EFFECT OF CROWDING ON RELATION BETWEEN EXPLOITATION AND YIELD IN *TILAPIA MACROCEPHALA*

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ABSTRACT

An experiment was performed to assess the effect of crowding on yield in *Tilapia macrocephala*. Populations of nearly equal number and weight were started in control (155.2 liter) and test (77.6 liter) tanks. Food amounts and environmental attributes other than space were the same for both tanks. Each of the two populations was exploited—first at a bimonthly rate of 10% for 14 months, then at a bimonthly rate of 25% for 10 months.

Equilibrium yields at each rate for each tank (four points) were fitted with a Fox exponential surplus-yield model. Deviations from this general population curve showed that yields were greater for the larger tank at the 25% rate and greater for the smaller tank at the 10% rate. This is believed to result from the fact that the entire yield came from growth at the lower rate whereas part of the yield came from recruitment at the higher rate. A low rate of conversion of food to fish (18%) is believed to be due to the large proportion of liver in the diet.

Current interest in aquaculture suggests an imminent increase in the holding of fish in restricted enclosures. Such holding, particularly at high densities, provides the fish with a drastically altered environment as compared with their native habitat. Some of the effects are undesirable, as is only too well known to hatchery men. Metabolic wastes accumulate rapidly and some communicable diseases spread easily among enclosed populations. There may also be undesirable effects due to reduced area for spawning—for example, spawning fish that are close together may use more energy defending their territory against the intrusion of other fish than spawners that are farther apart. Effects of crowding can also be beneficial, such as increased growth rate with less expenditure of energy in swimming.

The purpose of the experiment described here was to investigate one class of results from crowding—those related to the yield in self-sustaining populations. Of many possible experimental animals, *Tilapia macrocephala* belongs to a genus which is already important in pond culture. This species is small enough to raise in laboratory tanks and has reasonably rapid reproduction and growth. A conventional control-test design was adopted in which the control population was in a tank that had been demonstrated as being of suitable size for *T. macrocephala*. The test population was in a tank exactly one-half the size of the control tank. Food, light, temperature, and initial populations were kept as nearly identical as possible.

MATERIALS AND METHODS

Two conventional glass-wall aquarium tanks were used. The water mass in the control (larger) tank (L) had a volume of 155.2 liters, with approximate dimensions 39 by 90 by 44 cm. Volume of the test (smaller) tank (S) was one-half that of L, or 77.6 liters. To keep proportions the same, linear dimensions of S and its equipment were $1/2^{1/3}$ those of L.

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Tank L was provided with two fiber-charcoal filters, each with an electric pump delivering 2,800 ml per min; tank S had one of these.

Aeration was by one airstone in tank L and two in tank S.[2] Oxygen concentrations varied from 4.4 to 7.4 ppm for L and 2.4 to 7.2 ppm for S.

Illumination was by overhead pink fluorescent lamps, which screened out violet-blue light, found by Perlmutter and White (1962) to be lethal to some fish eggs. Lights were controlled by an automatic switch, turned on from 6 AM to 6 PM each day.

Each tank had shelter in the form of cords suspended from plastic floats. Forty-four cords 30 cm long were attached to a 49- by 15-cm float in tank L; numbers and dimensions of the shelter were proportional in tank S. A floating fiber brush type shelter, 4 cm in diameter by 25 cm long, was in L, and a proportional one was in S. The back, one side, and part of the front of each tank were rendered opaque with black plastic; the front area was 44 by 20 cm in L and proportional in S.

Refuges for young fish were enclosed at the end of each tank by fences consisting of 5-mm diameter plastic rods spaced 3 mm apart. The enclosed area was 14 cm wide in L and proportional in S. Aquarium gravel was placed in the bottom of each tank for nesting activity.

Both tanks were maintained at room temperature, which was thermostatically controlled except that cooling was not available in the summer. Weekly mean temperatures were 24 ± 2°C for both tanks.

Fish were fed daily according to a fixed schedule (Table 1). Uneaten food, feces, and other detritus were siphoned out daily, and two-thirds of the water mass was changed each week, using tap water brought to tank temperature. Charcoal and fiber in the filters were changed once weekly.

TABLE 1.—Amounts (grams) of food placed in each tank.

Day of week	Trout pellets		Tropical fish food	Liver	Total
	Moist	Dry			
Sunday	6.0	1.5	1.5	--	9.0
Monday	1.5	1.5	0.9	9.0	12.9
Tuesday	1.5	1.5	0.9	9.0	12.9
Wednesday	1.5	1.5	0.9	9.0	12.9
Thursday	1.5	1.5	0.9	9.0	12.9
Friday	1.5	1.5	0.9	9.0	12.9
Saturday	1.5	1.5	0.9	9.0	12.9
Total	15.0	10.5	6.9	54.0	86.4

Populations were counted and weighed every 2 months. Since *T. macrocephala* is a mouth breeder, it was not desirable to handle the fish more often. Aronson (1949) stated that the mean spawning interval for the species was 15 days, so the counting interval was about four brood intervals. Exploitation was performed at the time of counting by removing the tenth or fourth fish for 10% and 25% exploitation rates. Weighing was done by draining fish in a net, placing them in a weighed container with water, weighing the container with fish, and subtracting the tare.

Exploitation started in December 1967, with 42 fish weighing 1,148 g in S and 45 fish weighing 1,167 g in L (Table 2). These fish were either survivors or descendants of a shipment of 10 adults and 50 young fish received on 10 February 1966 by air from the Honolulu Biological Laboratory of the Bureau of Commercial Fisheries (now National Marine Fisheries Service).

Although numbers of fish declined at the 10% bimonthly exploitation rate (Figure 1), biomass remained relatively constant (Figure 2) and no evidence of recruitment was observed. To determine if recruitment would occur at a lower biomass, the exploitation rate was increased to 25% at month 16 and was continued at that rate until the end of the experiment. It will be shown below that recruitment did occur under the higher exploitation rate.

RESULTS

VITAL PROCESSES

Significant results from exploitation experiments require that recruitment and growth occur during the course of the experiment. It is also desirable to know whether natural (nonfishing) mortality was occurring. Evidence relating to these vital processes can be obtained by exam-

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[2] Although these numbers may appear to be reversed, they are as used. The oxygen concentrations show that they provided approximately equal aeration.

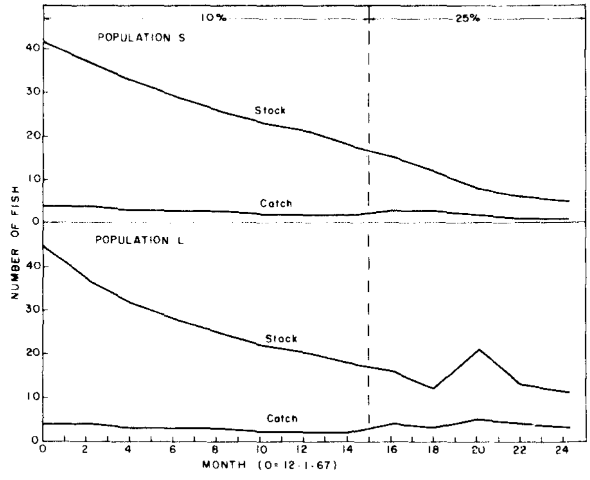

FIGURE 1.—Bimonthly stocks and catches, numbers, *Tilapia macrocephala*, 77.6-liter (S) and 155.2-liter (L) tanks. Percentages indicate target bimonthly exploitation rates.

ining net changes in number (R_{INT}) during the intervals between counts (Table 3).

Recruitment is defined here as survival of young fish to the size that could not pass through the 3-mm openings of the refuge fence. On this basis, no recruitment was apparent during the period of 10% exploitation, months 0-14 (Table 3). However, it is possible that some did occur, balanced by unrecorded mortality. Deaths not recorded are indicated by negative values of R_{INT} (Table 3). Also, it is almost certain that spawning occurred in which the resulting young were victims of cannibalism before reaching recruit size. Positive values of R_{INT} after month 14 show that recruitment occurred in both S and L under the 25% exploitation rate, with recruitment in L about double that in S.

Growth of individual fish can be detected by observing concurrent changes in numbers and biomass. Growth was demonstrated from month 0 to month 12.3, when biomass increased and numbers decreased in both S and L (Table 2, Figures 1 and 2).

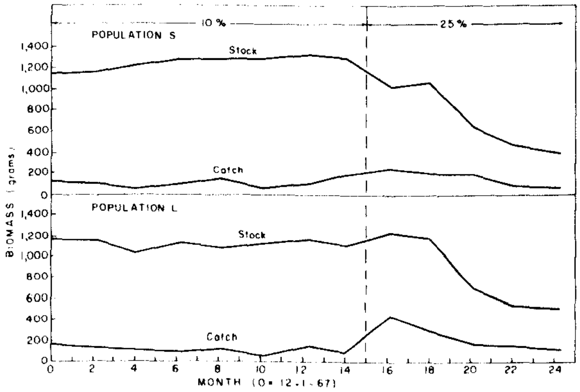

FIGURE 2.—Bimonthly stocks and catches, weights, *Tilapia macrocephala*, 77.6-liter (S) and 155.2-liter (L) tanks. Percentages indicate target bimonthly exploitation rates.

TABLE 2.—Population[1] and catch, *Tilapia macrocephala*, in two sizes of tanks during bimonthly exploitation.

Target exploitation rate[2]	Month[3]	S—77.6-liter tank				L—155.2-liter tank			
		Number		Weight (g)		Number		Weight (g)	
		Stock	Catch	Stock	Catch	Stock	Catch	Stock	Catch
0.10	0.0	42	4	1,148	132	45	4	1,167	178
	2.2	37	4	1,159	103	37	4	1,159	143
	4.0	33	3	1,216	47	32	3	1,026	122
	6.2	29	3	1,293	100	28	3	1,142	104
	8.1	26	3	1,288	153	25	3	1,076	126
	10.1	23	2	1,299	63	22	2	1,137	62
	12.3	21	2	1,338	109	20	2	1,181	160
	14.0	18	2	1,308	205	18	2	1,120	101
0.25	16.2	15	3	1,028	262	16	4	1,246	450
	18.0	12	3	1,080	216	12	3	1,195	297
	20.1	8	2	676	211	21	5	725	183
	22.0	6	1	496	102	13	4	562	156
	24.3	5	1	419	81	11	3	529	134

[1] In the 77.6 liter tank the population was replaced after accidental mortality at month 19. Also, sex ratio was changed from 1 male:5 females to 3 males:3 females at month 21.2.

[2] Because of the relatively small numbers of fish, the effective exploitation rates varied considerably from these. In fitting the population model, the effective rates in terms of weight were used.

[3] 0 = December 1, 1967.

Both recorded and unrecorded natural mortalities occurred. Recorded mortality represented finding of dead fish in the tanks. Unrecorded mortality, as mentioned above, is demonstrated by negative values of R_{INT} (Table 3).

TABLE 3.—Recruitment and unrecorded mortality, *Tilapia macrocephala.* $R_{INT} = P_{n+1} - P_n + M_{INT} + C_{INT}$, where INT is interval between counts n and $n+1$, R is net change,[1] P is stock, M is recorded mortality, and C is catch, all in numbers.

Interval (months)	R_{INT} for:	
	Population S—77.6-liter tank	Population L—155.2-liter tank
0- 2.2	−1	−2
2.2- 4.0	0	−1
4.0- 6.2	−1	0
6.2- 8.1	0	0
8.1-10.1	0	0
10.1-12.3	0	0
12.3-14.0	−1	0
14.0-16.2	+1	0
16.2-18.0	0	0
18.0-20.1	+4	+12
20.1-22.0	0	−2
22.0-24.3	+3	+3

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

CHANGES UNDER EXPLOITATION

Responses of the populations varied with exploitation rate. At the 10% rate, numbers in each population declined while biomass remained relatively constant (Figures 1 and 2). At the 25% rate, both numbers and weights declined. Further consideration of stock changes will be limited to data of biomass, since the biomass curves are more regular than those of numbers and represent both recruitment and growth. It is evident that the initial rise in weight of catch at the 25% rate was due almost entirely to cropping off the biomass accumulated at the 10% rate (Figure 2). The response of both populations to an increase in exploitation rate thus followed classical conceptions based on theoretical grounds (for instance, those of Thompson and Bell, 1934).

EQUILIBRIUM YIELDS

In a relatively short experiment, such as this, covering only 13 exploitation periods, the attainment of complete equilibrium at either of the exploitation rates is obviously impossible. The last two exploitation periods at each rate encompass relatively small changes in stock and catch (Figure 2); they will thus be considered equilibrium periods for the purposes of the analyses reported below.

POPULATION MODEL

The exponential surplus-yield model of Fox (1970) is simple to fit and has been found suitable for experimental populations with short brood intervals (Silliman, 1971); it was therefore chosen for use with the data from the *T. macrocephala* experiment. Ideally, the model would be fitted to S and L separately. The regression method employed for fitting does not perform well when only two points are available. There is no opportunity for compensating errors, and slight errors are greatly magnified when the regression is extrapolated to the Y-intercept to estimate the maximum stock. Also, since there are zero degrees of freedom, there is no way of assessing variability.

The above difficulties can be circumvented by fitting a single general curve to both populations. For individual population characteristics, deviations from the general curve can be studied. Four points were available for fitting the regression line—two from each population (Figure 3). The fit seems reasonably good for an experiment of this type.

COMPARISON OF YIELDS

Deviations from the general curve (Figure 3) may be considered with respect to the crowding effect. It is seen that at the lower exploitation rate (10% target) and larger population, the population in the smaller tank (S) has a large positive deviation whereas that in the larger tank (L) is close to the curve. Conversely, at the higher exploitation date (25% target) and

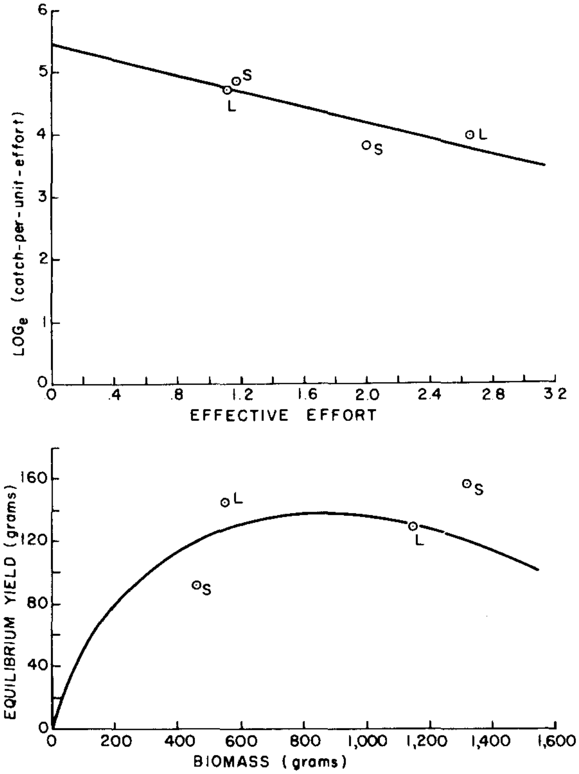

FIGURE 3.—Effort-CPUE line (least squares fit) and biomass-yield curve, fitting of Fox (1970) model. CPUE assumed proportional to population size. L indicates population in 155.2-liter tank and S in 77.6-liter tank.

smaller population, L has a positive deviation and S a negative.

An explanation for this seemingly paradoxical finding may be found in the source of the yield at each exploitation rate. At the lower rate, during months 0-14, the populations were large and no recruitment occurred (Figure 2, Table 3). The yield that did occur, then, resulted entirely from growth. Under the higher exploitation rate prevailing during months 16-24.3, the population was smaller and recruitment did occur (Figure 2, Table 3), furnishing part of the yield. Growth could have been retarded in the larger tank by greater expenditure of energy in swimming. Recruitment could have been favored in that tank by psychological factors controlling spawning, by greater opportunity for newly released young to escape cannibalism, or by a combination of these factors.

The finding of greater growth in the smaller tank is in contradiction to the conclusions of Chen and Prowse (1964) for *T. mossambica.* Examination of their data, however, shows that these conclusions were based on results from their largest ponds (0.10-0.40 ha) after a year of growth. Data comparing their smaller ponds were available only to 6-months' growth and are less clear cut. For instance, at 6 months their 0.04-ha pond showed greater growth than their 0.20-ha pond. Even their smallest pond (0.004 ha and 76 cm depth) had a volume of 31,000 liters, or 200 times that of the larger tank in the *T. macrocephala* experiments. With a different species (even though in the same genus) and such a vast difference in size of habitat it is perhaps not surprising that their findings are at variance with those reported here.

In both the present experiment and that of Chen and Prowse, the term "crowding" can be used only in a relative sense and not in the sense of lack of space to move about. Assuming the fish have the same density as water (nearly true), the maximum population in the smaller tank of the present experiment occupied only 1.72% of the water. The maximum concentration in Chen and Prowse's experiments was 0.02%. Thus, whatever effects occur must result from such factors as relative distance swum or sociological phenomena, like aggression. Chen and Prowse chose the latter, although it is a bit difficult to imagine when there are 2 or less kg of fish per 10,000 liters of water.

Finally, yields may be compared as measures of conversion[3] of food to fish flesh. The maximum bimonthly sustainable yield from the general population curve (Figure 3) is about 140 g (calculated value, 137.8 g). Food provided during each 2-month period weighed 749 g ($8\frac{2}{3}$ weeks × 86.4 g weekly total fed, as shown in Table 1). Apparent conversion was thus 18%.

The above results may be compared with those from the growth experiments of Swingle (1960)

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[3] Used here in the sense of net growth in weight (= sustainable yield) expressed as a percentage of weight of food made available to the population.

in 0.40-ha ponds. His data are not directly comparable, however, as he fertilized the ponds in addition to feeding the fish. A rough correction may be made by subtracting growth achieved in unfed groups of fish. By doing so, a mean of 42% is obtained for *T. mossambica* in seven experiments starting with brood stock and lasting a single growing season. The much poorer showing of *T. macrocephala* in the present experiment is believed to be partly due to the large proportion of liver included in the diet (Table 1). Substantial amounts of uneaten liver were often removed from the tanks during daily cleaning. Also, the population density in Swingle's ponds was about two orders of magnitude less than in the present experiment, which may bear on the difference in food conversion. His ponds were about the size of the larger ones used by Chen and Prowse (1964), so their finding of greater growth in larger ponds may account for some of the superiority in growth found by Swingle.

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As part of the O. E. Sette dedicatory volume, I gratefully dedicate this small contribution to him. He was my first research supervisor (1938-45), and I owe a very great deal indeed to his encouragement, advice, and instruction during those formative years of my career.

LITERATURE CITED

ARONSON, L. R.
1949. An analysis of reproductive behavior in the mouthbreeding cichlid fish, *Tilapia macrocephala* (Bleeker). Zoologica 34:133-158.

CHEN, F. Y., AND G. A. PROWSE.
1964. The effect of living space on the growth rate of fish. Ichthyologica 3:11-20.

FOX, W. W., JR.
1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99:80-88.

PERLMUTTER, A., AND E. WHITE.
1962. Lethal effect of fluorescent light on the eggs of the brook trout. Progr. Fish-Cult. 24:26-30.

SILLIMAN, R. P.
1971. Advantages and limitations of "simple" fishery models in light of laboratory experiments. J. Fish. Res. Board Can. 28:1211-1214.

SWINGLE, H. S.
1960. Comparative evaluation of two tilapias as pondfishes in Alabama. Trans. Am. Fish. Soc. 89: 142-148.

THOMPSON, W. F., AND F. H. BELL.
1934. Biological statistics of the Pacific halibut fishery. (2). Effect of changes in intensity upon total yield and yield per unit of gear. Rep. Int. Fish. Comm. 8, 49 p.