of clearly defined length classes amongst the *T. nigra* stock may be a response to the presence of the predator.

This environment was ideal for the growth of Nile Perch in respect of prey fish supply and the failure of the Nile Perch to breed allows some idea of the stocking limits which could operate using a monosex group of predators. In this case 23.9 kg. were produced from 1.6 hectares (four acres) of water having a predator to forage (prey fish) ratio of 20: 1 by weight at the end of 423 days. Production of this level does not compare favourably with the expected production of 842 kg./hectare/year upwards using non-predators alone (Hickling 1962, p.231).

LUWALA SUGAR ESTATE DAM

In this dam of about two acres Nile Perch introduced during October 1959 successfully established a breeding population amongst a stock of *T. zillii.* The sizes of Nile Perch caught in the dam during the experiment are shown in Table A4 together with the measurement of the original stock.

As it was impractical to drain and poison this dam a short period mark-and-recapture technique described by Schnabel (1938) was used to estimate the population of *Tilapia zillii* and *Lates niloticus* within the selection range of 16 mm. seine-net. The results are shown in Table A5, and the length frequency distributions of *T. zillii* at various times between August 1959 and February 1962 appear in Table A6.

The *Tilapia* were abundant in August 1959 but were of small size. The sample of *T. zillii* taken on 22nd December 1960, fourteen months after the introduction of the Nile Perch, was more markedly bimodal than any previous sample and was also the last sample to show more than one distinct length class. The *Lates* progeny were discovered on 5th October 1961, ten months after the latter sample was taken and two years after the introduction of the original stock. The December 1961 sample gave the first information about the *T. zillii* stocks after the discovery of the Nile Perch progeny. Only one mode of length frequency was represented and the *Tilapia* were noticeably fewer in number; the small samples of 1961 and 1962 were taken by five hauls of the seine-net whereas only two or three hauls secured the much greater samples of 1959 and 1960.

The size range in 1961 and 1962 was much the same as in the earlier two years. Male fish (14.0 to 15.0 em. total length) in breeding dress were present, indicating the small size at which breeding was taking place compared to the normal breeding size of males at 23.7 em. total length (Hamblyn 1960, p. 32). The growth of the *Tilapia* from December 1961 through to January 1962 may be followed by the movement of the mode. The growth rate of about 2.0 em. per month of this size range does not suggest an inadequate food supply *(vide* Cridland 1960, p. 139).

The population estimates given in Table A5 show about thirteen times more *Tilapia* than *Lates* living in this dam. By February 1962 no Nile Perch larger than 32.0 em. had been captured and there is no reason to believe that fish larger than thIS SIze were present. Every effort was made to recover members of the parent stock which could have achieved a length of 80-100 cm. by this time (Hamblyn *in press).*

The top end of the length range of *T. zillii,* Le. above 8.5 cm., is beyond the predation range of the Nile Perch which do not eat fish more than one-quarter of their own body length (Hamblyn *in press).* The group of *Tilapia* above 8.5 em. and outside this range susceptible to predation includes the males in breeding dress, so that a reproducing group of *Tilapia* free of direct predation are able to breed at a size smaller than observed amongst wild fish and undesirably small for fish culture.

The Nile Perch were introduced on 16th October 1959 when the *Tilapia* population was in this runted condition and *Lates* appear to have been effective in reducing the numbers present but perhaps not to a density low enough to produce a sustained growth improvement in the *Tilapia* population. The stocks of prey fish *(Tilapia)* present calculated at a density above 1,000 per acre foot does not suggest a failing food supply as a factor controlling the size of the Nile Perch population, nor the *size* attained by individuals.

Whether a growth improvement by the *Tilapia* was possible in an environment carrying a stock at subsistence level, if indeed the stock was at this level, and whether the *Tilapia* were genetically capable of greater growth at the lower density, are undecided questions. Also, behavioural responses to the presence of a predator could be influential in isolating part of the dam as more or less safe areas, and the direct competition between *Tilapia* species in the post-larval stages for the same food organisms *is* yet another form of interaction. An inexplicable growth inhibition which may have affected the Nile Perch suggests that a population density of more than 100 *Lates* per square foot away may be too high. Thus this Nile Perch population may represent a runted stock.

THE MEASUREMENT OF PREDATION

Figures for the actual impact of the predators or a known population of *Tilapia* were obtained in an experiment at Sagana using eight of the fish which later lived in the four-acre dam.

In this experiment, detailed in Table A7, three one-acre dams were each stocked with 2,000 *Tilapia nigra.* Eight Nile Perch were added to one pond, eight Black Bass *(Mieropterus salmoides)* to another, while the third pond was used as a control. At the end of thirty-five days a total count of the fish population was made in all three ponds. In the control pond 25 per cent of the stock were missing while the reduction of the *Tilapia* population in the *Lates* pond was 62.5 per cent and in the *Micropterus* pond was 55.0 per cent. The eight *Lates* had eaten about *750 Tilapia* during this time and had gained 600 gm. in weight as a group (it was assumed that no invertebrate food was taken during the experiment). Disregarding differential growth increments and treating each Nile Perch as equal to one another, each had consumed the 4.0 to 8.0 cm. *Tilapia* (total length) at a rate of 2.68 fish per day. It is also shown that the Black Bass achieved a comparable predation rate of 2.0 to 2.3 fish per day when allowance is made for the death of one Black Bass during the early stages of the experiment.

The total weight increment of the *Tilapia* during the course of the experiment was 0.5 kg. in spite of the destruction of 62.5 per cent of their numbers in the most heavily predated Nile Perch pond. The *Tilapia* in the Black Bass pond did better in this respect, showing an increase of 5.9 kg., but not so well as the control *Tilapia* which gave a net weight increment of 8.8 kg.

THE ESTABLISHMENT OF A PREY POPULATION AND SUBSEQUENT PREDATION

In the experiments described so far there was little known about the establishment of the prey population. Some information about this aspect of fish-culture was gained by stocking a control pond and a predator prey pond, each of 0.25 acres, with three pairs of *Tilapia nigra* and adding twelve small Nile Perch to the predatory-prey pond only. The measurements of the fish used are given in Table A8 which shows the length classes of the original populations and those of the same populations just over five months later.

At the end of the experiment the control pond contained three distinct length frequency modes, each representing a generation amongst the progeny of the original pairs. The predator-prey pond showed a length frequency distribution lacking well marked modes except for a group representing a recent breeding at the lowest limit of the range. Only two of the original twelve Nile Perch were recovered, while all but two parent *T. nigra* were recaptured. The Nile Perch had an average total length of 30.6 em. showing an average monthly growth increment of 3.7 em. At the beginning there were no fish prey of a suitable size present to support the Nile Perch, but at the end of the experiment they had the capacity to prey upon all *Tilapia* less than 8 ern. total length since the maximum size of prey for *Lates* approximates to 25 per cent of the predator length (Hamblyn *in press).* Observations showed the presence of small *Tilapia* in both ponds three weeks after the experiment began, so the Nile Perch may have utilized food other than *Tilapia* (e.g. Odonata nymphs, *Xenopus* larvae) until this time.

The length-frequency distributions given in Table A8 suggest that the first *Tilapia* progeny in the predator-prey pond suffered the heaviest predation (the 12.0 em. group was weak in this pond) and that the smaller *Tilapia* are most vulnerable. In this context Hamblyn *(in press)* has shown that although small *Lates* take small prey and that large fish can take larger prey, large fish still feed largely upon small prey.

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TABLE A1—THE LENGTH FREQUENCY DISTRIBUTIONS OF THE PRINCIPAL *Tilapia* SPECIES IN THE 4-ACRE DAM AT SAGANA ON 19-1-62 AND 22-3-62

Total Length (em.)	NUMBERS OF FISH			
	T. nigra 19-1-62	*T. nigra* 22-3-62	*T. melanopleura* 19-1-62	*T. melanopleura* 22-3-62
1·0- 1·9		2		
2·0- 2·9		27		16
3·0- 3·9	4	99	3	52
4·0- 4·9	19	69	39	135
5·0- 5·9	16	41	39	230
6·0- 6·9	65	155	18	49
7·0- 7·9	196	68	23	18
8·0- 8·9	90	73	11	6
9·0- 9·9	56	138		3
10·0-10·9	32	30		2
11·0-11·9	17	18	1	
12·0-12·9	5	1	2	1
13·0-13·9	1			
14·0-14·9		1		
15·0-15·9		2		
16·0-16·9		1		
TOTAL	501	725	136	512

NOTE :—The division at 5·0 em. represents the lowest size limit retained by the 16 mm. seine-net.

TABLE A2—STATISTICS FROM SUCCESSIVE SAMPLES OF THE PRINCIPAL *Tilapia* SPECIES IN THE 4-ACRE DAM AT SAGANA ON 22-3-62

Sample Number	Species	Number	Range of Total Length (em.)	Weight (gm.)	Mean Weight (gm.)
1	*T. melanopleura* ..	57	4·0- 9'0	170	3·2
	T. nigra	46	3,5-11,0	445	9·7
2	*T. melanopleura* ..	65	4·0- 7·0	165	2·5
	T. nigra	32	3'5-11,5	255	8·2
3	*T. melonopleura* ..	57	3,5- 7·9	145	2·5
	T. nigra	41	4·0-11·0	395	9·6
4	*T. melanopleura* ..	54	3,5- 9·0	185	3·4
	T. nigra	46	4·0-15·0	610	13·3
5	*T. melanopleura* ..	7	2,5- 7·0	1,085	-
	T. nigra	110	2·0-11'5		
6	*T. melanopleura* ..	28	2·0- 8·9	524	—
	T. nigra	71	2·0-11·9		
7	*T. melanopleura* ..	27	2·0- 8·9	545	—
	T. nigra	76	2,5-11'5		
8	*T. melanopleura* ..	29	4·0- 7·4	580	—
	T. nigra	76	3,5-10,5		
9	*T. melanopleura* ..	39	2·0-12·5	665	—
	T. nigra	88	2·0-11·4		
10	*T. melanopleura* ..	50	2,5- 6·9	160	—
	T. nigra	50	2·0- 9·4		
11	*T. melanopleura* ..	63	2·0-10·4	217	—
	T. nigra	37	2·0- 9·9		
12	*T. melanopleura* ..	47	3·0- 8·9	215	-
	T. nigra ..	53	1·0-10·0		

TABLE A3—THE TOTAL FISH POPULATION OF THE 4-ACRE DAM AT SAGANA ON 21-3-62 AND 22-3-62

Date	Time (hr.)	Water Level	Method of Capture	Total Number of Fish	Total Weight of Fish (kg.)
21-3-62	1100	⅓ full	1 seine haul (16 mm.) ..	15,825	126·9
21-3-62	1400	¼ full	1 seine haul (16 mm.) ..	18,934	134·8
22-3-62	0930	Pools	Many seine hauls (16 mm.).	37,965	284·2
22-3-62	1400	Pools	Poisoning, hand collection.	4,737	9·4
22-3-62	1800	Pools	Poisoning, digital counter.	17,590	36·0
22-3-62	Fish selected for consumption			40	3·0
	Total of *Lates niloticus*			9	30·4
	TOTAL			95,100	624·7

TABLE A4—LENGTH FREQUENCY DISTRIBUTION OF *Lates niloticus* IN THE LUWALA SUGAR ESTATE DAM

Total length (cm.)	16-10-59	5-10-61	18-1-62	Numbers of Fish 26-1-62	3-2-62	16-2-62
6·0- 7·9	1	-	-	-	-	-
8·0- 9·9	3	2	1	-	-	-
10·0-11·9	3	5	1	2	2	-
12·0-13·9	5	6	6	5	2	2
14·0-15·9	2	4	5	4	3	3
16·0-17·9	1	3	-	2	2	2
18·0-19·9	-	2	3	2	-	-
20·0-21·9	-	-	1	1	1	-
22·0-23·9	-	-	2	2	4	-
24·0-25·9	-	-	1	-	2	1
26·0-27·9	-	-	-	-	3	1
28·0-29·9	-	-	1	-	-	1
30·0-31·9	-	-	-	1	1	-
32·0-33·9	-	-	-	-	-	-
34·0-35·9	-	-	2	-	-	-
36·0	-	-	-	-	-	-
TOTALS ..	15	22	23	19	20	10

TABLE A5-POPULATION ESTIMATES FOR *Tilapia zillii* AND *Lates niloticus* IN THE LUWALA SUGAR ESTATE DAM
(Within the selection range of a 16 em. seine-net)

Date	N	C	R	M	A	B	C x M	C x M / R	EC x M	ER	EC x M / R
					Tilapia zillii						
18-1-62	5	138	-	-	138	138	-	-	-	-	-
26-1-62	3	134	4	138	134	272	18,492	4,623	18,492	4	4,623
3-2-62	3	70	4	272	70	342	19,040	4,760	37,532	8	4,692
7-2-62	2	4	1	342	4	346	1,368	1,368	38,900	9	4,322
16-2-62	3	24	2	346	-	-	8,304	4,152	47,204	11	4,291
					Lares niloticus						
18-1-62	5	22	-	-	22	22	-	-	-	-	-
26-1-62	3	19	1	22	19	41	418	418	418	1	418
3-2-62	3	20	3	41	20	61	820	273	1,238	4	310
7-2-62	2	2	1	61	2	63	122	122	1,360	5	272
16-2-62	3	16	1	63	-	-	1,008	1,008	2.368	6	395

NOTE.- Where N = Number of seine hauls.
C = Number of unmarked fish captured.
R = Number of marked fish captured.
M = Number of marked fish previously released.
A = Number of new fish marked and released.
B = Total number of fish marked released.
E C x M = Progressive total of C x M
E R = Progressive total of R

C x M / R Population estimate on one day's results.

EC x M / R Population estimate on results to date.

TABLE A6-LENGTH FREQUENCY DISTRIBUTIONS OF *Tilapia zillii* IN THE LUWALA SUGAR ESTATE DAM

Total Length (em.)	13-8-59	15-10-60	6-1-61	22-12-61	29-12-61	18-1-62	26-1-62	3-2-62	7-2-62	16-2-62
4·0– 4·9	1					1		3		
5·0– 5·9	11			9	3	3	3			
6·0– 6·9	6	3	9	45	2	6	1	1		
7·0– 7·9	34	10	46	53	15	6	1	3		
8·0– 8·9	90	18	32	31	21	16	3	5		
9·0– 9·9	66	42	42	11	48	20	10	8		
10·0-10·9	41	88	31	15	24	29	14	9	Results not significant	Results not significant
11·0-11·9	21	94	19	7	13	17	29	13		
12·0-12·9	26	43	5	7	1	10	13	13		
13·0-13·9	35	50	6	3	1	7	11	3		
14·0-14·9	26	76	7	14		2	12	3		
15·0-15·9	8	56	9	24	1	1	10	4		
16·0-16·9	1	20		19	1	1	1			
17·0-17·9	1	6	1	1			2			
18·0-18·9		1					4	1		
19·0-19·9		1	1				1			
20·0-20·9						1	1	1		
TOTALS ..	367	508	208	239	130	120	116	67	4	24

TABLE A7—THE POPULATION OF FISH IN THE 1-ACRE DAMS AT SAGANA DURING PREDATION PRESSURE EXPERIMENTS

Pond	Fish	Number 20-12-60	Number 23-1-61	Weight 20-12-60 (kg.)	Weight 23-1-61 (kg.)	Weight increment (kg.)
Control ..	Prey ..	2,000	1,441	4·4	13·2	8·8
(A2) ..	Predator	nil	nil	nil	nil	nil
Lates ..	Prey ..	2,000	748	4·4	4·9	0·5
(A5) ..	Predator	8	8	5'7	6·3	0·6
Micropterus	Prey ..	2,000	869	4·4	10·3	5·9
(A7) ..	Predator	8	7	7·6	5·45	-

TABLE A8—LENGTH FREQUENCY DISTRIBUTIONS OF PREDATORS AND PREY DURING PREY POPULATION ESTABLISHMENT EXPERIMENTS AT SAGANA

Total Length (em.)	(M=Male F=Female) Population Numbers on 31-1-61			Population Numbers on 5-7-61		
	Control	Predation and Prey		Control	Predation and Prey	
	T. nigra	*Lates*	*T. nigra*	*T. nigra*	*T. nigra*	*Lates*
2·0- 2·9 "	-	-	-	8	-	Number = 2 Average length 30·6 cm
3·0- 3·9 ..	-	-	-	97	19	
4·0- 4·9 ..	-	-	-	7	1	
5·0- 5·9 ..	-	-	-	201	70	
6·0- 6·9 ..	-	-	-	22	88	
7·0- 7·9 ..	-	-	-	-	77	
8·0- 8·9 ..	-	-	-	-	59	
9·0- 9·9 ..	-	-	-	-	85	
10'0-10·9 ..	-	2	-	1	42	
11·0-11·9 ..	-	4	-	32	22	
12·0-12·9 ..	-	3	-	47	11	
13·0-13·9 ..	-	2	-	37	3	
14·0-14·9 ..	-	0	-	12	4	
15·0-15·9 ..	-	1	IF	16	3	
16·0-16·9 ..	3F	-	2F	11	6	
17'0-17·9 ..	-	-	-	-	-	
18·0-18·9 ..	-	-	-	1	-	
19·0-19·9 ..	-	-	-	-	-	
20·0-20·9 ..	-	-	-	-	-	
21·0-21'9 "	-	-	-	-	-	
22·0-22·9 ..	3M	-	3M	1	2	
23·0-23·9 ..	-	-	-	2	-	