SELECTIVE AND UNSELECTIVE EXPLOITATION OF EXPERIMENTAL POPULATIONS OF *TILAPIA MOSSAMBICA*

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ABSTRACT

Two populations of *Tilapia mossambica* were grown under controlled conditions. After a period of growth and stabilization at about 10 kg and 200 fish, exploitation was started; about 50 fish of outside stock were added to each population to increase genetic variability.

Initial exploitation at 10% (later 20%) per 2 mo encompassed all sizes above fry in the unselectively fished population. In the selectively fished population, exploitation was practiced only on fish that could not pass through 25-mm (later 22-mm) vertical slots between glass bars.

Recruitment was estimated from data of stock, mortality, and catch. Parabolas fitted to the stock-recruitment relation suggested greater recruitment in the selectively fished stock than in the unselectively fished one.

Rectilinear thickness-length regressions were calculated for immature and male fish and separately for females.

The exploitation-yield relation was assessed by fitting Fox surplus-yield models to both populations. These revealed a greater maximum sustainable yield in weight from the unselectively fished population than from the selectively fished one. Efficiency of food conversion was 29-36%.

To test for genetic effect of selection, a group of 46 fish, matched as closely as possible in size and sex composition, was selected from each population. Growth in length over a period of 150 days was significantly greater among males from the unselectively fished population than among those from the selectively fished one. Growth in length of females was practically identical for both groups. Growth in total weight was distinctly greater for the group from the unselectively fished population than from the selectively fished one.

As applied to commercial fisheries, the experimental results suggested fishing as wide a range of sizes as possible. If economic gains from selection are indicated, they should be balanced against possible costs in reduced yield and retarded growth rate.

Controlled selective breeding for desirable attributes in plants and animals is a well-recognized technique in agriculture. This technique has also had limited application in fish culture, particularly with trout. Claimed achievements have included increased size and earlier age at maturity. Fishery biologists have speculated whether the reverse process, attainment of undesirable attributes, may have occurred in some fished populations because of inadvertent imposition of selection by the fishery. Although gill nets and trawls are perhaps the most obvious gear elements causing selection, the phenomenon is probably present to some extent with practically all fishing gears. It thus becomes a matter of considerable economic importance to determine if gear selectivity has adversely affected fish stocks.

The general subject of selection for slow growth by fishing was briefly reviewed by Miller (1957). He adduced no data, however, and drew no firm conclusions, merely noting that he knew of no instances where changed growth rates in fish could not be attributed to some cause other than genetic change. It seems entirely possible, nevertheless, that such a change could occur, if selection were of sufficient strength and continued during a sufficient number of generations. Such a possibility is indicated by the success of artificial selection in altering quantitative characters in a wide variety of organisms.

The purpose of the work reported herein was to test experimentally whether selective fishing could produce a genetic change in the growth pattern of the fish in the fished stock. This problem was approached by growing two populations of Mozambique tilapia, *Tilapia mossambica*, under as nearly identical conditions as possible. One of these was then fished selectively from only those fish above a fixed thickness. The other was fished over the entire range of sizes, except the small "fry."

A secondary purpose was to compare amount and size composition of the yields under selective

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and unselective fishing. To achieve this comparison, records of weight and size composition were kept for each catch made during the experiments.

MATERIALS AND METHODS

For the experimental animal, *Tilapia mossambica* was chosen. This species is hardy and will grow readily in experimental tanks. It also is used widely in tropical pond culture and thus has some economic importance. Since it is a mouth breeder, handling and exploitation were done only at approximately 2-mo intervals.

Tanks, feeding, etc. were as reported in Silliman (1970) and represented a modification of the methods of Uchida and King (1962). Briefly summarized, the procedures were to raise the two populations in hatchery-type troughs of 850-liter (225-gallon) capacity. Water condition was maintained either by changing it biweekly or by a continuous dribbling flow into the head of each trough plus bimonthly partial changing. Temperature was maintained at 80° ± 5°F or 26.7°C (weekly means). Illumination was by fluorescent light 12 h per day. Feeding schedules and water condition are detailed in Tables 1 and 2.

Rectangular enclosures at the standpipe ends were separated from the rest of the troughs by plates with 3-mm holes through which the newly expectorated "fry" could escape, thus furnishing them refuges from cannibalism by the adults. After each counting, all fish in the refuges were placed in the main part of the tanks.

Fishing was done at approximately 2-mo intervals by removing each nth fish for fishing rate $1/n$ (n was always an integer). For the selectively fished population, all fish were placed on one side of a grid consisting of 25-mm diameter vertical glass rods spaced 25 mm (22 mm in latter part of experiment) apart. All fish were provided an opportunity to swim through the spaces between the rods; only those which could not do so were fished. In the unselectively fished population all sizes were fished except the fry (under 4-mm thickness).

Counting was done simply by netting fish from one container to another. For weighing, fish were drained in a net and then placed in a previously weighed container of water. Fish weight was obtained by subtracting the tare from the total.

All caught fish and the preexploitation stocks were measured for thickness and length. They were categorized as immature (where sex could not be determined by external inspection), male, and female. Sex determination was based on the characteristics set forth by St. Amant (1966). Length (total length to outermost tip of caudal fin) was measured on a board with millimeter scale and head block. Thickness was measured on the same device, plus a sliding block; the fish were held upright between the sliding block and the head block with firm pressure for the thickness measurement. Fish for the pretest measurements

TABLE 1.—Food placed in tanks, grams.

			Trout pellets		Tropical fish food		
Date[1]	Month	Day of week	Moist	Dry	A[2]	B[2]	Total
15 Aug. 1966	0.5-40.2	Sun.	30	10	4	5	49
to		Mon.	40	10	4	10	64
6 Dec. 1969		Tues.	40	10	4	10	64
		Wed.	40	10	4	10	64
		Thurs.	40	10	4	10	64
		Fri.	40	10	4	10	64
		Sat.	40	10	4	10	64
		Total	270	70	28	65	433
7 Dec. 1969	40.2-82.2	Sun.	30	10	4	5	49
to		Mon.	40	10	4	10	64
5 June 1973		Tues.	40	10	4	10	64
		Wed.	40	10	4	10	64
		Thurs.	40	10	4	10	64
		Fri. A.M.	40	10	4	10	64
		Fri. P.M.[3]	40	10	4	10	64
		Total	270	70	28	65	433

[1] Diet was varied initially to achieve optimal reproduction and growth; it was stabilized at the listed amounts on 18 June 1967, month 10.6.

[2] Commercal makes of dry food.

[3] This feeding was combined with the Friday A.M. feeding in 37 out of 183 wk. and with the Sunday feeding once.

TABLE 2.—Water condition on selected dates.[1]

Date	Month	O_2 (ppm.)		CO_2 (ppm.)		pH	
		Test[2]	Control[3]	Test[2]	Control[3]	Test[2]	Control[3]
1968:							
9 Aug.	24.3	5.2	5.0	—	—	—	—
16	24.5	4.6	4.4	—	—	—	—
29	24.9	4.8	4.8	10	10	6.9	6.9
6 Sept.	25.2	3.6	3.8	—	—	—	—
13	25.4	3.6	3.6	—	—	—	—
20	25.7	4.0	4.4	10	10	—	—
27	25.9	4.0	4.0	—	—	—	—
4 Oct.	26.1	4.0	4.4	—	—	—	—
11	26.4	3.8	4.0	—	—	—	—
18	26.6	3.0	3.8	—	—	—	—
25	26.8	3.0	4.0	—	—	—	—
8 Nov.	27.3	3.6	4.0	—	—	—	—
15	27.5	3.4	4.0	—	—	—	—
28	27.9	4.2	4.4	—	—	—	—
6 Dec.	28.2	3.8	4.0	—	—	—	—
13	28.4	3.4	4.0	—	—	—	—
26	28.8	3.0	3.4	—	—	—	—
1969:							
2 Jan.	29.1	3.4	3.6	—	—	—	—
17 Sept.	37.6	5.2	4.8	10	10	6.5	6.7
2 Oct.	38.1	5.4	5.4	—	—	—	—
9	38.3	5.0	4.8	—	—	—	—
23	38.7	5.0	4.8	—	—	—	—
30	39.0	5.4	5.0	—	—	—	—
1971:							
25-26 Feb.	54.9	4.6	4.4	20	20	6.0	6.0
1972:							
23 Mar.	67.7	3.4	[4]2.6	20	25	6.5	6.5
1973:							
29 May	81.9	3.4	3.2	15	15	7.0	7.0

[1] With the exception noted in footnote 4, all values were within (or above for oxygen) the ranges stated to be suitable for warmwater fishes by Lewis (1963). These were: oxygen, 3-5 ppm.; carbon dioxide, below 30 ppm.; pH, 5-9.

[2] Selectively fished.

[3] Unselectively fished.

[4] Aeration was increased and O_2 had risen to 3.8 ppm. by the next day.

were anesthetized with MS-222 [2] (tricaine methanesulfonate) in a 1:2,500 solution. Caught fish were measured some time after removal. They were usually alive or freshly dead, and rigor mortis was rare. The group selected for growth study at the end of the experiment was measured alive without an anesthetic.

COURSE OF POPULATIONS

A single population was started on 15 August 1966, but this was divided into two populations as nearly equal as possible after 2 mo. A period of population growth then ensued (Table 3, Figures 1, 2). This growth was extensively discussed by Silliman (1970), who found growth in biomass of the two populations to be practically identical. He therefore combined the two populations for growth analysis. A Gompertz curve fitted to the total biomass of both populations had the formula $W_t = 1.337 \exp[2.85 - 2.85 \exp(-0.2\,(t-3.6))]$, where W_t is biomass in kilograms at the time t in months. The asymptote of this curve was 23.1 kg or 11.55 kg per population. An accidental interruption to population growth (Figures 1, 2) resulted from temporary relocation of the fish during refinishing of the laboratory floor. After recovery and re-equalization, the populations did not approach the asymptote predicted by the Gompertz curve but leveled off at about 10 kg each.

Because the fish were descendants of an original three males and three females, I felt that in-

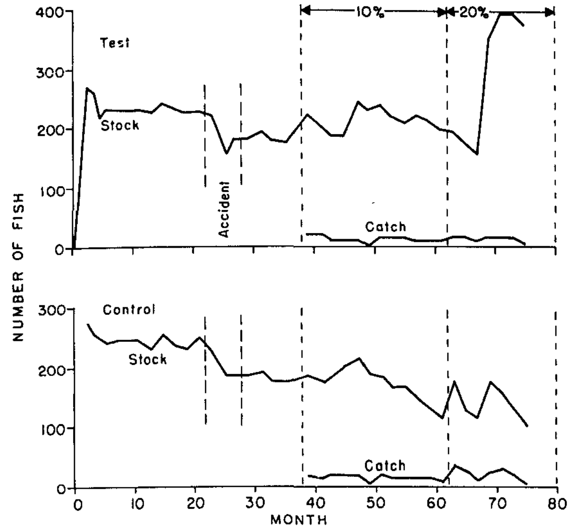

FIGURE 1.—Population size and catch, numbers. Percentages indicate target exploitation rates. Test population was selectively fished; control, unselectively.

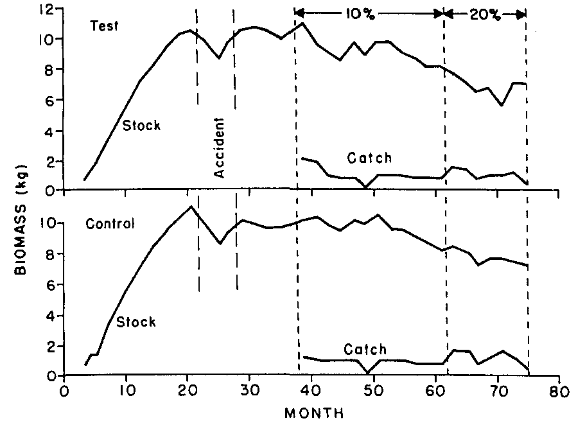

FIGURE 2.—Population size and catch, weight. Percentages indicate target exploitation rates. Test population was selectively fished; control, unselectively.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 3.–Population and catch, *Tilapia mossambica.*

		Test (selectively fished) population				Control (unselectively fished) population			
	Target expl.	Number		Weight (g)		Number		Weight (g)	
Month[1]	rate[2]	Stock	Catch	Stock	Catch	Stock	Catch	Stock	Catch
0.5	0.00	6	—	—	—	—	—	—	—
2.5		272	—	—	—	273	—	—	—
3.6		258	—	856	—	253	—	825	—
4.5		220	—	1,318	—	251	—	1,325	—
5.5		231	—	1,924	—	239	—	1,447	—
7.5		228	—	3,306	—	247	—	3,303	—
10.5		228	—	5,614	—	246	—	5,749	—
13.0		224	—	7,420	—	232	—	7,313	—
15.0		239	—	8,275	—	253	—	8,692	—
17.1		228	—	9,346	—	237	—	9,448	—
19.2		226	—	10,174	—	232	—	10,244	—
21.1		224	—	10,459	—	251	—	10,907	—
23.2		[3]221	—	[3]9,859	—	[3]226	—	[3]9,826	—
25.4		[3]156	—	[3]8,567	—	[3]186	—	[3]8,561	—
27.2		181	—	9,560	—	184	—	9,431	—
29.1		180	—	10,415	—	183	—	9,967	—
31.3		189	—	10,525	—	189	—	9,791	—
33.1		181	—	10,348	—	177	—	9,622	—
35.3		177	—	9,881	—	173	—	9,661	—
39.2	0.10	218	19	10,760	2,023	183	18	10,009	1,168
41.3		201	18	9,468	1,714	174	17	10,139	1,033
43.2		187	8	8,984	906	187	18	9,743	974
45.2		187	8	8,311	794	199	19	9,300	956
47.3		[4]240	8	[4]9,534	883	[4]217	22	[4]9,917	909
48.9		231	2	8,860	182	191	4	9,843	191
51.2		233	14	9,690	960	186	18	10,368	1,057
53.2		217	14	9,575	991	163	16	9,532	927
55.1		207	14	9,037	929	165	16	9,315	951
57.2		221	12	8,542	848	148	15	8,956	895
59.0		210	10	8,056	806	131	13	8,507	827
61.1		196	10	7,935	853	117	12	8,287	824
63.2	0.20	191	17	7,687	1,575	177	35	8,322	1,681
65.4		172	17	6,944	1,377	124	25	7,965	1,531
67.1		157	11	6,382	738	114	12	7,261	840
69.1		345	15	6,684	1,050	176	26	7,592	1,217
71.2		388	14	5,465	1,061	155	31	7,664	1,574
73.2		389	14	7,046	1,170	123	21	7,389	1,272
75.1		371	6	6,901	438	101	6	7,280	459

[1] 0 = 1 August 1966.

[2] Because of selection problems, actual rates varied considerably from these. In analyses, effective rates in terms of weight were used.

[3] Populations re-equalized after accidental mortality from temporary relocation of fish.

[4] New fish added for genetic variability.

sufficient genetic variability might exist in the populations to permit a genetic effect of selection. Since one of the major objectives of the experiment was to detect such an effect, I decided to add outside stock. During the 2-mo period preceding month 47.3 (Table 3), I added 45-47 (2 fish uncertainty due to counting difficulties) immature *Tilapia mossambica* from Arizona to each population. These fish were descendants of ones from Malacca.

Exploitation was started at month 39.2 (Table 3, Figures 1, 2) at a conservative 10% per 2 mo. This exploitation period included 1.0 to 2.6 of the brood intervals reported by various authors (Kelly 1957, 30-40 days; Swingle 1960, 30-40 days; Uchida and King 1962, 23-61 days). Because of irregularities in recruitment, population numbers (Figure 1) reflected population responses less well than population biomasses (Figure 2). The latter, however, generally reflected the expected population decrease from imposition of the 10% exploitation rate. When the rate was increased to 20% at month 63.2 (Table 3, Figure 2), further declines in population biomasses occurred.

BASIC RELATIONS

Recruitment was estimated from changes (R_{INT}) in stock number and data of mortality and catch (Table 4), using the approach of Silliman (1972). Because of variations in length of period between counts, values of R_{INT} were adjusted to a standard 2-mo interval (Table 4). Observation of large numbers of fry in the refuges, followed by the later appearance of peaks of recruitment (Table 4), indicated that the "reproductive lag" was about 2

TABLE 4.—Recruitment and stock. $R_{\mathrm{INT}} = P_{n+1} - P_n + M_{\mathrm{INT}} + C_{\mathrm{INT}}$, where P is stock, INT is interval between counts n and $n+1$, R is net change[1], M is recorded mortality and C is catch, all in numbers. $\bar{S}$ is mean stock in kilograms for previous interval.

Interval (months)	Interval length (months)	Selectively fished population			Unselectively fished population		
		R_{INT}	$^2R_{\mathrm{INT}}$	$\bar{S}$	R_{INT}	$^2R_{\mathrm{INT}}$	$\bar{S}$
5.5- 7.5	2.0	−3	−3.0	1.4	+9	+9.0	1.1
7.5-10.5	3.0	+1	+0.7	2.6	+1	+0.7	2.4
10.5-13.0	2.5	+4	+3.2	4.4	−13	−10.4	4.5
13.0-15.0	2.0	+15	+15.0	6.5	+21	+21.0	6.5
15.0-17.1	2.1	−5	−4.8	7.8	−5	−4.8	8.0
17.1-19.2	2.1	−2	−1.9	8.8	−5	−4.8	9.0
19.2-21.1	1.9	0	.0	9.8	+19	+20.0	9.8
25.4-27.2	1.8	+25	+27.8	—[3]	−1	−1.1	—[3]
27.2-29.1	1.9	−1	−1.1	9.1	−1	−1.1	9.0
29.1-31.3	2.2	+9	+8.2	10.0	+6	+5.5	9.7
31.3-33.1	1.8	−6	−6.7	10.4	−12	−13.3	9.9
33.1-35.3	2.2	−2	−1.8	10.4	−2	−1.8	9.7
35.3-39.2	3.9	+44	+22.6	10.1	+16	+8.2	9.6
39.2-41.3	2.1	+7	+6.7	10.8	+10	+9.5	9.8
41.3-43.2	1.9	+4	+4.2	9.1	+30	+31.6	9.4
43.2-45.2	2.0	+8	+8.0	8.4	+30	+30.0	9.4
45.2-47.3	2.1	[4]+16	+15.2	8.2	[4]−6	−5.7	9.0
47.3-48.9	1.6	+2	+2.5	8.5	0	.0	9.1
48.9-51.2	2.3	+4	+3.5	8.8	−1	−0.9	9.4
51.2-53.2	2.0	−1	−1.0	9.2	−3	−3.0	10.0
53.2-55.1	1.9	+5	+5.3	9.2	+18	+18.9	9.4
55.1-57.2	2.1	+31	+29.5	8.8	0	.0	9.0
57.2-59.0	1.8	+3	+3.3	8.3	−1	−1.1	8.7
59.0-61.1	2.1	−2	−1.9	7.9	+2	+1.9	8.3
61.1-63.2	2.1	+5	+4.8	7.6	+73	+69.5	8.0
63.2-65.4	2.2	−1	−0.9	7.4	−16	−14.5	7.9
65.4-67.1	1.7	+3	+3.5	6.5	+15	+17.6	7.3
67.1-69.1	2.0	+199	+199.0	6.0	+75	+75.0	6.8
69.1-71.2	2.1	+62	+59.0	6.2	+6	+5.7	7.0
71.2-73.2	2.0	+16	+16.0	5.6	−1	−1.0	7.0
73.2-75.1	1.9	−2	−2.1	5.7	+1	+1.1	6.8

[1] $R_{\mathrm{INT}} > 0$ indicates recruitment of at least the indicated number of fish; $R_{\mathrm{INT}} < 0$ indicates unrecorded mortality of at least the indicated number and $R_{\mathrm{INT}} = 0$ indicates either no recruitment and unrecorded mortality or the two exactly balanced.

[2] Adjusted to a standard 2-mo interval length.

[3] Indicated intervals omitted because of re-equalization of stocks.

[4] Exclusive of 46 new fish added for genetic variability.

mo. Each value of R_{INT} was therefore compared with the mean stock ($\bar{S}$) for the preceding 2-mo interval (Table 4).

The stock-recruitment data were highly variable and were, therefore, treated as group means based on 5-kg intervals of $\bar{S}$, considering negative values of R_{INT} to be equal to zero. Although the data indicated no regular relation (Figure 3), they were fitted with parabolas to indicate central tendency, even though fits were poor. These, based on 30 pairs of observations each, were:

Selectively fished stock

$$R_{N+1} = 6.163\ \bar{S}_N - 0.5209\ \bar{S}_N^2.$$

Unselectively fished stock

$$R_{N+1} = 3.304\ \bar{S}_N - 0.2158\ \bar{S}_N^2,$$

where N is number of the 2-mo interval, R is in

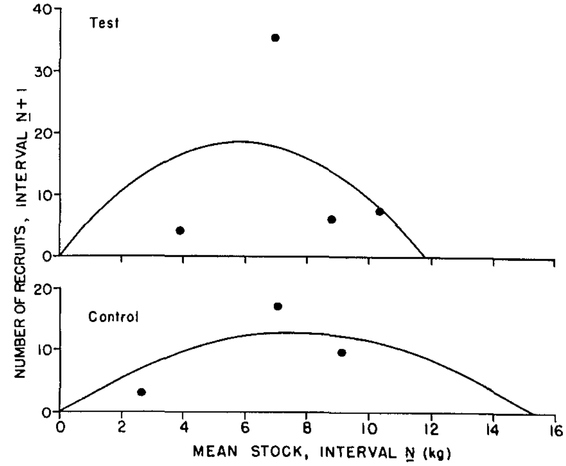

FIGURE 3.—Stock and recruitment. Test population was selectively fished; control, unselectively. Parabolas shown were fitted by least squares.

numbers, and S is in kilograms. The somewhat higher maximum for the selectively fished stock may have resulted from its changed size composition; it included fewer extremely large males than the unselectively fished population.

Since selection reflected the ability of fish to escape through vertical slots between glass bars, thickness was the controlling dimension. Most of the fish-size data in this report are therefore in thickness. However, to reduce fish handling to a minimum, the growth measurements of live fish during the final part of the experiment were in lengths. Because of this, and because other biologists may wish to compare their length data with my thickness data, I calculated thickness-length relations.

Measurements for the relation were from the caught fish, for which both thickness and length were recorded. Preliminary analysis showed that data for immature and male fish could be combined into a single rectilinear regression of length on thickness. The regression for females was also rectilinear but had a gentler slope, probably because of the distention of mature fish carrying eggs. It was therefore calculated separately. The regression equations, numbers of pairs of observations in parentheses, and correlation coefficients were (fitting was by least squares):

Immature and male

$$L = 7.027\,T \qquad (368) \qquad r = 0.987 \qquad r^2 = 0.974.$$

Female

$$L = 26.89 + 5.037\,T \qquad (207) \qquad r = 0.866 \qquad r^2 = 0.750,$$

where L is length and T is thickness, both in millimeters. The squared coefficients suggest that 97 and 75% of variations in length were associated with variations in thickness.

RESULTS

Exploitation and Response

Before selective exploitation could be started, it was necessary to determine the selection point. To aid in this the thickness of all of the fish in both populations was measured at month 33.5. At this time the population to be selectively fished (pretest) consisted of 85 males and 95 females—that to be unselectively fished (precontrol), 77 and 98, respectively. The thickness frequencies (Figure 4) revealed a low point in the pretest population between males and females at about 25 mm. This was used as the initial selection point and it meant, of course, that the early catches were mostly males. It will be shown below, however, that later catches were composed of roughly equal proportions of males and females.

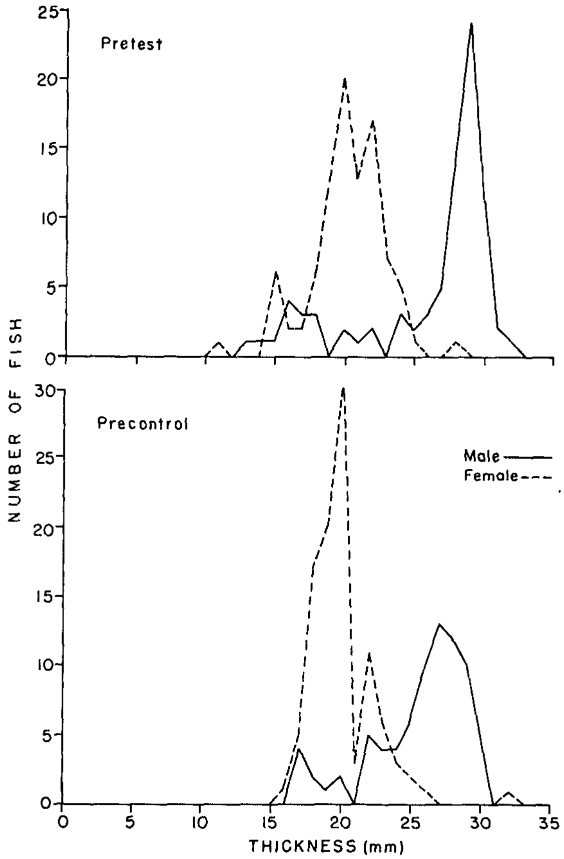

FIGURE 4.—Thickness frequencies at month 33.5. Test population was to be selectively fished; control, unselectively.

Changes from exploitation, in addition to those described under "Course of Populations," were reflected in the size composition of the catches (Figures 5, 6). In the test population, the catches were roughly the target percentage of the selected group; the percentages in the control population were adjusted to take the same proportion of the entire population as taken in the test population. Percentages were by number at months 39.2 and 41.3, but it became evident that this procedure took too large a proportion of the biomass. At months 43.2-75.1, the percentages were by weight

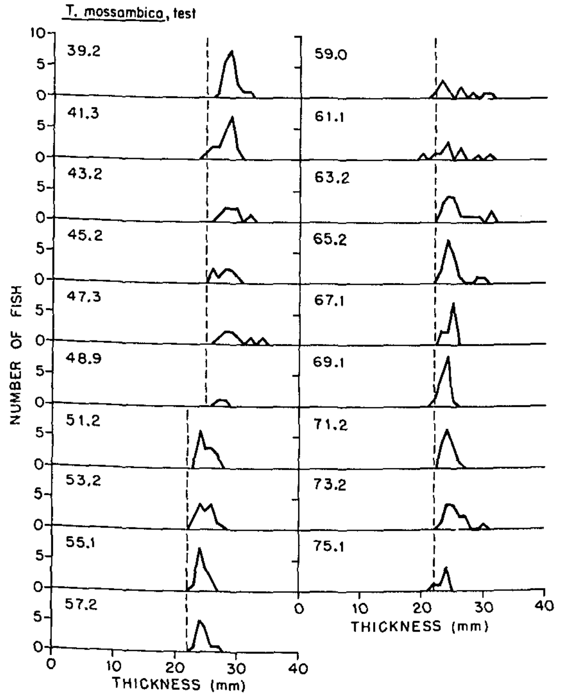

FIGURE 5.—Bimonthly thickness frequencies of catches, test (selectively fished) population. Vertical broken lines indicate selection points. Numbers in panels indicate months from start.

(Table 3). Numbers of fish growing above the selection point rapidly diminished in the test population (Figure 5) so that insufficient numbers were available from which to catch the target percentage. To continue exploitation, it was necessary to lower the selection point to 22 mm as shown. With few exceptions, all fish caught from the test population were above the selection point.

Catches from the control population were taken representatively over all sizes larger than fry and, therefore, represented the size composition of the stock above the fry size (Figure 6). Significant amounts of recruitment at months 43.2, 45.2, 55.1, 63.2, 67.1, and 69.1 (Table 4) appear as modes of small fish in the size frequencies, and the more prominent ones can be traced through succeeding frequencies.

A summary of catch size frequencies (Figure 7) clearly reveals the differences between catches from test and control populations. It is evident that the selection device employed was almost completely effective. The appearance of roughly equal proportions of males and females in the test catches, after lowering the selection point, is also apparent. It can be seen that a selection curve was at work, such that fish were not fully retained until they had reached a thickness of about 2-4 mm above the selection point.

The relation of yield to exploitation was assessed by fitting a Fox (1970) exponential surplus-yield model to data of catches and stock (Figure 8). The method of fitting used requires equilibrium yields. Although absolute equilibrium obviously was not attained, it was considered that the biomass and catch levels (Figure 2) at months 29-35 (zero exploitation), 59-61 (10% target rate), and 69-73 (20% target rate) represented sufficiently close approximations to equilibrium for fitting the model. The calculated maximum sustainable yield (1.39 kg per 2 mo) from the selectively fished test population was substantially lower than that for the unselectively fished control (2.36 kg). If we wish to consider a comparable commercial fishery, however, we might assume that only the fish above the selection point are commercially desirable. Catch thickness frequencies for the 22-mm selection point (Figure 7) showed that 97% of the fish in test catches were above the selection point as compared with 40% for the control catches. Although these data cannot be

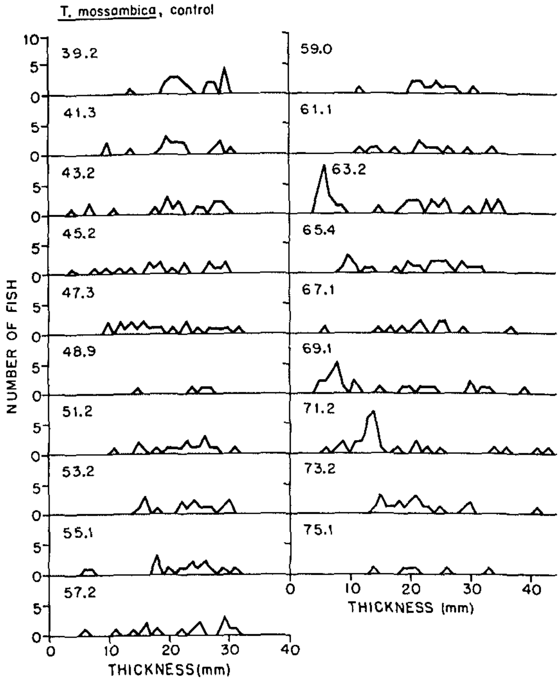

FIGURE 6.—Bimonthly thickness frequencies of catches, control (unselectively fished) population. Numbers in panels indicate months from start.

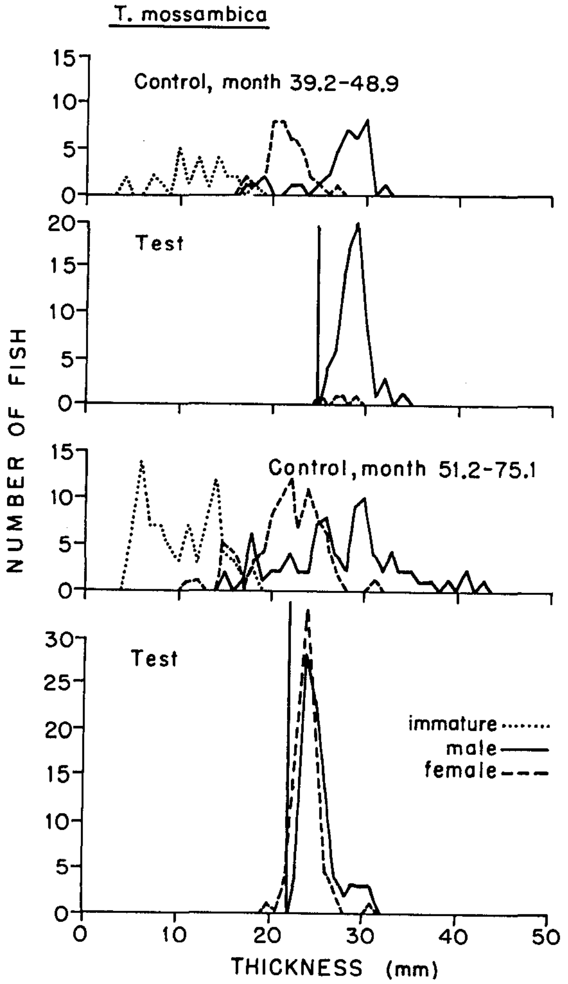

Figure 7.—Summary of catch thickness frequencies. Test population was fished selectively; control, unselectively. Vertical lines indicate selection points.

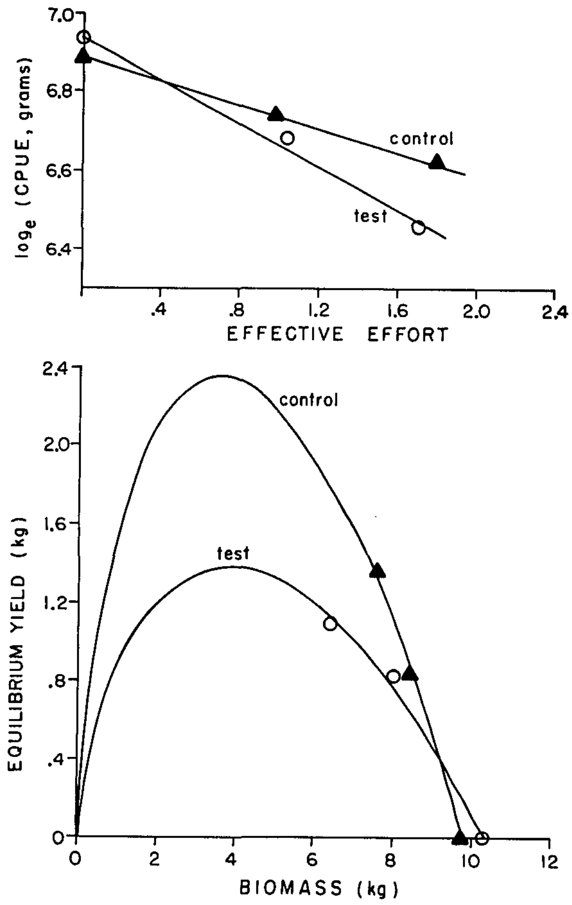

Figure 8.—Fitting of Fox (1970) model. Catch-per-unit-effort (CPUE) is considered proportional to biomass; effort is in arbitrary units. Regression lines shown are least-squares fits. Target exploitation rates were 0, 10%, and 20% per 2 mo, left-to-right in upper panel, reversed in lower panel.

converted to weights, it is certain that the comparison for fish above the selection point would be more favorable to the test catches than was true for all sizes of fish.

It is possible to calculate the efficiency of conversion of food to fish flesh under both types of fishing. The amount fed per 2-mo period was 3.75 kg (433 g per week from Table 1, for 8⅔ wk). Maximum sustainable yields (MSY's) of 1.39 kg and 2.36 kg indicate 37 and 63% conversion efficiencies for selective and unselective fishing, respectively. Since the theoretical MSY's represent a considerable extrapolation (Figure 8), it is of interest to calculate from equilibrium yields actually attained during the experiment. The largest yields were under the 20% per 2-mo target rate for both populations. Effective exploitation rates and corresponding yields were: selectively fished, 17.1% and 1.09 kg; unselectively fished, 17.9% and 1.35 kg. These yields indicate 29 and 36% efficiency, respectively. The values are in fair agreement with the 33% calculated by Silliman (1970) for the initial growth of the populations.

Genetic Response

Knowledge of the number of generations involved is essential to any genetic experiment. Progression of the two most prominent thickness frequency modes (months 63.2 and 69.1) in the unselectively fished population (Figure 6) gave an indication of the growth rate of the fish. Frequencies of thickness for immature and mature fish (Figure 7) suggested a thickness at maturity of about 15-20 mm. The two prominent modes in the frequencies seemed to require about 4 mo (63.2-67.1, 69.1-73.2) to reach this size. To this must be added the 2-mo "reproductive lag" mentioned above under "Basic Relations," suggesting a generation length of about 6 mo. The 36-mo period of selective fishing would thus include about six potential generations. Because of irregularities in recruitment, however, the effective number of generations was less, and it was necessary to make an estimate.

Such an estimate can be derived from the record of recruitment numbers (R_{INT}, Table 4, Figure 9). An arbitrary criterion for significant recruitment was established, requiring at least 15 recruits per 2 mo. A generation was considered to be such a peak separated from the previous filial generation by a period of at least 6 mo (the parental generation for the test group had been fished selectively at month 40). Under the arbitrary criterion the estimated generations (Figure 9) during the selection period were only three for the selectively fished test and four for the unselectively fished control population. Experiments with other animals, such as those of Robertson with thorax length of *Drosophila* cited by Falconer (1960), have shown that measurable change in a size character can occur in as few as three generations of selection.

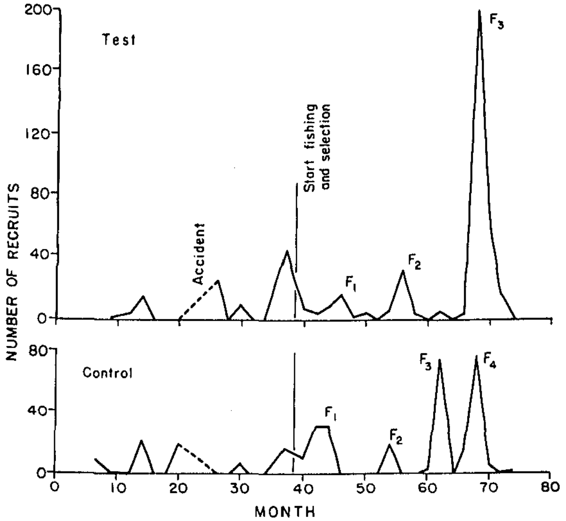

Figure 9.–Recruitment numbers from R_{INT} in Table 4, with negative values considered zero. Test population was selectively fished; control, unselectively.

TABLE 5.–Growth of selected groups of fish. Lengths are from snout to tip of tail.

		Male		Female		Total	
Group	Day[1]	No.	Mean length (mm)	No.	Mean length (mm)	No.	Wt. (g)
Test	0	10	152.0	36	140.6	46	2,158
	56	[2]9	180.0	[2,3]36	155.0	45	3,199
	118	9	197.8	[4]34	165.0	43	3,794
	150	9	207.2	[3]33	169.8	42	4,078
Control	0	10	148.0	36	141.4	46	2,561
	55	[5]8	195.0	[3,5]37	153.4	45	3,504
	119	8	235.6	[6]35	164.4	43	4,455
	151	8	253.1	[7]34	169.1	42	4,819

[1] 0 = 5 January 1973.
[2] One female misclassified as male on day 0.
[3] One female died.
[4] Two females died.
[5] Two females misclassified as males on day 0.
[6] Two females removed to match mortalities in test group.
[7] One female removed to match mortality in test group.

To test whether genetic response to selection did occur, groups of 46 mature fish as similar in sex and length composition as possible were selected from test and control populations on 5 January 1973 at month 77.2 (Table 5). It was not possible to match these fish as closely as desired by total weight, and that of the control group exceeded that of the test group by 19%. These fish were fed the standard diet (Table 1) which furnished them, even at the end of the growth period, with 1.5% (test) or 1.3% (control) of body weight of food per day. This was 2.5 (test) or 2.1 (control) times as much as was received by the 10 kg preexploitation stocks. Any offspring that appeared were removed as soon as possible.

Growth of the selected fish was measured by determining the lengths of individual fish and the total weight of each group at 55-56, 118-119, and 150-151 days after the start of the growth period (Table 5, Figures 10, 11). The length frequencies reveal the general correspondence of the groups at the beginning of the period, in addition to the expected more rapid growth of the males than the females in each group. They also reveal that the males in the unselectively fished control group grew more rapidly than those in the selectively fished test group.

Growth was further studied by curves based on mean lengths and total weights of the selected groups. Gompertz curves fitted to lengths had the equation:

$$L_{t'} = L_0 \exp[G - G \exp(-gt')],$$

where L is mean length in millimeters, t' is time in days, and G and g are empirical constants. This curve and all other Gompertz curves were fitted by

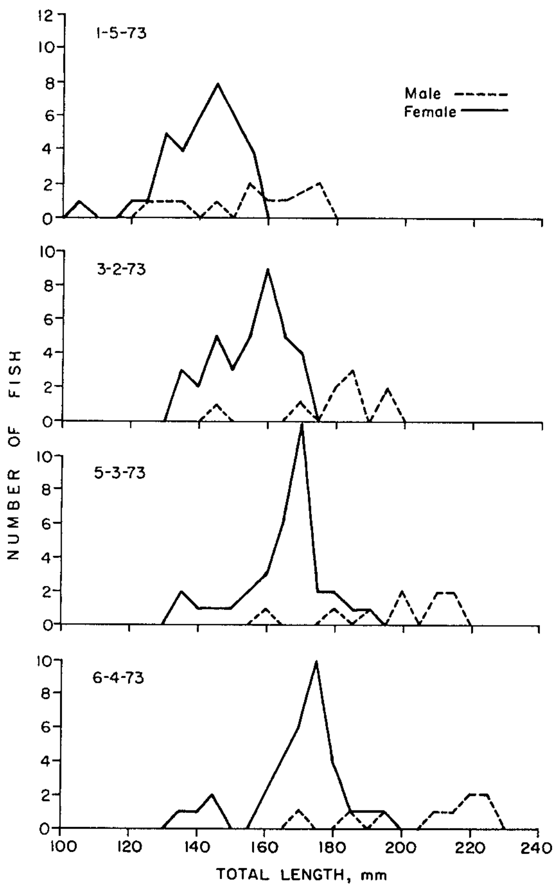

Figure 10.—Length frequencies of group selected from selectively fished test population. Lengths are from snout to tip of tail.

the analog computer method of Silliman (1967). Growth in length was essentially identical in the two groups for the females (Table 5, Figure 12), and a single curve was fitted. Constants are given in Table 6. For males, however, growth was significantly greater in the unselectively fished control group than in the selectively fished test group.

The sexual misclassification of one fish in the test group and two in the control group (Table 5) must be considered in relation to possible effects on the results. These fish were misclassified at the beginning of the growth period, when the fish were relatively small (chosen so to provide room for growth) and sex determination was difficult. As the fish grew and determination became easier, the errors were discovered and corrected. To test the effect of the errors it was assumed that they occurred in the manner most contrary to the conclusion adopted—that growth was greater among males in the control than in the test group.

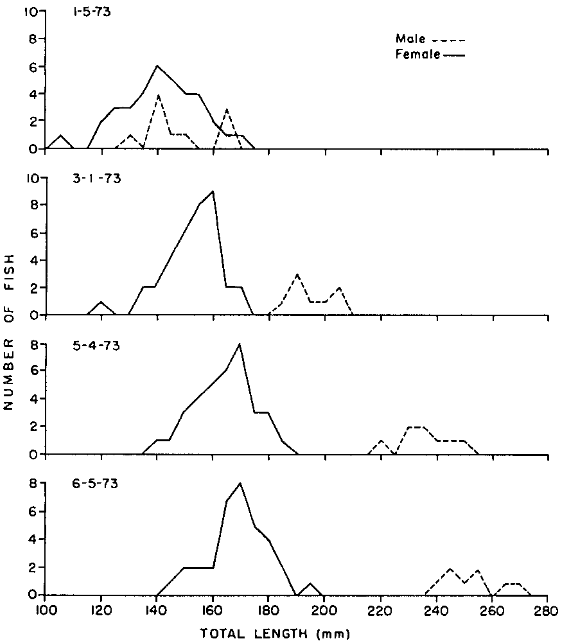

Figure 11.—Length frequencies of group selected from unselectively fished control population. Lengths are from snout to tip of tail.

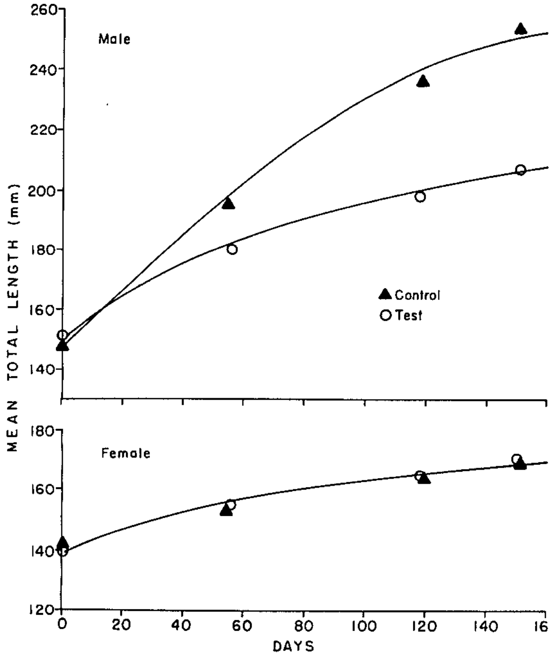

Figure 12.—Gompertz curves fitted to mean lengths in group selected from selectively fished test population and unselectively fished control population.

TABLE 6.—Constants of Gompertz curves for growth of selected groups of fish.

Sex	Variable	Population	L_0 (mm)	L_∞ (mm)	W_0 (kg)	W_∞ (kg)	g	G
♂	Length	Test	148	214	—	—	0.0150	0.367
		Control	146	274	—	—	0.0127	0.630
♀	Length	Both	141	174	—	—	0.0128	0.211
Both	Weight	Test	—	—	2.23	4.45	0.0130	0.692
		Control	—	—	2.49	5.65	0.0105	0.819

Note: L_0 = Length at time zero.
L_∞ = Asymptotic limit of length.
W_0 = Weight at time zero.
W_∞ = Asymptotic limit of weight.
g and G = Empirical constants of the Gompertz curve.

Thus it was assumed that at day 0 one of the two males at maximum length in the test group was misclassified as a female and, similarly, for the two smallest males in the control group. Resulting mean lengths in millimeters comparable to those for day 0 in Table 5 are: test male, 149.4; test female, 141.5; control male, 151.2; control female, 141.1. Percentage differences are 1.7, 0.6, 2.2, and 0.2, respectively. The means under the "most contrary assumption" are indistinguishable from the values used on the scale of Figure 12. It is evident that substitution of the most contrary values would not change the conclusion of greater male growth in the controls.

Gompertz curves were also fitted to biomasses of the two groups (Table 5, Figure 13). Here the equation was:

$$W_{t'} = W_0 \exp[G - G \exp(-gt')],$$

where W is total weight in kilograms, t' is time in days, and G and g are empirical constants. Constants are given in Table 6. In weighings, fish were not separated as to sex, and only a single growth curve was available for each population. Because of the initial difference in total weight, the curve for the control population is shown moved over to the time when weight of the test group had grown to the initial weight of the control group. Even so treated, the control group exhibits markedly greater growth than the test group, reflecting greater growth of the males in it. This is even more striking when it is considered that the amount of food per weight of fish was somewhat less in the control than in the test group. The observed growth in biomass supports the conclusion of diminished genetic growth in males as a result of selective fishing.

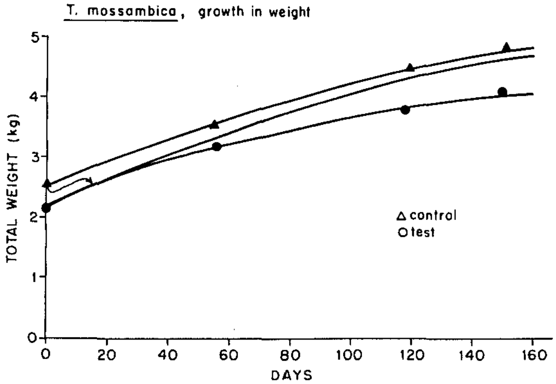

FIGURE 13.—Gompertz curves fitted to total weights of groups from selectively fished test population and unselectively fished control population. Line branching upward from test curve indicates control curve moved over to same starting point as test curve.

CONCLUSIONS

Analyses presented above have revealed significant differences of responses to exploitation between the selectively fished test population and the unselectively fished control population. These differences were demonstrated both in catches obtained and in genetic growth patterns.

Yield models fitted demonstrated marked differences in the catches obtained under selective and unselective fishing. It is clear that, with the particular populations studied and under the assumptions of stability made, weight of yield under unselective fishing was greater than that under selection. This yield included a large proportion of fish below the selection point, however. To the extent that one may generalize from this experiment, it appears that unselective fishing would be preferable if maximum physical yield were the sole objective. If selection is required to secure fish that are of appropriate size for the market, the objective may be achieved only at the sacrifice of part of the weight of the catch.

That three generations of selective fishing caused a change in the genetic growth pattern of males, resulting in slower growth than in the controls, seems certain from the results. It is necessary to explain, however, why a similar change did not occur in the females. This may have resulted from the phenomenon of epistasis. In this it is considered that a single gene may control the hormone which permits males to grow to larger ultimate size than females. Since females have less of this hormone than males, they are unable to express genotypic differences which otherwise might cause changed growth patterns. In other words, the degree of selection imposed did not work against females because they were unable to achieve extra large size in any event. This hypothesis cannot be tested with data from the present experiment.

Fishing in the experiment was similar to that in a commercial fishery, with the vertical slots in the apparatus corresponding to the meshes of commercial gear. Results may, therefore, be of some significance in fishery management. They suggest that as wide a range of sizes as possible be included in the catch. An appropriate balance should be struck between the possible higher market value of large fish and the lesser yields that may be achieved under selection. Also, the possibility of a genetic change in growth pattern under selection should not be overlooked.

SUMMARY

1. Two populations of *Tilapia mossambica* were grown with as nearly identical space, water condition, and food as possible.
2. After a period of initial growth each population stabilized at a weight of about 10 kg. Numbers were less stable at this time and ranged from 173 to 218 fish.
3. To increase genetic variability, 45-47 immature fish of Malacca descent were added to each population at month 47.3.
4. Exploitation was started at month 39.2, at 10% per 2 mo (1.0-2.6 brood intervals) and increased to 20% at month 63.2. Selective fishing was from fish which could not pass through 25-mm (later 22-mm) vertical slots between glass rods. Unselective fishing was from all fish except fry (under 4-mm thickness).
5. Recruitment was estimated from data of stock number, mortality, and catch. Reproductive lag was 2 mo. The stock-recruitment relations, roughly fitted with parabolas, suggested greater recruitment in the selectively fished stock than in the unselectively fished one.
6. Two rectilinear thickness-length relations were calculated, one for immature and male fish and another for females.
7. Catch thickness frequencies for the unselectively fish population revealed modes corresponding to peaks of recruitment.
8. Catch thickness frequencies for the selectively fished population, compared with those for the unselectively fished population, demonstrated that the device for selection at 25 and 22 mm was almost completely effective.
9. The exploitation-yield relation was assessed by fitting Fox exponential surplus-yield models to data from both populations. Fitted models indicated a higher maximum sustainable yield in weight for the unselectively fished population than for the selectively fished one. Efficiency of food conversion was 29-36%.
10. Growth rates from catch thickness frequencies, together with the 2-mo reproductive lag, suggested a generation length of 6 mo. Recruitment records indicated three generations under exploitation for the selectively fished population and four during the same period for the unselectively fished one.
11. To test for genetic effect of selection, a group of 46 fish was selected from each population. These were matched as closely as possible by size and sex composition and grown under previously established standard conditions.
12. Growth in length over a period of 150 days was significantly greater among males from the unselectively fished population than among males from the selectively fished one. Growth for females in the two groups was practically identical.
13. Growth in total weight was distinctly greater for the group from the unselectively fished population than in that from the selectively fished one.
14. It was concluded that these experiments demonstrated diminished total yield and retarded male growth in the selectively fished population compared with the unselectively fished one. An hypothesis based on epistasis was advanced to explain lack of growth response among females.
15. As applied to commercial fisheries, the experimental results suggest fishing as wide a range of sizes as possible. If economic gains from selection are indicated, they should be balanced against possible costs in reduced total yield and retarded growth rate.

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My special thanks are due Alban R. Essbach of the Arizona Game and Fish Department. He generously shipped stocks of fish on two different occasions.

Experimental populations were maintained during various periods by George F. Slusser, Christopher E. Mathews, Martin G. Beam, Jimmy R. Chrnaoski, and Judy A. Trauth. I also thank George F. Slusser for furnishing the initial stock of fish. All of these persons are present or former members of the National Marine Fisheries Service, NOAA (formerly Bureau of Commercial Fisheries).

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