

AN ANALYSIS OF  
AGGRESSIVE BEHAVIOR, GROWTH, AND COMPETITION FOR FOOD AND SPACE  
IN MEDAKA (ORYZIAS LATIPES) - PISCES, CYPRINODONTIDAE

by

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PISCES, CYPRINODONTIDAE

ABSTRACT

The role and consequences of aggressive behavior in competition for food and space were studied among laboratory populations of juvenile medaka. Growth rate and relative condition were used to measure the success of an individual fish in different competitive situations. Both were measured relative to sibs of the same age and size raised in isolation under the same conditions.

Temperature, day length, and light intensity were held constant, and fresh water was circulated. All fish were raised in nylon baskets (30 meshes/cm) suspended into a common water bath. Length or weight, or both, of each fish was measured every 6 days for at least 24 days between 0 and 66 days after hatching. Quantitative records of aggression, activity and location preference were taken throughout the day. *Paramecium*, *Artemia salina* nauplii and pellets (diameter = 0.25 mm to 0.5 mm) were used as food. *A. salina* were assumed to be "in excess" if active nauplii were present at all times. Limited food was 10 pellets per fish per day (0.68 mg per fish per day). Growth was followed for 648 fish in populations of 1, 2, 4, 8, or 16 fish in 1, 4, or 8 liter baskets.

No difference in average growth was observed at different densities, and growth depensation was no greater than would be expected from genetic differences in growth potential, as long as food was supplied "in excess" and the accumulation of waste products was prevented. Aggressiveness was at a low level, and both large and small fish were equally aggressive. Spatially localizing excess food did not alter the relationship.

When food supply was limited, a social hierarchy developed in which large fish were socially dominant, chased small fish away from food, and grew faster than small fish. Aggressive actions increased in frequency just after limited food was presented. If food was localized spatially the social hierarchical society changed into a territorial society in which the dominant defended the food area, and the dominant's competitive advantage increased. Aggressive behavior was initiated by an internal state of "hunger" and the presence of food stimuli and smaller medaka.

Visual isolation between competitors increased the dominant's advantage if food was contagiously distributed, but decreased it if food was evenly distributed. When food was evenly distributed and the environment had a semi-isolated subsection for each fish, both dominant and subordinate grew equally well.

If population size was large the dominant could not chase all subordinates from the food area, and consequently the growth advantage of social dominance was in part lost. In addition frequency of aggressive actions by the dominant decreased. Aggressive behavior only dispersed medaka through the habitat if food was evenly distributed.

Small fish could not eat pellets as fast as large fish and if all fish had equal access to the limited food supply the rate at which they ate was important in determining their growth rate.

Action of aggressive behavior as a competitive mechanism for space or *Lebensraum* and the influence of environment on both the expression of aggressive behavior and the extent to which it reserves the food supply is discussed. Applicability of these findings to field situations and other species of fish is also considered.

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The role and consequences of aggressive behavior in competition for food and space were studied among laboratory populations of juvenile medaka. Growth rate and relative condition were used to measure the success of an individual fish in different competitive situations. Both were measured relative to sibs of the same age and size raised in isolation under the same conditions.

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## TABLE OF CONTENTS

	Page
INTRODUCTION . . . . .	1
MATERIALS AND METHODS . . . . .	4
Experimental Animal . . . . .	4
Laboratory Installations . . . . .	4
Physical Constants . . . . .	6
Breeding and Hatching . . . . .	6
Foods and Feeding . . . . .	7
Length and Weight Measurements . . . . .	7
Quantification of Behavior . . . . .	8
COMPETITION FOR SPACE (EXPERIMENT I) . . . . .	10
Introduction . . . . .	10
Description of Experiment . . . . .	10
Results . . . . .	11
Growth variability among isolates . . . . .	11
Growth variability in populations relative to control . . . . .	15
Average growth at different densities . . . . .	17
Aggressive behavior . . . . .	18
Summary of Results . . . . .	19
COMPETITION FOR LIMITED FOOD (EXPERIMENT II) . . . . .	21
Introduction . . . . .	21
Description of Experiment . . . . .	21
Results . . . . .	24
Growth rates . . . . .	24
Condition (Relative weight) . . . . .	29



Relative condition and growth . . . . .	32
Aggressive behavior and activity comparisons . . . . .	34
Diurnal rhythms in behavior . . . . .	40
Relation between growth and behavior . . . . .	47
Summary of Results . . . . .	58
COMPETITION FOR EXCESS FOOD (EXPERIMENT III) . . . . .	60
Introduction and Description of Experiment . . . . .	60
Results and Conclusions . . . . .	60
Summary of Results . . . . .	61
COMPETITION FOR LIMITED FOOD IN LARGER POPULATIONS (EXPERIMENT IV) . .	62
Introduction . . . . .	62
Description of Experiment . . . . .	62
Results . . . . .	65
Growth rates . . . . .	65
Behavior . . . . .	67
Relation between growth and behavior . . . . .	72
Summary of Results . . . . .	75
DISCUSSION . . . . .	77
SUMMARY OF RESULTS . . . . .	95
LITERATURE CITED . . . . .	98
APPENDIX . . . . .	103

## FIGURES

	Page
Figure 1. A water bath with nylon baskets (above) and with baskets and thermostat removed (below). See overlay for individual items. . . . .	5
Figure 2. Growth depensation among isolated medaka sibs grown under "identical" environmental conditions, compared from date of fertilization. Solid line = male, broken line = female. . . . .	13
Figure 3. Growth depensation among isolated medaka sibs grown under "identical" environmental conditions, compared from date of hatching. Solid line = male, broken line = female. . . . .	14
Figure 4. Diagram of treatments used in experiment II showing location and amount of food, size and number of fish, and size and topography of basket. . . . .	23
Figure 5. Multiple comparisons of size-specific growth rates of large fish, small fish, and both for each treatment, except XF, relative to the size-specific growth rates of controls ( $\Delta W - \Delta \hat{W}$ ); (any two means not enclosed by the same bracket are different, $p \leq 0.05$ ). ● = large fish, ○ = small fish, — = mean for whole treatment. . . . .	28
Figure 6. Multiple comparisons of relative condition of large fish, small fish, and both for each treatment, except XF, as measured as a deviation from the weight on length regression of controls ( $W - \hat{W}$ ); (any two means not enclosed by the same bracket are different, $p \leq 0.05$ ). ● = large fish, ○ = small fish, — = mean for whole treatment. . . . .	31
Figure 7. Relation between mean relative growth and mean relative condition of large and small fish in each treatment, except XF. ○ = small fish, ● = large fish. . . . .	33

- Figure 8. Multiple comparisons of aggressiveness of large fish, small fish, and both for each treatment as calculated from days 27;21, 39;33, and 51;45 (any two means not enclosed by the same bracket are different,  $p \leq 0.05$ ).  
● = large fish, ○ = small fish, — = mean for whole treatment. . . . . 37
- Figure 9. Multiple comparisons of activity of large fish, small fish, and both for each treatment as calculated from days 27;21, 39;33, and 51;45 (any two means not enclosed by the same bracket are different,  $p \leq 0.05$ ).  
● = large fish, ○ = small fish, — = mean for whole treatment. . . . . 39
- Figure 10. Diurnal changes in activity and aggressiveness of large and small fish in the isolate controls (CL1, CS1), in plain 1-liter limited food treatment (L1), and in the excess food treatment (XF). ● = large fish, ○ = small fish. . . . . 41
- Figure 11. Diurnal changes in activity and aggressiveness of large and small fish in the no-food treatment (NF), and activity, aggressiveness, and location preference of large and small fish in the limited food localized on bottom treatment (LB). ● = large fish, ○ = small fish. . . . . 42
- Figure 12. Diurnal changes in activity, aggressiveness, and location preference of large and small fish in treatments with a partial partition across the basket which were fed on one side (LP1) and both sides (LP2) of the partition.  
● = large fish, ○ = small fish. . . . . 43
- Figure 13. Diurnal changes in activity and aggressiveness of large and small fish in shallow limited food treatment (LSH), 4-liter isolate treatment (CL4, CS4), and plain 4-liter limited food treatment (L4). ● = large fish, ○ = small fish. . . . . 44
- Figure 14. Differences in the growth rates of large and small fish in each treatment plotted against the differences in their aggressiveness during the 2.5 hours after food was presented. . . . . 55

- Figure 15. Efficiency of aggression to the large dominant fish as influenced by (a) amount of food, (b) localization of food supply, and (c) size of environment. Efficiency =  $(G_L - G_S) / (\text{Aggressive actions by large fish in 2.5 hours after food was supplied})$  . . . . . 57
- Figure 16. Diagram showing partitions and food locations of the 8-liter baskets used in experiment IV. (top view) . . . . . 64
- Figure 17. Relation between growth depensation  $\left[ (s_{t+6}^2)^{\frac{1}{3}} - (s_t^2)^{\frac{1}{3}} \right]$  and (a) the spatial distribution of limited food in a subdivided habitat and (b) the extent to which the habitat is subdivided. (Brackets enclose means which do not differ at  $p \leq 0.05$ ) . . . . . 66
- Figure 18. Relation between frequency of aggressive actions in populations of 8 fish and (a) the spatial distribution of limited food in a subdivided habitat and (b) the extent to which the habitat is subdivided in evenly distributed food treatments. (Brackets enclose those means which are not different at  $p \leq 0.05$ ) . . . . . 69
- Figure 19. Average number of fish in subsections during the 5 minutes after food was introduced. . . . . 71

# TABLES

	Page
Table 1. Design of experiment I showing treatments and number of replications. . . . .	11
Table 2. Mean 12-day length increments (mm) of male and female sibs grown in isolation under "identical" conditions calculated for fish 10 mm, 15 mm, 20 mm, and 25 mm long. . . . .	12
Table 3. Design of experiment II showing treatments and number of replications, with treatment codes and descriptions. . . . .	22
Table 4. Linear regressions of $(W_{t+6} - W_t)$ on $W_t$ in milligrams for each 6-day interval for large and small isolated fish in 1-liter baskets, CL1 and CS1, while food supply was limited ( $y = W_{t+6} - W_t$ , $x = W_t$ ). . . . .	25
Table 5. Average size-specific growth rates ( $\Delta W - \hat{\Delta W}$ ) and relative conditions ( $W - \hat{W}$ ) of large and small fish and of the whole treatment relative to the growth and condition of control fish of the same size, presented for each treatment, except XF. . . . .	26
Table 6. Average aggressiveness and activity during the daylight hours for large and small fish in each treatment and for the whole treatment as calculated from days 27;21, 39;33, and 51;45. . . . .	36
Table 7. Differences in average growth, condition, aggressiveness, and activity between large and small fish in each treatment averaged for days 27;21, 39;33, and 51;45. . . . .	52
Table 8. Simple, partial, and multiple correlation coefficients for $y_1 = (G_L - G_S)$ , $y_2 = (C_L - C_S)$ , $x_1 = (Agg_L - Agg_S)$ and $x_2 = (Act_L - Act_S)$ . (See text for explanation.) . . . . .	54
Table 9. Design of experiment IV showing treatments and number of replications with treatment codes and descriptions. . . . .	63

Table 10. The average increase in variability of weight-frequency distributions during a 6-day period due to differences in growth rate in populations of 8 fish. . . . .	65
Table 11. Frequency of aggressive actions/2.5 min by 8 fish and the coefficient of variation (%) resulting from differences in frequency of aggression on different days of observation during the 5 minutes after food was provided. . . . .	67
Appendix Table. Mean values of relative condition for large and small fish in each treatment, except XF, expressed as $(W-\hat{W})$ and $(\log_{10}W - \log_{10}\hat{W})$ . . . . .	105

## INTRODUCTION

Although growth depensation<sup>1/</sup> is a common phenomenon in fish, it is difficult to determine whether intraspecific competition is one of its causes. Hubbs and Cooper (1935) observed growth depensation in two centrarchid species and postulated that either: (i) larger fish had a competitive advantage over smaller fish for food; (ii) there was a consistent difference in the habitat of fish; (iii) fast growth in one year had a physiological effect upon growth rate in the following year; or (iv) there were genetic differences in growth potentials within the populations.

Larkin et al. (1950) observed a negative association between average annual growth increments and the annual change in variability of size frequency distributions within year classes of rainbow trout, Salmo gairdneri Richardson (Salmo gairdneri kamloops Jordan); and concluded that both the mean size and the changes in variability are measures of competitive intensity.

Brown (1946, 1951, 1957) observed growth depensation in laboratory populations of young-of-the-year brown trout, Salmo trutta Linnaeus, and postulated physiological "stress" as a mechanism which resulted in poor growth among the smaller fish due to the presence of larger fish even when food was "in excess."

The influence of a water-borne growth inhibiting agent described by Richards (1958), Rose (1960), and West (1960) also results in a reduced growth rate under more crowded conditions and in growth depensation

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<sup>1/</sup> Growth depensation refers to the increase in variance of a size-frequency distribution with time due to differences in growth rates (Ricker, 1958).

among Rana pipiens tadpoles.

Aggressive behavior expressed as social hierarchy or territoriality has often been postulated as a mechanism of competition for food and space which benefits the larger animals and therefore results in growth depensation (Allee et al. 1948; Collias, 1944; Kalleberg, 1958; Kawanabe, 1958; M. Newman, 1956; Noble, 1939; Noble and Borne, 1938). Carpenter (1958) listed increased access to food and to space, per se, as two possible functions of territoriality, but stated that these functions are ascribed "mainly on inferential basis, since controlled experimentation has not yet clearly defined and delineated the area of its [territoriality's] possible effects."

Aggressive behavior, the mechanism studied in this paper, has not been isolated previously as a competitive mechanism which results in growth depensation (see discussion) because: (i) genetic differences in growth potential have been assumed negligible; (ii) some of the associations between growth rate, relative size, and appetite would exist in the absence of aggressive behavior; (iii) social rank is largely determined by relative size, and conclusions that social rank determines relative size may be a misinterpretation of the correlation; (iv) supplying food "in excess" is a relative condition and may be misleading if considered as an absolute.

If aggressive behavior is an important competitive mechanism, its action should be isolated under different environmental conditions, and its utility to the animal should be measured in the quest of specific resources. If growth depensation is to be used as a measure of competitive intensity it is necessary to remove the extraneous influence of other factors, such as genetics and conditioning of the water.

In the following experiments, the role and consequences of aggressive



behavior as a mechanism of intraspecific competition for food and space are investigated. Attention is given to the influence of such factors as the relative size of a fish, the amount and the spatial distribution of the food, the amount of spatial isolation between competitors, population density, and population size. Growth rate and relative condition are used to measure the success of individual fish in different competitive situations.

In experiment I the effects of crowding on growth and growth depensation are investigated when food is supplied "in excess." In experiment II the effects of limited food are studied. Modifying factors such as the topography of the habitat and the amount and spatial distribution of the food are considered. In experiment III the consequences of localized supplies of excess food are investigated. In experiment IV the action and consequences of aggressive behavior are examined among larger populations in more complicated environments. In all cases biological conditioning of the water is removed as a factor, genetic differences are accounted for, and aggressive behavior is studied as a possible competitive mechanism.

## MATERIALS AND METHODS

### Experimental Animal

A domestic stock of "golden" medaka, Oryzias latipes (Temminck and Schlegel), a small cyprinodont fish, was used as an experimental animal. Briggs and Egami (1959) outline some features which make it a useful laboratory animal. Medaka are easily raised, mature at lengths near 27 mm, and breed readily on successive days for several months. Juveniles exhibit agonistic behavior, are tolerant to starvation, and can be weighed and measured alive with little handling mortality.

### Laboratory Installations

Controlled environment apparatus was built in the Vancouver Public Aquarium, Vancouver, B.C., in the summer, 1959, and the experiments were conducted periodically from August, 1959, through March, 1961. The laboratory contained six controlled-temperature water baths (213.4 liters) with adjustable water inflows (Figure 1). The medaka populations were placed in 1- or 4-liter baskets made from nylon "horsehair" crinoline (10 meshes/cm) with nylon chiffon liners (30 meshes/cm). For some treatments the 1 liter baskets were divided into two equal sections by a partial partition made from nylon "horsehair" crinoline with a 5 x 4 cm hole in it. All baskets were suspended into the water baths. Each water bath held either eight 4-liter baskets (20 x 20 x 10 cm) plus two 1-liter baskets (10 x 10 x 10 cm), or thirty-eight 1-liter baskets. Movable opaque baffles penetrated the upper 10 cm of water and prevented fish vision between baskets. Glass and wax paper covers, placed over each basket, prevented undue interference from the experimenter.

BIMETAL THERMOSTAT  
/

1-LITER BASKET  
/

4-LITER BASKET  
/

WATER INLET  
/

STAND PIPE DRAIN  
/

AIR STONE  
/

STAINLESS STEEL  
HEATING ELEMENT  
/

MOVABLE OPAQUE BAFFLES  
/

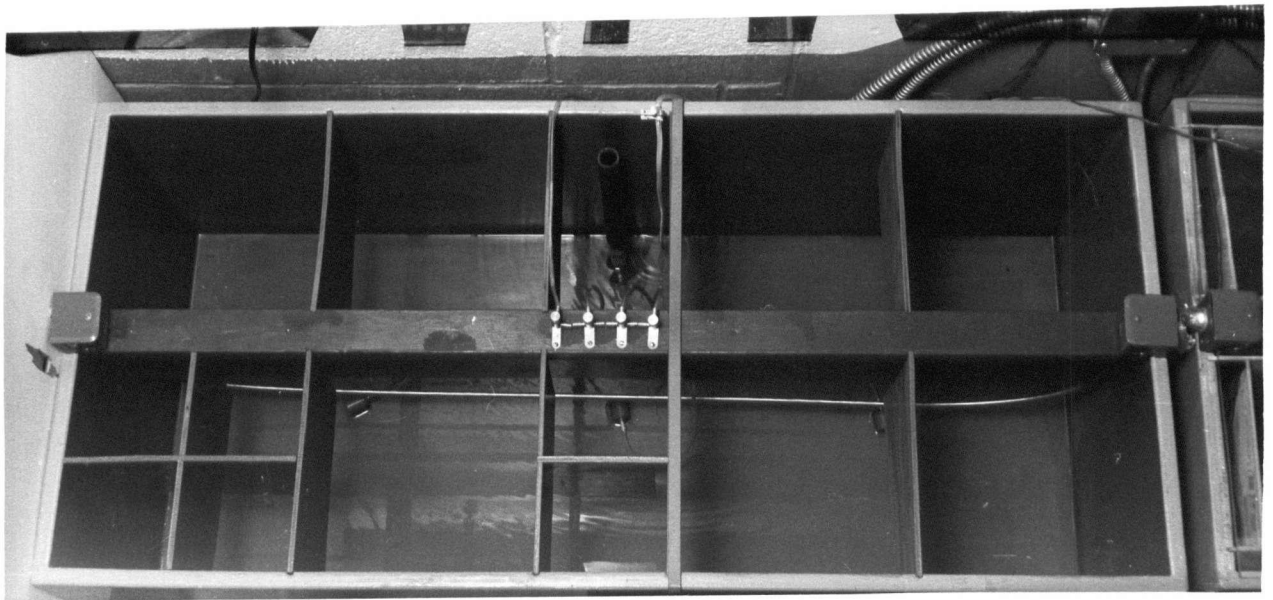


Figure 1. A water bath with nylon baskets (above) and with baskets and thermostat removed (below). See overlay for individual items.

Fluorescent lights were arranged evenly over the water baths, and a time clock controlled day length.

A behavior observation water bath (90 liters) was built with an inclined mirror above it. This bath held either two 4-liter baskets and two 1-liter baskets or ten 1-liter baskets, and had the same light and temperature characteristics as the six mentioned above. Behavior was observed through a narrow slit in a masking screen.

### Physical Constants

All experiments were conducted in fresh dechlorinated water from the Vancouver city water supply, at a 16 hour daylength, and at a light intensity (water surface) which slowly decreased from 19-23 ft-c at the beginning of the experiments to 13-18 ft-c at the end due to exhaustion of the fluorescent tubes. Water temperature was held at 24°C with a maximum deviation between days and baths of  $\pm 0.4$  degrees and a usual deviation of  $< \pm 0.1$  degrees. Between basket locations in a bath the range was  $< 0.1$  degrees at any one time. A water flow of 4.5 liters per hour provided a minimum volume exchange of 95% every 4 days. Each basket was washed under a faucet every 6 days when the fish were removed for measurements. Three air stones created a slight current in the baskets and especially in the small baskets near the center of the bath (Figure 1).

### Breeding and Hatching

The brood stock was held at 24°C. One pair was used in experiment I, three pairs in II, and one pair in III, and many pairs in experiment IV. Breeding occurred soon after the lights went on, and the eggs adhered to the female's abdomen. Eggs were removed immediately by the experimenter, and

each egg was separated. Malachite green (1:100,000) was used periodically to inhibit fungus during incubation, and egg mortality was less than 5%. Hatching occurred naturally in experiment I, but was induced 23 days after fertilization in II, and 11 days after fertilization in III, and 10 days after fertilization in IV, by fluctuating the water temperature between 24 and 28°C. The latter procedure results in a uniform hatching date.

#### Foods and Feeding

In all experiments, living Paramecium sp. were fed to the newly-hatched medaka three times each day for at least 7 days. After the third day, living brine shrimp nauplii, Artemia salina, were also supplied three times each day either until the end of the experiment or until a small pelleted food was substituted. If active nauplii were still present in the basket before each feeding, food was assumed to be in excess. The pelleted food was prepared from "Dina-fish; super-fry ration"<sup>2/</sup> by grinding and sieving until a homogeneous collection of small sized particles was obtained which would pass through a 0.5 mm but not a 0.25 mm soil sieve.

All fish in limited food treatments were fed 10 pellets per fish per day (0.68 mg per fish per day). This amount was eaten in less than five minutes. Pellets floated until they were forcefully nudged by a fish at which time they sank if not eaten. The fish swam to the bottom and ate the pellets which had sunk after the surface food was eaten. If a bottom pellet was desired, the pellets were dampened before being placed in the basket.

#### Length and Weight Measurements

Small fish were handled entirely with eyedroppers. As the fish grew

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<sup>2/</sup> Manufactured by Willis H. Small Feed Co., Eugene, Oregon.

larger, plastic tubes with larger bores and suction bulbs were used.

Total fish length was measured under magnification with a calibrated movable substage. A fish was placed on its side in a V-shaped groove between two parallel glass tubes lying on the bottom of a small glass petri dish. The water in the dish just covered the fish, and surface tension held the fish in place. No anesthetic was necessary. The tip of the fish's snout was aligned at a fixed point in the field, and the displacement of the movable substage which was necessary to align the tip of the fish's tail at the fixed point in the field was the measure of total fish length. Calibrations on the substage vernier were to 0.1 mm, and when care was taken to orient the fish in a consistent manner, measurements of this accuracy could be replicated exactly.

Total weight of an individual fish was measured on a Mettler H-5 balance. A fish was placed in a plastic cylinder (8 mm in diameter and 12 mm high) covered with silk bolting cloth on the bottom. Water was blotted out through the bolting cloth onto paper toweling and adhering droplets were removed with a small paper blotter. The fish plus cylinder were weighed, and fish weight was determined by subtraction. Weights were made to the nearest 0.1 mg and could be replicated within  $\pm 0.6$  mg with 95% confidence. Each fish was measured twice to reduce measurement error.

A fish could be weighed and measured in a 5-minute period during which it was out of the water for about 30 seconds (time on the balance pan). When the fish was placed back in its basket it appeared to behave normally and would take food within 5 minutes.

#### Quantification of Behavior

In experiment I and IV observations were made with the baskets in situ, but in experiment II selected baskets with their fish were removed from their

bath and placed in the observation bath 8 hours prior to observation. An observation consisted of a 2.5-minute period and was immediately replicated. A grid of strings (5 cm intervals and parallel to sides of the baskets) was placed over each basket. Activity was recorded as the number of times a fish swam under the strings. Agonistic behavior was recorded as a total count of aggressive actions by each fish (nips, chases, frontal and lateral threats). Location preference was measured by accumulating the time a fish spent in specific locations and by expressing this as a percentage of the observation period. In experiment I the records for different fish in the same basket were taken in consecutive time periods, but in experiment II all records for all fish in a basket were taken synchronously.



## COMPETITION FOR SPACE (EXPERIMENT I)

### Introduction

Aggressive behavior expressed as social hierarchy or territoriality is often postulated as a mechanism used in competition for space, per se (i.e. where space is a vague and undefined something, not including any specified resources in limited supply, but which animals nevertheless compete for with density dependent consequences). This hypothesis was explored by comparing variability in growth within populations of different densities after removing the variability which resulted from genetic differences within the populations and by comparing average growth rates at different densities. Aggressive behavior and social hierarchies were investigated to determine whether the postulated mechanism was present.

### Description of Experiment

Medaka were reared at 1, 4, and 16 fish per liter, and isolates were raised as controls to estimate genetic variability of the stock (Table 1). Effects of biological conditioning were removed not only by circulating new water, but also by allowing the water in each bath to circulate freely through baskets containing all population densities and isolated controls. Variability in size-frequency distributions occurring in the populations and exceeding the genetic base was considered to result from interactions between fish in the population.

Eggs from a single pair on 10 consecutive spawning days were used. Each day's eggs were randomly allocated to treatments with the restrictions that a single replicate only contained eggs from the same spawning day, and that

Table 1. Design of experiment I showing treatments and number of replications.

Size of Baskets		Population Size		
		1	4	16
1 liter	No. fish	18	48	96
	No. baskets	18	12	6
	Density	control fish	4/liter	16/liter
4 liters	No. fish	18	48	96
	No. baskets	18	12	6
	Density	control fish	1/liter	4/liter
		Total fish		324
		Total baskets		72

eggs from each spawning day were distributed proportionately to all treatments. Treatments were randomly allocated to positions in water baths with the restriction that equal proportions of a treatment's replicates were placed in each of the six water baths.

Total fish length was measured every 6 days for 66 days after hatching, except for populations of 16 which were measured every 6 days for the first 24 days, and every 12 days thereafter. Quantitative observations of activity and aggressive behavior were made at 1-hour intervals and just after each feeding approximately 30 and 60 days after hatching. One basket from each treatment was observed. In populations of 4 or 16 fish, records were kept for a large, medium, and small sized fish.

## Results

### Growth Variability Among Isolates

Even medaka of the same age and parentage varied in size when grown

under environmental conditions as similar as possible with the facilities used (Figure 2). Much of this variation in size was a result of variable hatching dates among eggs fertilized on the same day. Yet when fish were compared using hatching date as age zero, variations in size still resulted from genetic differences in growth potential (Figure 3). Each fish also tended to maintain its relative position in the size distribution of isolates graphed together for comparison.

Some variation in growth might have been due to a difference in growth potential between the two sexes. The 12-day length increments<sup>3/</sup> of all isolated males were compared with the increments of all isolated females when the fish were 10 mm, 15 mm, 20 mm, and 25 mm long (Table 2). No difference existed in 12-day length increments between the sexes at 10, 15, and 20 mm lengths (sign test,  $n = 16$ ,  $p = \text{ca.}0.50$  in each case), but females grew

Table 2. Mean 12-day length increments (mm) of male and female sibs grown in isolation under "identical" conditions calculated for fish 10 mm, 15 mm, 20 mm, and 25 mm long.

Sex	$n_i$	Length of fish (mm)			
		10	15	20	25
M	16	6.7	6.1	5.1	3.2
F	16	6.7	6.0	5.3	4.0
Mean		6.7	6.0	5.2	3.6

<sup>3/</sup> A 12-day increment for each fish at each of these sizes was determined graphically by plotting the length of a fish at age  $t + 12$  days against the length of the same fish at age  $t$  (Walford plot; Ricker, 1958). The points were connected by straight lines, and the distance between this broken line and a  $45^\circ$  line passing through the origin (line of no growth) is a 12-day increment of a fish at any particular length at age  $t$ .

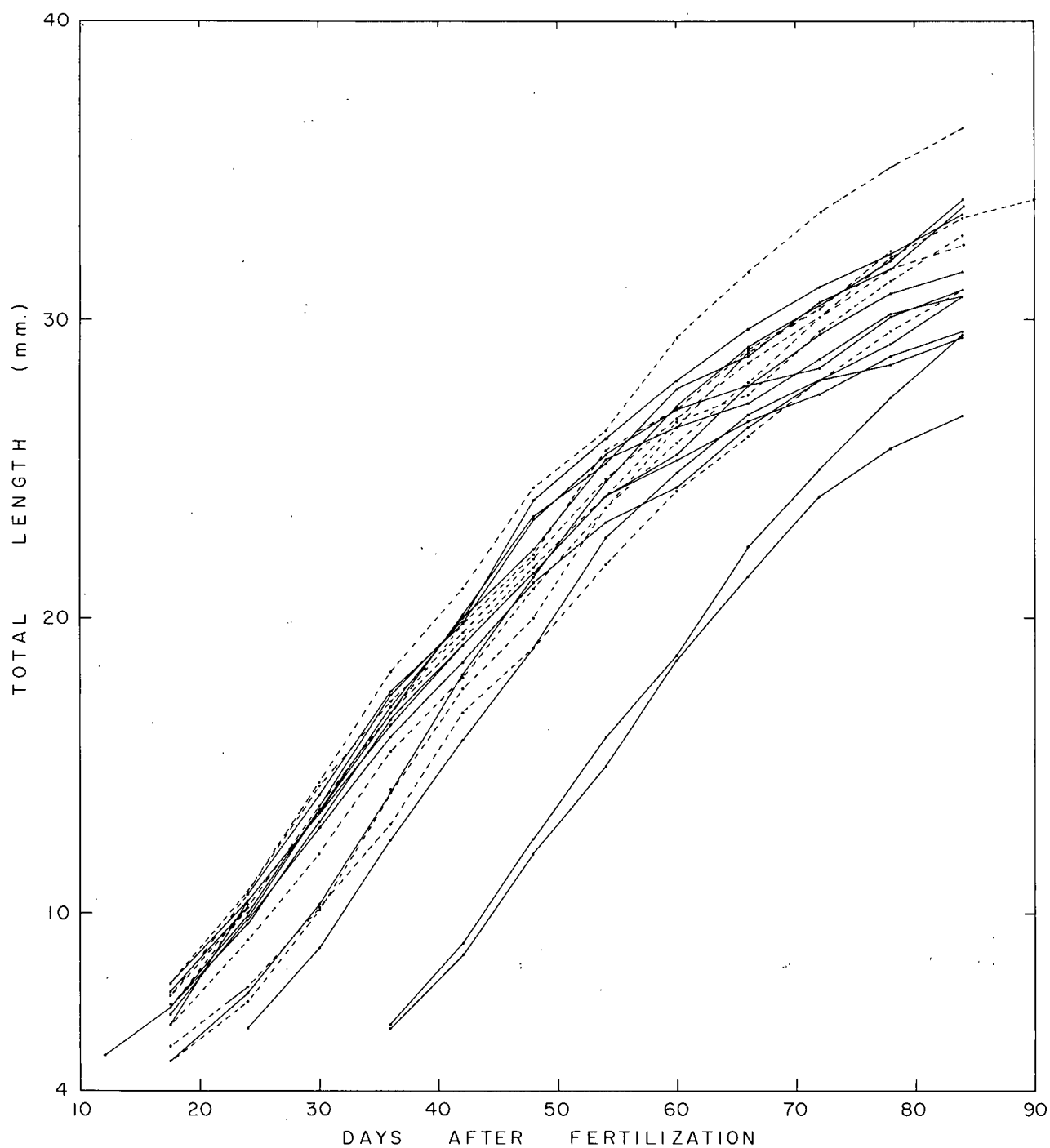


Figure 2. Growth depensation among isolated medaka sibs grown under "identical" environmental conditions, compared from date of fertilization. Solid line = male, broken line = female.

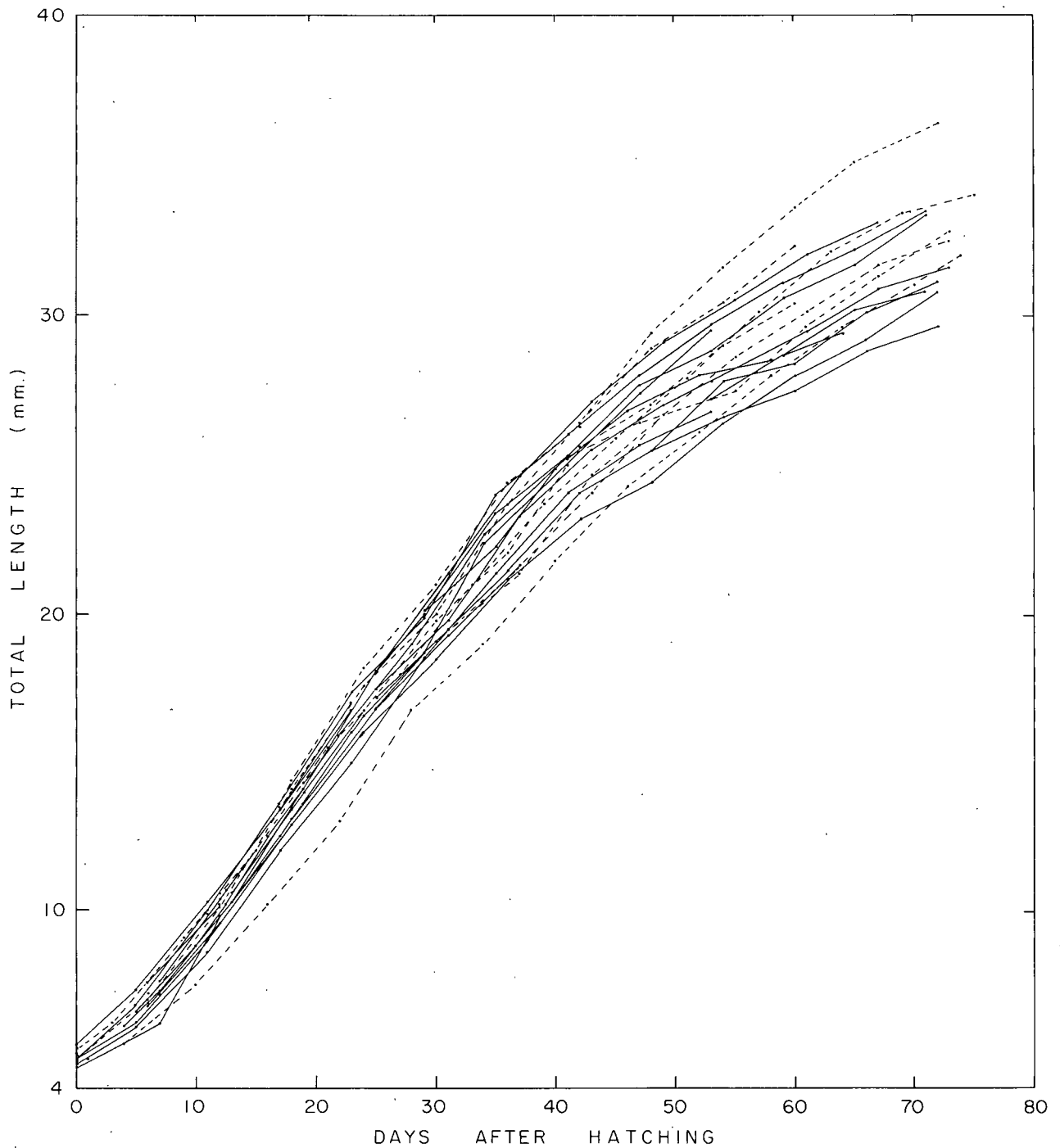


Figure 3. Growth depensation among isolated medaka sibs grown under "identical" environmental conditions, compared from date of hatching. Solid line = male, broken line = female.

faster than males at 25 mm lengths (sign test,  $n = 16$ ,  $p = 0.04$ ). When females reached approximately 28 mm in length, they began to lay eggs, and the reduced growth rate among the males occurred at the onset of sexual activity.

As males and females grew larger, the successive 12-day length increments decreased (Table 2). The 12-day increments were less at 15 mm than at 10 mm, less at 20 mm than at 15 mm, and less at 25 mm than at 20 mm. This was true of both sexes for each of the above comparisons (sign test,  $n = 16$ ,  $p < 0.02$  in each case).

#### Growth Variability in Populations Relative to Control

Growth rates could be traced for individual isolated control fish, but not for each fish in populations because the latter could not be individually identified at successive measuring days. Since direct growth comparisons of large or small isolated control fish could not be made with large or small fish in the treatment populations, a measure of growth depensation was developed to compare the treatment populations with the controls. This measure of divergence among treatment populations, when compared to the control, was indicative of the variability in growth rates exceeding that expected from genetic variability in the stock. All comparisons were made between groups of immature fish growing from 10 mm to 20 mm in length, and extraneous sources of variation such as hatching dates were removed by regression analysis. The above was accomplished by making comparisons from a regression of the variation in time after fertilization for a group of fish to reach a length of 20 mm ( $s^2_{t_{20}}$ ) on the variation in time they took to reach a length of 10 mm ( $s^2_{t_{10}}$ ). The resulting regressions were linear if the cube roots of each variance were plotted. Isolate control fish were divided randomly into groups of four, the cube roots of the above variances

were computed for each group, and the linear regression of y on x was calculated. The control regression is:  $y = 0.46066 + 0.85859 x$ , where  $y = (s^2_{t_{20}})^{\frac{1}{3}}$ , and  $x = (s^2_{t_{10}})^{\frac{1}{3}}$  (95% C.I.,  $n = 8$ ,  $b = 0.85859 \pm 0.2415$  and  $\bar{y} = 2.7135 \pm 0.3624$ ;  $s_x = 1.6051$ ,  $s_{yx} = 0.4197$ ,  $s_y = 1.4318$ ). Values of y and x were also calculated for each population of 4 and 16 fish, and the average deviation of y from the control regression was determined. A significant positive deviation would indicate a more rapid growth rate among larger fish in a population relative to the smaller fish than would be expected from genetic differences alone. The mean deviation from the control regression was  $+0.33$  ( $t_8 = 0.24$ ,  $p > 0.25$ ) for populations of 4 in 4-liter baskets,  $-0.047$  ( $t_8 = 0.33$ ,  $p > 0.25$ ) for populations of 4 in 1-liter baskets,  $+0.065$  ( $t_5 = 0.79$ ,  $p > 0.25$ ) for populations of 16 in 4-liter baskets, and  $+0.183$  ( $t_5 = 1.81$ ,  $p = 0.13$ ) for populations of 16 in 1-liter baskets. None of these mean deviations were different from zero and populations of high density were no more variable than would be expected from genetic differences in growth potential. This conclusion was reached even though the t test used was biased towards decisions of significant differences where none existed.<sup>4/</sup>

The above analysis demonstrated that growth depensation was no larger or smaller in populations of high density with less space per fish than among isolated control fish. Larger fish had no competitive advantage for space, per se, when food was provided in excess, and smaller fish did as well in groups as in isolation.

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<sup>4/</sup> The control regression was assumed to be a parameter, and average deviation from regression for each treatment was tested against zero using a t test. The estimate of standard error of these means was calculated from the deviations of the treatment populations from the control regression.

### Average Growth at Different Densities

A general reduction in growth is often used to measure the consequences of competition when a specific resource is limited. Mean growth rates in mm/day for fish growing between 10 mm and 20 mm were calculated for the controls and for each population in each treatment. Growth rates of the isolated controls were averaged by fours to get a range of variation similar to the variations in mean growth between populations within a treatment. The data were analyzed in factorial design with 2 levels of basket size and 3 levels of population size.

The 0.52 mm/day growth rate of all fish in 1-liter baskets was not different from the 0.53 mm/day growth rate of fish in 4-liter baskets ( $F_{1,32} = 0.826$ ;  $p = 0.40$ ), but the 0.53 mm/day growth for all isolates and 0.53 mm/day for populations of 4 fish were different from the 0.51 mm/day for populations of 16 fish ( $F_{2,32} = 4.06$ ;  $p = 0.04$ ). Interaction between basket size and population size was not significant ( $F_{2,32} = 0.010$ ;  $p > 0.25$ ). Only populations of 16 were growing slower than the controls. Decreasing the amount of space by 4 times did not affect the growth rate of equal sized populations, but increasing the population's size by 4 times, even when space was increased proportionately, reduced the growth rate.

It appears that space, per se, is not the influential factor. The reason that fish in populations of 16 grew more slowly was not determined in this experiment, but perhaps it was a result of a scarcity of food. At the beginning of the experiment the amount of brine shrimp solution was fed in proportion to the basket size rather than in proportion to population size. After about 2 weeks, populations of 16 were able to eat most of the food provided whereas large numbers of dead brine shrimp collected in baskets with 1 or 4 fish. The amount of food given to the populations of 16 was doubled,



but after about 1 week a depletion was noticed again. Finally each population was fed in proportion to its size, and there was no further evidence of food depletion. By this time, however, the fish had reached a size of approximately 16 mm.

### Aggressive Behavior

During experiment I aggressive behavior was observed in three different situations. First, aggressive actions appeared to be more common just before and after feeding or near local concentrations of food. Second, medaka satiated with food would lie motionless at the surface and chase or threaten those fish which approached too closely. Third, sexually mature males fought vigorously with each other and would often nip females which did not respond during courtship. Behavior patterns used in these experiments as measures of aggressive behavior are familiar aspects of fish ethology and are not described here in detail. The relationships between environment and behavior presented below are from preliminary data, and the same relationships are demonstrated in detail in experiments II through IV.

Aggressive behavior included chases, hips, frontal threats, and lateral threats. Social hierarchies were established in which larger medaka were most aggressive. Both males and females were able to assume social dominance until the onset of reproductive behavior. Then a new social order was formed in which males dominated females regardless of body size. Subordinate fish did occasionally nip or threaten a dominant fish.

A daily rhythm in behavior was associated with the feeding schedule. Activity increased immediately after food was introduced (sign test,  $n = 14$ ,  $p = 0.006$ ) but one hour later decreased to a level even lower than before food was introduced (sign test,  $n = 10$ ,  $p = 0.001$ ). The medaka were satiated and lay almost motionless near the surface. Subordinates were occasionally

chased from the surface by the dominant fish, and the smallest fish often set up residence near the bottom. Two to three hours after the fish were fed, activity slowly increased as fish began to search for more food. At the next feeding time there was again a burst of feeding activity, and the pattern was repeated.

Aggressive actions followed a diurnal pattern similar to general activity, but were often more frequent just before a feeding time. A comparison between treatments demonstrated no increase in aggressive actions when space was more limited (populations of higher density). The lowest frequency of aggressive actions, 0.3 per fish per 2.5 minutes, was observed at the greatest population density or at 16 fish per liter (sign test comparison to next lowest,  $n = 12$ ,  $p = 0.003$ ).

#### Summary of Results

Limited space had no measurable effect on growth rates of medaka when the influence of biological conditioning of the water was eliminated and food was supplied "in excess." Definite social hierarchies were established in which larger fish were dominant, but large dominant fish had no negative influence on the growth of small subordinates. Differences in size within a population could be accounted for by variations in hatching date and genetic variability in the growth potential of the stock. Growth depensation occurred among sibs grown in isolation under "identical" environmental conditions. There was no interaction between these control fish, yet each tended to maintain its relative position in a composite size-frequency distribution.

Aggressive actions were not more frequent when space was more limited, but occurred at all densities apparently in response to food. After food was presented, medaka fed to satiation, but three or four hours later a food

stimulus again initiated intense feeding behavior. Apparently, the fish were fed in excess only in relative terms, for ostensibly if they were fed more frequently they would have eaten more.

In summary, aggressive behavior did not appear to be a mechanism used in competition for space, per se. Also limited space had no detrimental effects upon any member of a population if other factors usually associated with limited space were either supplied in excess (food) or eliminated (biological conditioning of water).

## COMPETITION FOR LIMITED FOOD (EXPERIMENT II)

### Introduction

The purpose of experiment II was to determine whether large fish had a competitive advantage over small fish for a limited food supply when space, per se, was eliminated as a factor. Spatial distribution of food, amount of food, and degree of environmental isolation between competitors were varied to determine the influence of these modifying factors. Aggressive behavior was investigated as a competitive mechanism, and effects of biological conditioning were removed as in experiment I.

### Description of Experiment

Each population was composed of two sibs with a 6-day difference in age, and pairs of isolated controls with 6-day age differences were maintained. All fish were fed in excess on brine shrimp nauplii until 24 days after the older fish hatched or 18 days after the younger fish hatched (day 24;18). At this date older fish averaged about 13 mm in total length or 3 mm longer than younger fish. This size difference persisted until the end of the experiment, and individual fish could easily be identified by their relative size. On day 24;18 a limited food supply of 10 pellets per fish per day was imposed. If either fish in a population had a competitive feeding advantage it would get 10 pellets plus some pellets provided for the other fish. This situation could be detected by comparing the growth of each with the growth of isolated controls of the same age and size. A description of each treatment and its letter code are given in Table 3 and Figure 4.

Eggs were used from three sets of spawning days from each of three

Table 3. Design of experiment II showing treatments and number of replications, with treatment codes and descriptions.

Treatment Code	No. of Replications	No. Fish Per Basket		Basket		Food	
		Small	Large	Size (liters)	Features	Total Amount Per Day	Location
CL1	9	-	1	1	plain	10 pellets	surface
CS1	9	1	-	1	plain	10 pellets	surface
L1	9	1	1	1	plain	20 pellets	surface
XF	9	1	1	1	plain	excess <u>Artemia salina</u>	scattered
NF	9	1	1	1	plain	0	-
LB	6	1	1	1	50 mm diam. petri dish on bottom	20 pellets	wet in bottom dish
LP1	6	1	1	1	incomplete partition across basket	20 pellets	surface, one side of partition
LP2	6	1	1	1	incomplete partition across basket	20 pellets	surface, both sides of partition
LSH	6	1	1	0.25	very shallow	20 pellets	surface
CL4	9	-	1	4	plain	10 pellets	surface
CS4	9	1	-	4	plain	10 pellets	surface
L4	9	1	1	4	plain	20 pellets	surface

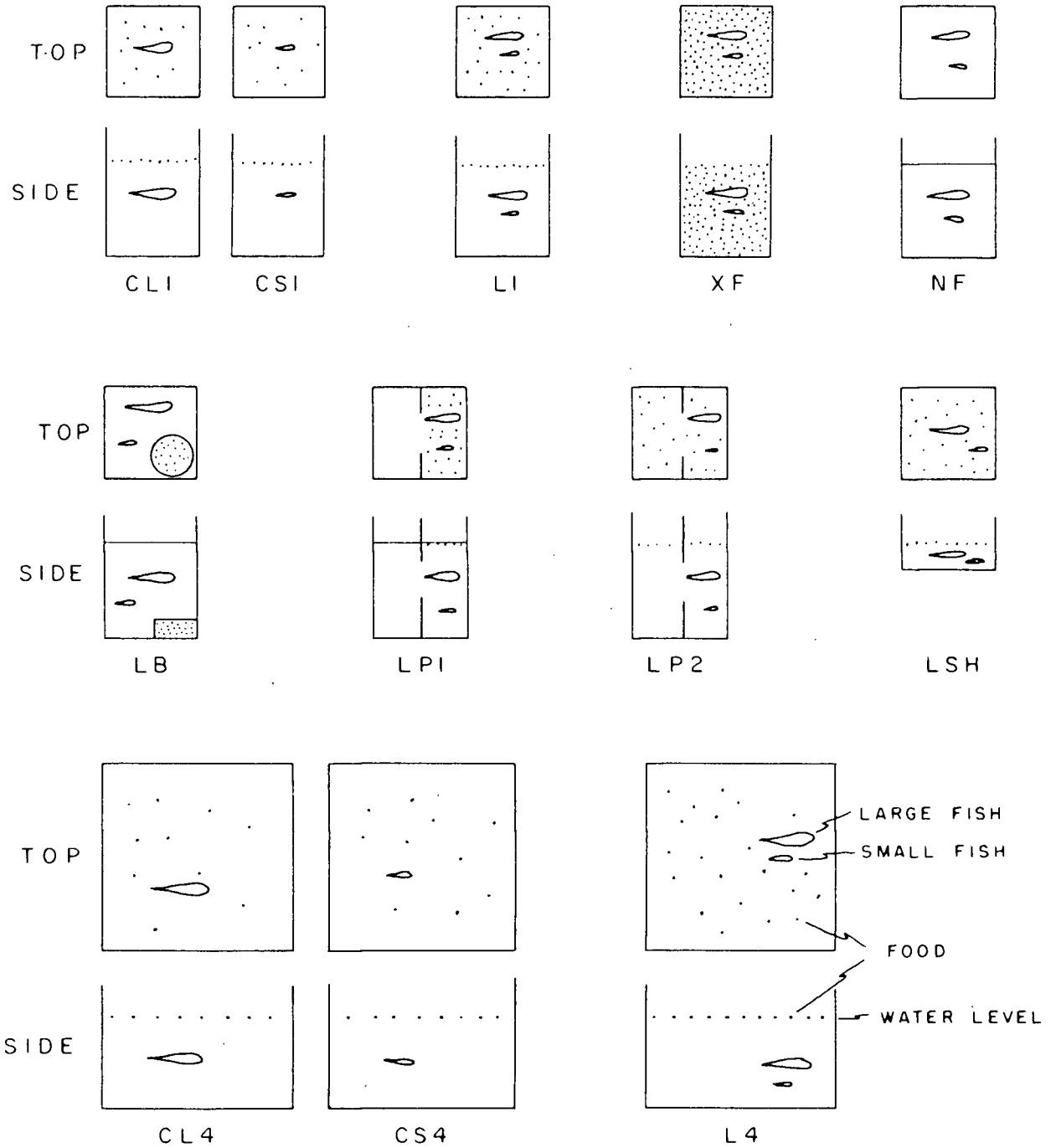


Figure 4. Diagram of treatments used in experiment II showing location and amount of food, size and number of fish, and size and topography of basket.

spawning pairs. A set of spawning days consisted of 2 spawning days which occurred 6 days apart. Hatching was induced 23 days after fertilization, and newly-hatched fish were allocated to treatments so that each had a matched pair in every other treatment in terms of spawning day and parentage. Those which hatched 6 days later were allocated in the same way except that they were also matched with the older fish by time of hatching. Treatments were randomly allocated to water bath positions with restrictions that each bath contained an equal proportion of replicates from each treatment, and no two replicates of a treatment occupied the same position in different baths.

Each fish was weighed and measured every 6 days from day 18;12 through day 48;42. Eight pairs of observations on aggressive behavior, activity, and location preference were made through the day at 2-hour intervals, and one pair of observations was made after each feeding. This sequence of observations was repeated at 12-day intervals from approximately day 15;9 through day 51;45. Three randomly chosen replicates were observed from each treatment at each date.

## Results

### Growth Rates

Growth rate was used to measure the relative success of a fish in different competitive situations. Isolates reared in 1-liter baskets served as controls from which the growth rates in all other treatments were compared. The regressions,  $(W_{t+6} - W_t) = a + bW_t$ , where  $W_t$  = weight in milligrams on day  $t$  and  $(W_{t+6} - W_t)$  = the six-day weight increment, were calculated for large and small isolates during the first three 6-day

intervals after limited feeding was begun (Table 4).<sup>5/</sup> Deviations of the size-specific 6-day weight increments ( $\Delta W - \hat{\Delta W}$ ) were calculated from the appropriate control regression for each treatment and control fish (Table 5), where  $\Delta W$  = the 6-day weight increment of a fish of a specific weight, and  $\hat{\Delta W}$  = the expected 6-day weight increment of fish of the same weight as determined from the controls. By definition, the average growth rate of control fish, CL1 and CS1, would be zero. If there were no competitive interactions within treatment populations, average growth rate of fish in any treatment relative to the controls would also be zero. If a large fish in a population had a competitive advantage, its growth rate relative to the

Table 4. Linear regressions of ( $W_{t+6} - W_t$ ) on  $W_t$  in milligrams for each 6-day interval for large and small isolated fish in 1-liter baskets, CL1 and CS1, while food supply was limited ( $y = W_{t+6} - W_t$ ,  $x = W_t$ ).

Fish Size	Interval After Limiting Food	t = Age Days After Hatching	$n_i$	a intercept	b slope	$\bar{y}$	$s_x$	$s_{yx}$	$s_y$
Large	1st	24	9	0.339	0.165	2.933	6.768	2.510	2.601
Small	1st	18	9	1.351	0.218	3.189	3.784	1.042	1.277
Large	2nd	30	9	0.128	0.120	2.367	8.229	1.413	1.764
Small	2nd	24	9	0.761	0.185	2.911	4.730	1.943	2.018
Large	3rd	36	9	2.179	0.001	2.200	9.311	1.044	0.977
Small	3rd	30	9	0.700	0.146	2.822	5.896	1.246	1.451

<sup>5/</sup> The six regressions in Table 4 could not be adequately described by a single regression equation because the pooled within groups regression coefficient ( $b_w$ ) was not equal to the linear regression coefficient ( $b_m$ ) of the group means ( $F_{1,47} = 5.98$ ,  $p = 0.01$ ) (Dixon and Massey, 1956). Even though slopes of the 6 regressions are not significantly different ( $F_{5,42} = 0.914$ ,  $p > 0.25$ ), individual slope estimates were maintained because the slopes appeared to be decreasing in a regular manner as the mean size of the fish increased.



Table 5. Average size-specific growth rates ( $\Delta W - \hat{\Delta W}$ ) and relative conditions ( $W - \hat{W}$ ) of large and small fish and of the whole treatment relative to the growth and condition of control fish of the same size, presented for each treatment, except XF.

Treatment Code	Fish Size	Growth		Condition	
		$(\Delta W - \hat{\Delta W})$ in mg	$n_i$ d.f. = $(n_i - 6)^{1/}$	$(W - \hat{W})$ in mg	$n_i$ d.f. = $(n_i - 2)^{2/}$
CL1	Large	0.00	27	0.00	27
CS1	Small	0.00	27	0.00	26
	Mean	0.00		0.00	
L1	Large	-0.60	20	+0.93	17
	Small	-2.23	20	-0.70	17
	Mean	-1.42		+0.12	
XF	compared by another method				
NF	Large	-2.87	27	-0.53	27
	Small	-2.94	25	-0.79	25
	Mean	-2.90		-0.66	
LB	Large	-0.27	16	+0.08	16
	Small	-2.74	16	+0.35	16
	Mean	-1.50		+0.22	
LP1	Large	+0.45	18	+1.15	17
	Small	-2.38	18	-0.52	17
	Mean	-0.96		+0.32	
LP2	Large	-0.21	18	-0.03	18
	Small	-0.89	18	+0.46	18
	Mean	-0.55		+0.22	
LSH	Large	-0.33	16	-0.08	16
	Small	-2.97	16	-0.86	16
	Mean	-1.65		-0.47	
CL4	Large	+1.43	27	+2.52	27
CS4	Small	+1.80	27	+2.59	26
	Mean	+1.62		+2.56	
L4	Large	+1.37	27	+1.86	27
	Small	-1.08	27	+0.15	27
	Mean	+0.14		+1.00	

- 1/ Two degrees of freedom were lost from each of the 3 regressions used for each mean deviation.
- 2/ Two degrees of freedom were lost because all values are deviations from 1 regression line.

controls would be greater than a small fish's. Comparisons made in the above manner are independent of genetic differences, and of physiological differences existing between fish of different ages and sizes.

Comparisons of average growth rates for large fish and for small fish in each treatment, except XF, were made by multiple comparison techniques (Duncan, 1955; Krammer, 1956).<sup>6/</sup> In Figure 5 average growth rates relative to the controls are plotted for the large fish in a treatment, the small fish in a treatment, and for the mean of the large and small fish combined. The vertical line connects these three values in a given treatment. Brackets on the left side of the figure enclose means of large or of small fish for within or among treatment comparisons which can not be distinguished at the 0.05 probability level. For example, the small fish in L4 was not growing slower than the large fish in LP2 ( $p > 0.05$ ), but was growing slower than the large fish in its own treatment ( $p < 0.05$ ). The brackets on the right side of the figure enclose the means for a whole treatment which can not be distinguished from the mean for another whole treatment at  $p \leq 0.05$ . For example, the mean growth of fish in LP2 was not less than the controls, CL1 and CS1 ( $p > 0.05$ ), but the mean growth of fish in LP1 was less than the growth of the controls ( $p < 0.05$ ).

Average growth of both fish in a treatment was usually less than growth of controls; for example, as shown on the right side of Figure 5, fish in LP1, L1, LB, and LSH were all growing slower than controls CL1 and CS1. Apparently a disoperative interaction which depressed their relative growth rates was occurring between the two fish in most treatment populations.

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<sup>6/</sup> Pooled variance for these comparisons equals 4.548 with d.f. =  $\frac{282}{2} = 141$ . Degrees of freedom were divided by two in appraising tabled probability levels (Snedecor, 1956) because the pooled variance of small fish 3.367 was not equal to the pooled variance for large fish 5.713.

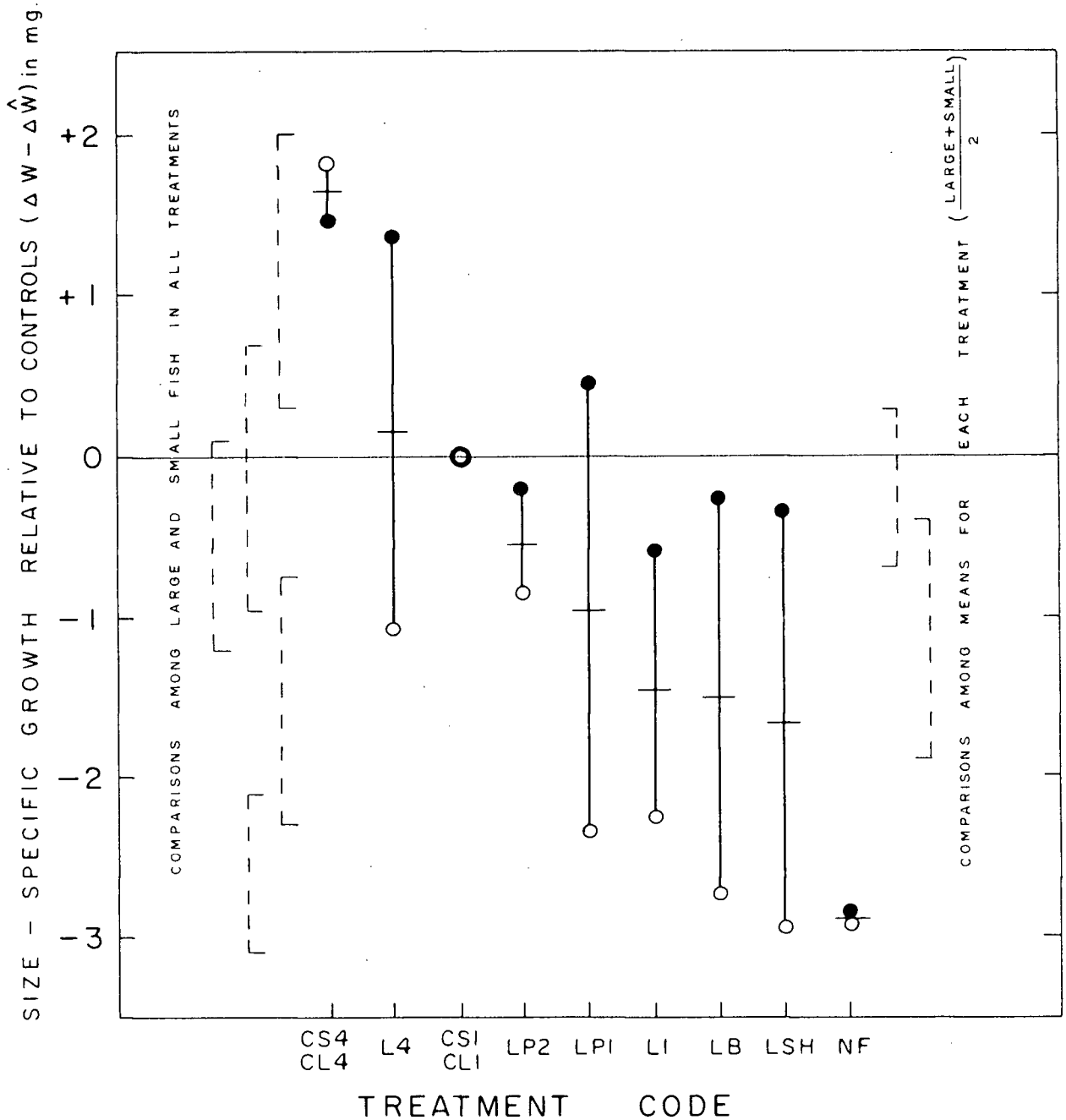


Figure 5. Multiple comparisons of size-specific growth rates of large fish, small fish, and both for each treatment, except XF, relative to the size-specific growth rates of controls ( $\Delta W - \Delta \hat{W}$ ); (any two means not enclosed by the same bracket are different,  $p \leq 0.05$ ).  
 ● = large fish, ○ = small fish, — = mean for whole treatment.

Small fish in a treatment population were usually more adversely influenced by the disoperative interaction; for example, as shown on the left side of Figure 5, small fish were growing slower than large fish in LP1, LB, LSH, L1, and L4. Excluding L4, these small fish were growing as poorly as those fish which were not fed, as in NF. There were several notable exceptions to the above generalizations; for example, the fish in LP2 grew as well as controls, and small fish did not grow slower than large fish. Isolated fish in 4-liter baskets grew faster than isolated fish in 1-liter baskets. Detailed analyses of these data are given following presentation of behavior data.

Fish in XF were not comparable to limited food isolates. Since both large and small fish in XF were fed in excess throughout the experiment, it was assumed that they would have equal size-specific growth rates if there were no interaction between them. The technique used for comparison was developed by Parker and Larkin (1959) who state that growth can be described by an equation comparable in form to  $B = W_{t+6}^c - W_t^c$ , where  $c$  is a constant which changes the slope of the Walford line to  $+1$  ( $c = 1-x$  in Parker and Larkin), and  $B$  is the adjusted size-specific growth increment. If two groups of fish have equal  $c$  values, the  $\bar{B}$  of each group is a comparable measure of growth rate which is independent of fish size. Large and small fish had a common  $c$  of 0.38 and the  $\bar{B} = 0.868$  for small fish was not different from the  $\bar{B} = 0.826$  for large fish ( $t_{78} = 0.168$ ,  $p > 0.25$ ). When food was supplied in excess individual growth rates of large and small fish were the same, and large fish had no competitive advantage.

#### Condition (Relative Weight)

Condition or relative weight of a fish might be expected to respond to competitive interactions between fish. As with growth comparisons, isolated fish in 1-liter baskets, CL1 and CS1, served as controls from which the

condition of all other fish was compared. The relation between weight and length for all control fish<sup>7/</sup> was  $\log_{10} W_t = -2.6329 + 3.4455 \log_{10} l_t$ , where  $\log_{10} W_t = y$  = logarithm of weight in milligrams on day t, and  $\log_{10} l_t = x$  = logarithm of length in millimeters on day t (95% C.I., n = 64, b = 3.4455  $\pm$  0.4742,  $\bar{y}$  = 1.2119  $\pm$  0.0295;  $s_x$  = 0.06204,  $s_{yx}$  = 0.1179,  $s_y$  = 0.24554). Relative condition of each control and treatment fish was measured as  $(W - \hat{W})$  where W is the actual weight of a fish of a specific length, and  $\hat{W}$  is the expected weight of a fish of that length according to the control regression. These measures of relative condition (Table 5) will be positive if fish are in better condition than controls and negative if they are in poorer condition. By definition the mean relative condition of control fish is zero. LeCren (1951) developed and used a different measure of relative condition  $\left(\frac{W}{\hat{W}}\right)$ . A comparable measure to LeCren's relative condition was tried in the present study but was rejected. These values and the reasons for not using them are presented in the appendix.

Relative conditions of large and small fish in each treatment, except XF, were compared by multiple comparison techniques in Figure 6 (Duncan, 1955; Krammer, 1956).<sup>8/</sup> No treatment with a limited food supply had a mean relative condition less than the controls. Yet relative conditions of small fish in treatment populations were often less than the relative condition of large

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<sup>7/</sup> Length-weight data for both large and small control fish from day 24;18 through day 42;36 were analyzed by covariance and found to be adequately described by a single regression of the logarithm of weight on the logarithm of length ( $F_{2,60} = 0.04$ ,  $p > 0.25$ ).

<sup>8/</sup> Pooled variance equalled 1.940, d.f. = 271/2 for comparisons between 1-liter basket treatments; equalled 6.778, d.f. = 73/2 for comparisons between 4-liter basket treatments; and 2.9668, d.f. = 344/2 for comparisons of 1-liter versus 4-liter basket treatments. Degrees of freedom were divided by two in appraising tabled probability levels (Snedecor, 1956) because the pooled variance among large fish was not equal to the pooled variance among small fish.

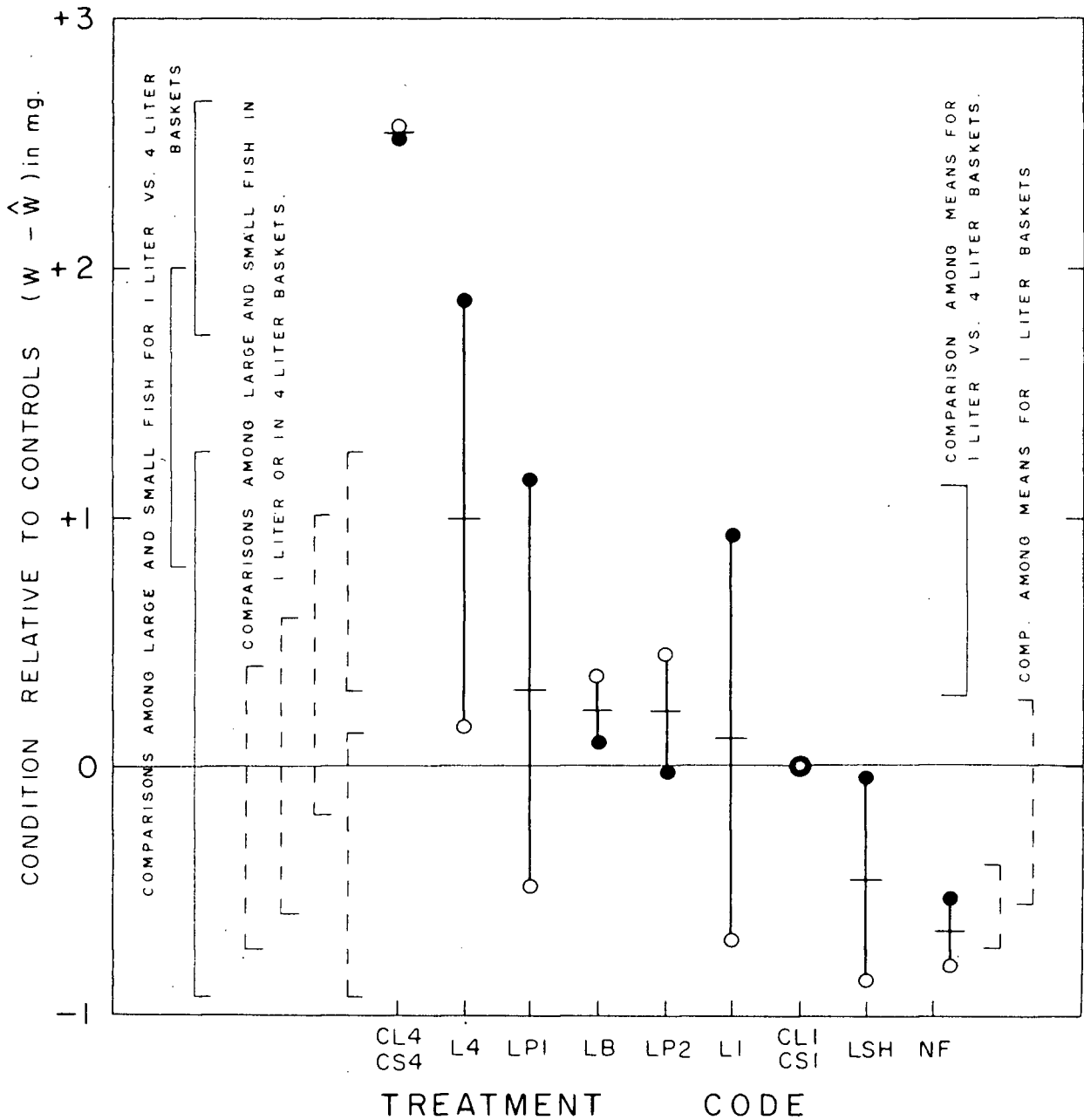


Figure 6. Multiple comparisons of relative condition of large fish, small fish, and both for each treatment, except XF, as measured as a deviation from the weight on length regression of controls ( $W - \hat{W}$ ); (any two means not enclosed by the same bracket are different,  $p \leq 0.05$ ). ● = large fish, ○ = small fish, — = mean for whole treatment.

fish; for example, as shown on the left side of Figure 6, small fish had a lower relative condition in L4, L1, and LP1. If there were competitive interactions in the populations, they did not result in a general lowering of relative condition, but resulted in a lower condition only among small fish in certain cases.

When fish were fed in excess, as in treatment XF, regressions of weight on length for large and for small fish were the same ( $F_{2,83} = 2.02$ ,  $p > 0.10$ ) and large fish had no competitive advantage. The combined regression for large and small fish in XF,  $\log_{10} W_t = -2.7189 + 3.5844 \log_{10} l_t$  (95% C.I.,  $n = 87$ ,  $b = 3.5844 \pm 0.1271$ ,  $\bar{y} = 1.6113 \pm 0.0143$ ;  $s_x = 0.11302$ ,  $s_{yx} = 0.0666$ ,  $s_y = 0.41050$ ), was compared to the control regression above. The intercepts are not different but the regression coefficient was greater for the XF treatment than for CL1 and CS1 controls ( $t_{147} = 3.28$ ,  $p < 0.01$ ) which demonstrates that fish fed in excess were in better condition than limited food controls over the whole range of observed sizes.

#### Relative Condition and Growth

Mean relative growth of fish-size treatment combinations was positively associated with mean relative condition ( $r = 0.84$ ,  $n = 18$ ,  $p < 0.01$ ). This association also existed among fish within a treatment. The correlation coefficient among fish in CS1 and CL1 was 0.68 ( $n = 18$ ,  $p < 0.01$ ) and among fish in L4 was 0.82 ( $n = 18$ ,  $p < 0.01$ ). Both relative condition and relative growth were measuring the same response but relative growth was more sensitive to differences in competitive situations.

Since both variables were measures of the same response the influence of different treatments on large and small fish was emphasized if both were considered at the same time (Figure 7). Each point in Figure 7 represents the average of large or small fish in a treatment. In terms of growth and

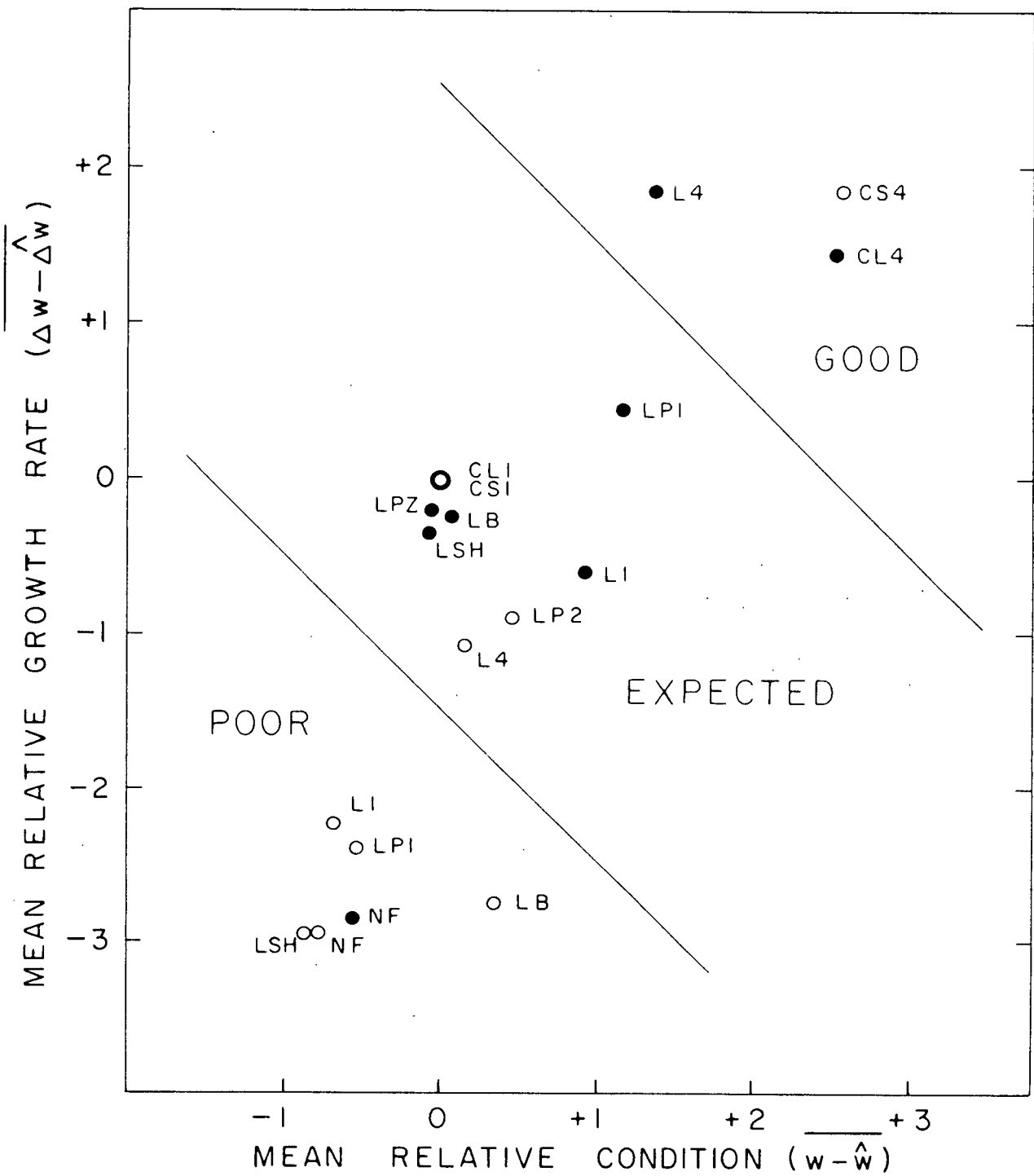


Figure 7. Relation between mean relative growth and mean relative condition of large and small fish in each treatment, except XF.  
 ○ = small fish, ● = large fish.



condition, the fish represented by points in the center of the figure were comparable to the isolated fish in 1-liter baskets fed 10 pellets/day. Those in the lower left were smaller and less robust than controls while those in the upper right were larger and in better condition than the controls. Fish fed in excess (XF) were not plotted but would be in the upper right.

The poorest environment, as judged by growth and condition of fish, was NF with no food, and the best was XF with excess food. All other baskets received a limited amount of food. Among these, larger 4-liter environments were more favorable than smaller 1-liter environments. The large fish was one component of a small fish's environment and likewise the small fish was a component of a large fish's environment. In general the presence of a large fish in limited food treatments resulted in a poorer environment for a small fish (L1, LB, LSH, and LP1), whereas the presence of a smaller fish did not result in a poorer environment for the large fish. In one treatment (LP2) the presence of the other fish did not reduce the quality of the environment for either the large or the small fish.

#### Aggressive Behavior and Activity Comparisons

Aggressive actions, activity counts, and location preferences were recorded from two 2.5-minute periods at 2-hour intervals during daylight hours for large and small fish. Three baskets from each treatment were observed. Activity counts were recorded for each treatment, aggressive actions for all except the isolates, and location preferences only in LB, LP1, and LP2. A description of each treatment with its code number was given in Table 2 and Figure 4.

Average number of aggressive actions/2.5 min during the day was calculated for the large and the small fish in each treatment on days 27;21, 39;33, and 51;45 by averaging the eighteen 2.5-minute observations made on

each fish in a day (Table 6). A mean value for the whole treatment was calculated by averaging the large fish with the small fish for a treatment. Large and small fish in each treatment were compared by multiple comparison techniques in Figure 8 (Duncan, 1955; Krammer, 1956).<sup>9/</sup>

Large fish were more aggressive than small fish (Figure 8) in all limited food treatments (L1, LB, LP1, LP2, LSH, and L4), and in the no-food treatment (NF), but large and small fish were equally aggressive in the excess food treatment (XF). Large fish in XF were less aggressive than large fish in all other treatments (Figure 8), but were not more aggressive than small fish in the other treatments. A localization of the food in a basket resulted in higher level of aggressiveness for large fish. For example, average aggressiveness for large fish in LP1 and LB, which had localized food supplies, was 2.87 aggressive actions/2.5 min while in L1, L4, LSH, and LP2, which had dispersed food supplies, it was only 1.82 aggressive actions/2.5 min (multiple comparisons,  $n = 15, 45; p \leq 0.05$ ). Another useful comparison was made by grouping treatments on the basis of previously observed growth rates (Table 5, Figure 5). All treatments in which large fish grew faster than small fish were called "competition" treatments (L1, LB, LP1, LSH, and L4), while those in which both fish grew equally well (excluding the isolates) were called "no competition" treatments (XF, NF, and LP2). Average aggressiveness was at a higher level in "competition" treatments, 1.24 aggressive actions/2.5 min, than in "no competition" treatments, 0.71 aggressive

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<sup>9/</sup> Pooled estimates of variance among fish treated alike and associated degrees of freedom used for comparisons among small fish were  $s^2_x = 0.132$ , d.f. = 60; among large fish were  $s^2_x = 1.92$ , d.f. = 60; between large and small fish were  $s^2_x = 0.972$ , d.f. = 120/2; and between the means of the large and small fish combined were  $s^2_x = 0.972$ , d.f. = 120. The degrees of freedom for comparisons between large and small fish were divided by two in appraising the tabled probability levels (Snedecor, 1956) because the variances of small and large fish were not equal.

Table 6. Average aggressiveness and activity during the daylight hours for large and small fish in each treatment and for the whole treatment as calculated from days 27;21, 39;33, and 51;45.

Treatment Code	Fish Size	n <sub>i</sub>	Aggressiveness (Aggressive Actions/2.5 min)	Activity (Counts/2.5 min)
CL1	Large	9	-	12.4
CS1	Small	9	-	12.5
	Mean	18	-	12.4
L1	Large	9	2.12	15.8
	Small	9	0.12	10.7
	Mean	18	1.12	13.2
XF	Large	9	0.44	8.2
	Small	9	0.35	8.5
	Mean	18	0.39	8.3
NF	Large	9	1.44	11.0
	Small	9	0.30	9.7
	Mean	18	0.87	10.3
LB	Large	9	2.42	16.5
	Small	9	0.16	12.4
	Mean	18	1.28	14.4
LP1	Large	6	3.54	15.5
	Small	6	0.24	10.2
	Mean	12	1.88	12.8
LP2	Large	9	1.54	9.1
	Small	9	0.17	8.1
	Mean	18	0.85	8.6
LSH	Large	9	1.58	11.0
	Small	9	0.21	8.6
	Mean	18	0.89	9.8
CL4	Large	9	-	24.4
CS4	Small	9	-	24.2
	Mean	18	-	24.3
L4	Large	9	2.06	28.0
	Small	9	0.07	28.4
	Mean	18	1.06	28.2

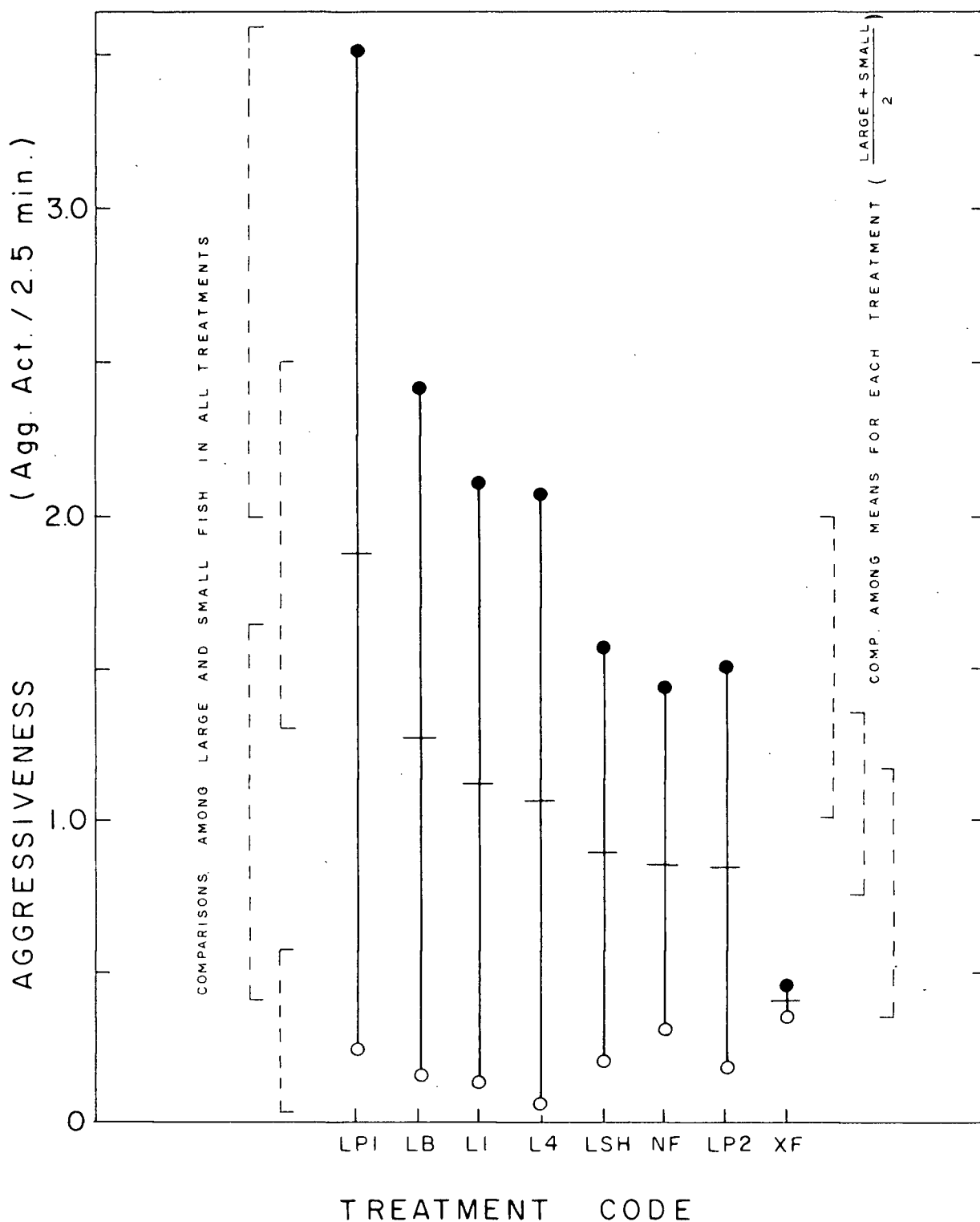


Figure 8. Multiple comparisons of aggressiveness of large fish, small fish, and both for each treatment as calculated from days 27;21, 39;33, and 51;45 (any two means not enclosed by the same bracket are different,  $p \leq 0.05$ ). ● = large fish, ○ = small fish, — = mean for whole treatment.

actions/2.5 min, (multiple comparison,  $n = 84, 54$ ;  $p \leq 0.05$ ).

Large fish were more aggressive and were socially dominant, while the small fish behaved as subordinates. The social dominance of the large fish was presumably determined more (on the average) by relative size than genotype because the size difference was initiated by rearing sibs of different ages. Aggressiveness of the large socially dominant fish was influenced by environmental factors and in general increased when food was limited and locally concentrated. If food was in excess the large fish was no more aggressive than the small fish.

Average daily activity counts/2.5 min of the large and the small fish in each treatment were calculated for days 27;21, 39;33, and 51;45 by averaging the eighteen 2.5-minute observations made on a fish in one day (Table 6). In addition the small fish was averaged with the large fish to get a mean value for the whole treatment. Multiple comparison techniques (Duncan, 1955; Kramer, 1956) were used in the analysis of the data (Figure 9).<sup>10/</sup>

Fish in 4-liter baskets apparently were more active than fish in 1-liter baskets (Figure 9), but this was at least in part a bias in the counting techniques. If a fish swam across a 4-liter basket, it passed under 3 strings and moved 20 cm (1.5 activity counts/10 cm of movement); but if a fish swam across a 1-liter basket, it passed under 1 string and moved 10 cm (1 activity count/10 cm of movement). At this rate a fish swimming 120 cm back and forth in a 4-liter basket would be recorded as 18 counts and in a 1-liter basket as 10 counts. Fish did not always swim back and forth however, and it was not possible to calculate a factor to equilibrate the activity data for 1-liter versus 4-liter comparisons.

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<sup>10/</sup> Pooled estimate of variance among fish treated alike was  $s^2_x = 602.1$  and degrees of freedom d.f. = 152.

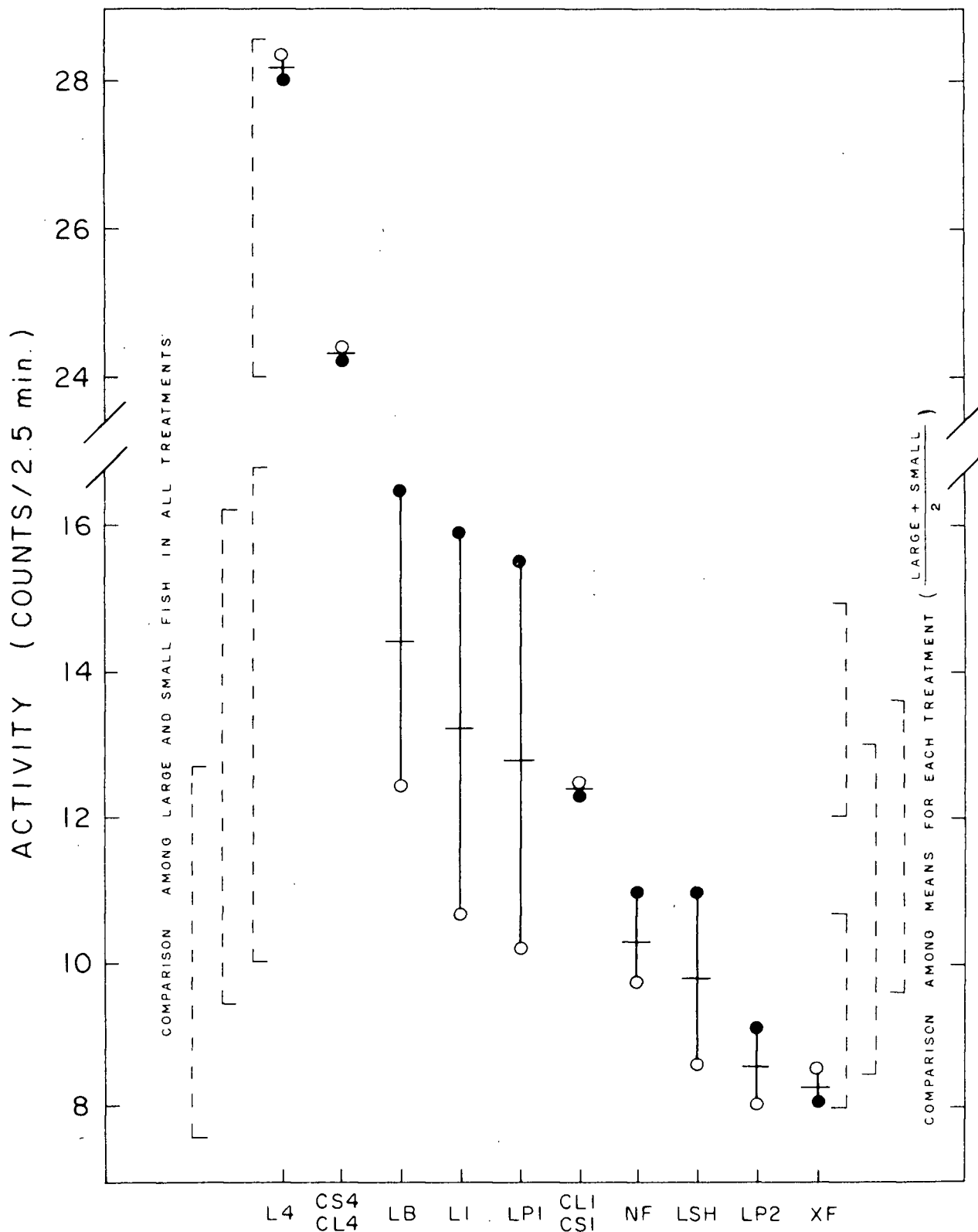


Figure 9. Multiple comparisons of activity of large fish, small fish, and both for each treatment as calculated from days 27;21, 39;33, and 51;45 (any two means not enclosed by the same bracket are different,  $p \leq 0.05$ ). ● = large fish, ○ = small fish, — = mean for whole treatment.

There were no significant differences between activities of a large and a small fish in the same treatment (Figure 9), and there were not many differences among average activities of whole treatments (Figure 9). Average activity in 1-liter treatments was never greater than activity of controls. Only fish in treatment XF were less active than isolate controls.

Some useful comparisons were made by grouping treatments on the basis of growth rates into "competition" treatments (L1, LB, LP1, LSH, and L4) and "no competition" treatments (CL1, CS1; XF; NF; LP2; and CL4, CS4). Average activity in "competition" treatments, 15.7 counts/2.5 min, was greater than average activity in "no competition" treatments, 12.8 counts/2.5 min (multiple comparison,  $n = 84, 90; p \leq 0.05$ ). In "no competition" treatments, activity of large fish, 13.0 counts/2.5 min, was not greater than activity of small fish, 12.7 counts/2.5 min (multiple comparison,  $n = 45, 45; p > 0.05$ ); but in "competition" treatments, large fish, 17.3 counts/2.5 min, were more active than small fish, 13.0 counts/2.5 min (multiple comparisons,  $n = 42, 42; p \leq 0.05$ ). Increased activity in "competition" treatments was primarily a result of increased activity of large fish. Even though activity counts of small fish were the same in both "competition" and "no competition" treatments, there was a difference in what they were doing while accumulating activity counts. Much of a small fish's activity in competition treatments consisted of escaping aggressive actions of the large fish, while in some of the "no competition" treatments (CL1, CS1 and CL4, CS4) there was none of this activity and in others, such as XF, little of this activity.

#### Diurnal Rhythms in Behavior

Behavior observations from each treatment on day 39;33 and 51;45 were averaged and graphed in Figures 10-13 for each time period. Each point represents twelve 2.5-minute periods of observation. Lights went on at 0 hours and off at 16 hours. In limited food treatments the single feeding

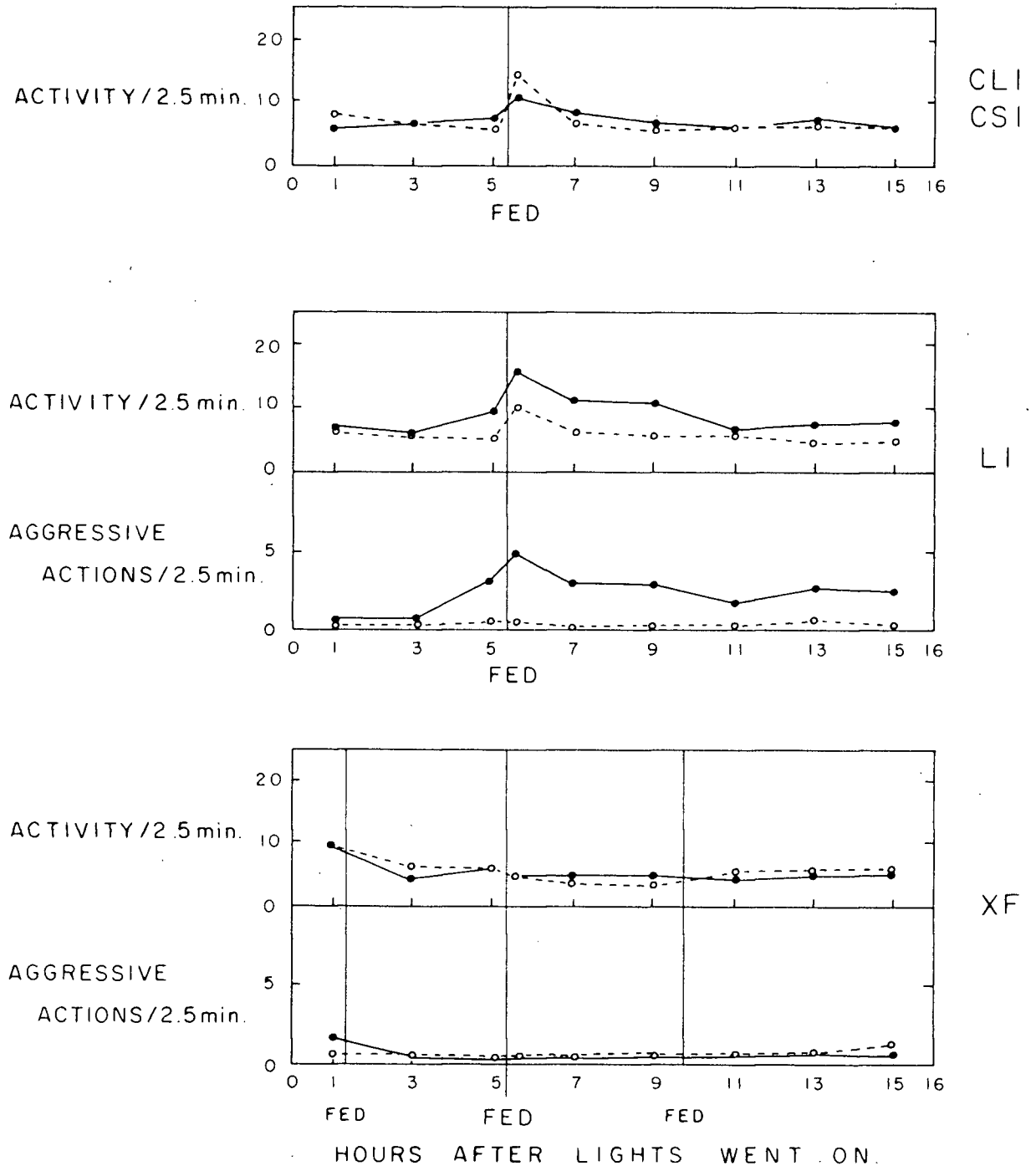


Figure 10. Diurnal changes in activity and aggressiveness of large and small fish in the isolate controls (CL1, CS1), in plain 1-liter limited food treatment (L1), and in the excess food treatment (XF).  
 ● = large fish, ○ = small fish.



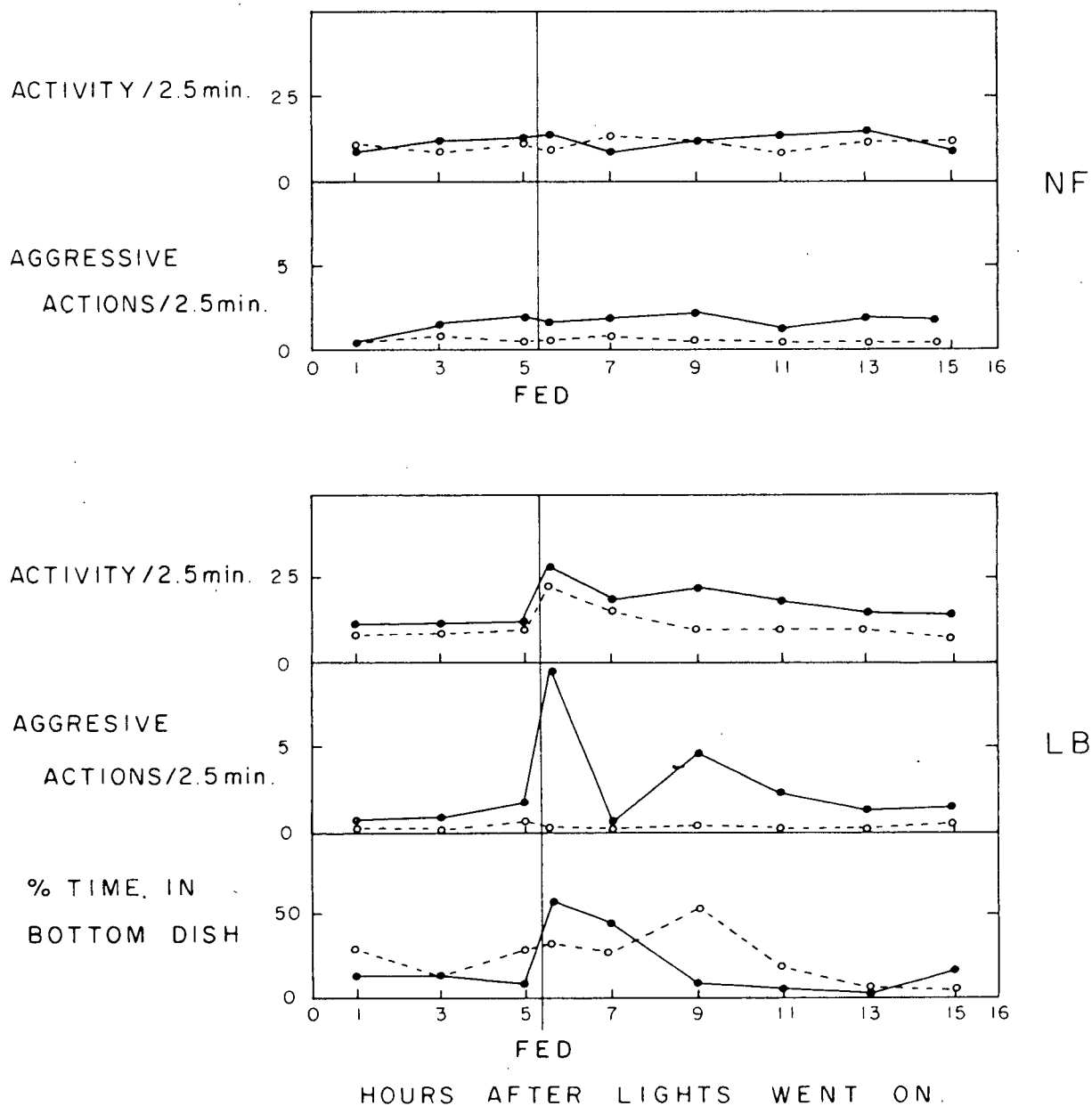


Figure 11. Diurnal changes in activity and aggressiveness of large and small fish in the no-food treatment (NF), and activity, aggressiveness, and location preference of large and small fish in the limited food localized on bottom treatment (LB). ● = large fish, ○ = small fish.

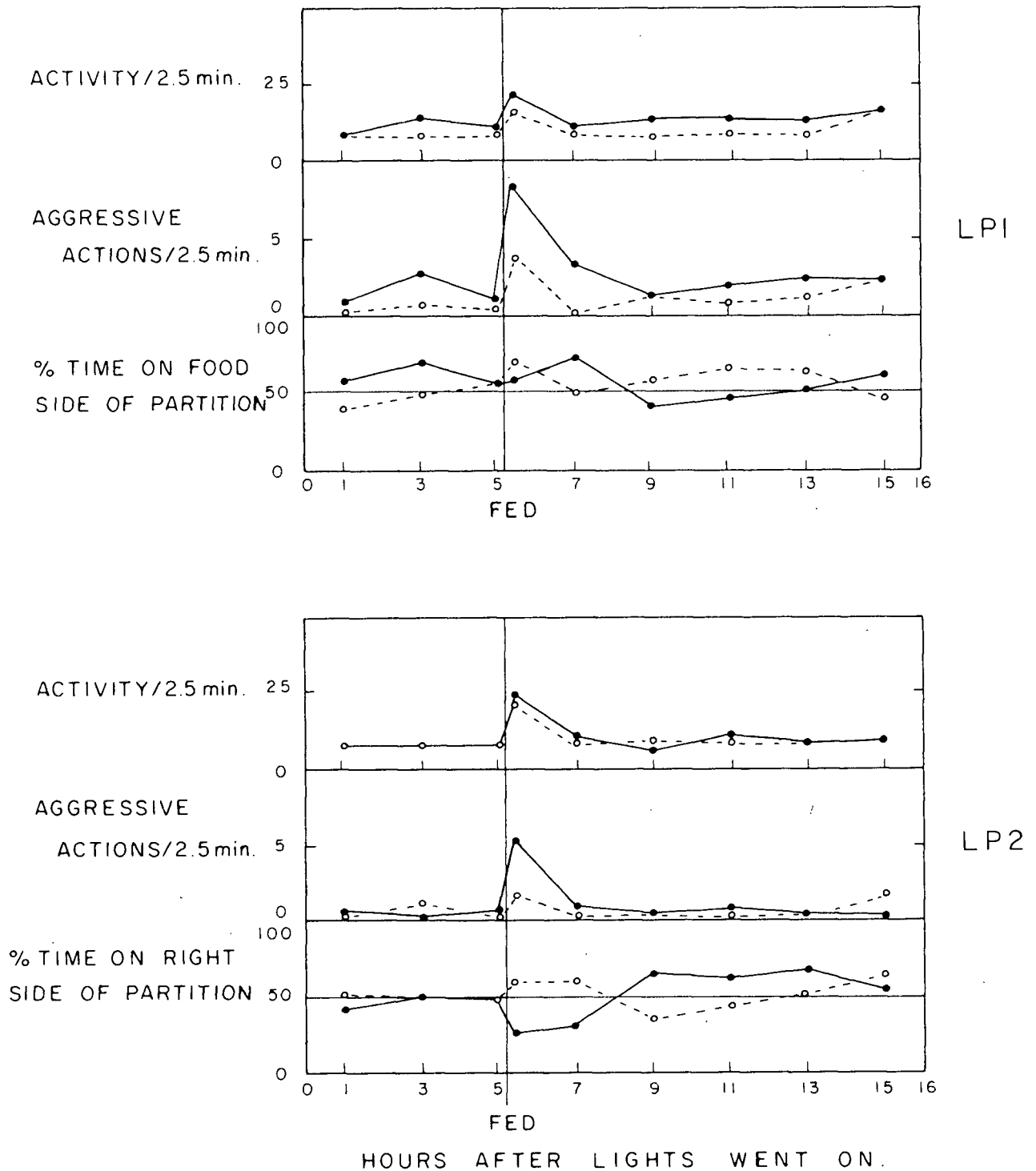


Figure 12. Diurnal changes in activity, aggressiveness, and location preference of large and small fish in treatments with a partial partition across the basket which were fed on one side (LP1) and both sides (LP2) of the partition. ● = large fish, ○ = small fish.

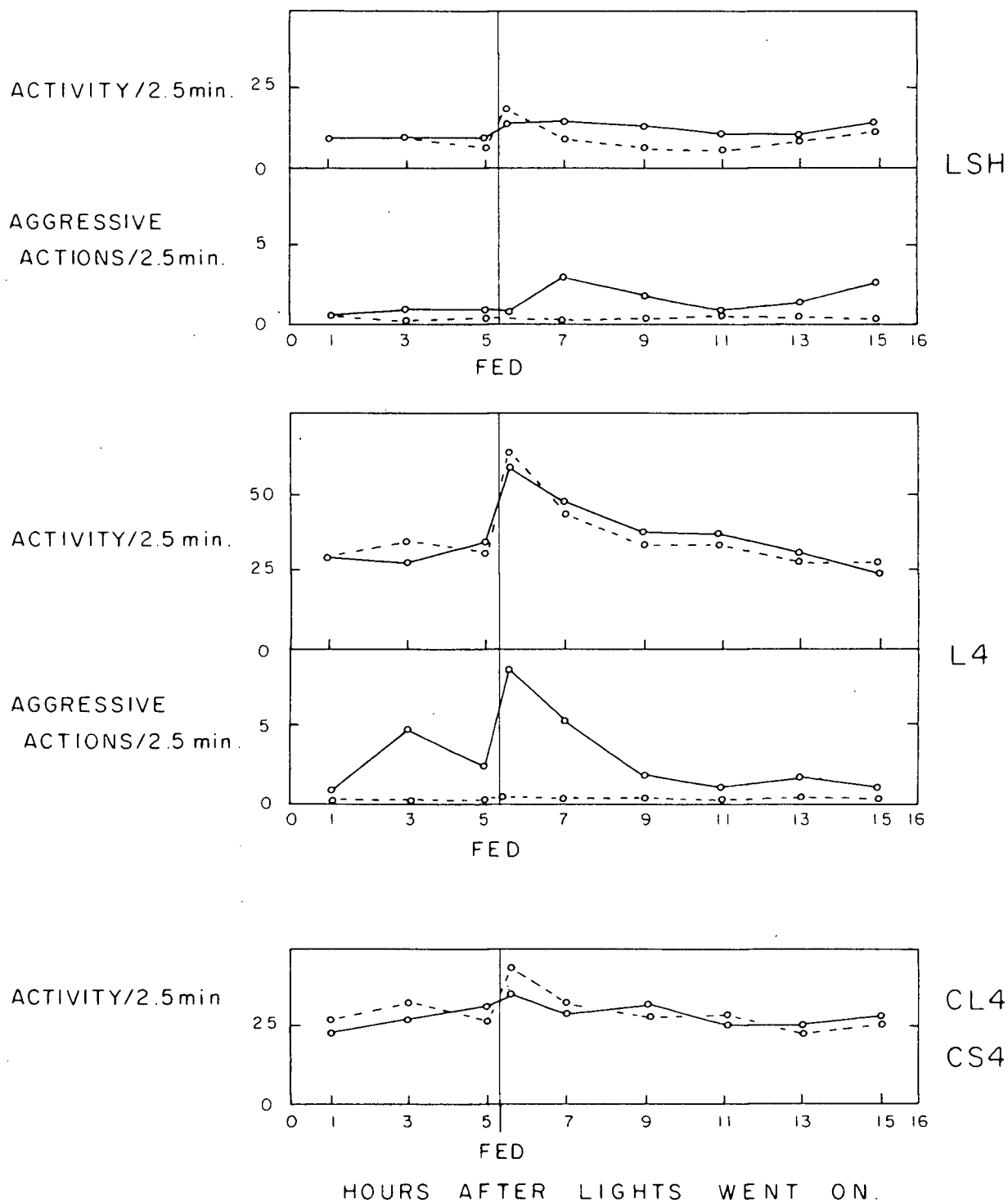


Figure 13. Diurnal changes in activity and aggressiveness of large and small fish in shallow limited food treatment (LSH), 4-liter isolate treatment (CL4, CS4), and plain 4-liter limited food treatment (L4). • = large fish, ○ = small fish.

was at 5.25 hours, and in XF the three feedings were at 1.25, 5.25, and 9.25 hours after the lights went on.

Activity of both large and small fish increased immediately after food was introduced in all limited food treatments (L1, LB, LP1, LP2, LSH, and L4) (Figures 10-13); and in the isolates (CL1, CS1, CL4, and CS4) (Figures 10, 13). Activity did not increase in the excess food treatment (XF) at feeding time (Figure 10), and in the no-food treatment (NF) activity was steady throughout the day (Figure 11). Activity in the form of general appetitive behavior was at a steady level among isolates during periods when no food was in the basket. At feeding time the fish swam rapidly back and forth among the food particles until all pellets had been eaten. The steady level of food searching behavior was then resumed. The same general pattern was observed in the limited food populations, but was further complicated by social interactions between the large and small fish. High activity at hour 1 in XF (Figure 10) was the consequence of sexual behavior. The fish in XF were the only ones which had grown fast enough to approach maturity by day 51;45.

Aggressiveness of the large fish increased within one or two minutes after food was presented in the limited food treatments (L1, LB, LP1, LP2, and L4) (Figures 10-13) and several hours after food was presented in the limited food treatment (LSH) (Figure 13). In excess food treatment (XF) no increase in aggressiveness occurred after food was introduced (Figure 10). When no food was provided (NF) the level of aggressiveness was steady throughout the day (Figure 11).

Aggressiveness of small fish remained steady or decreased at feeding time in limited food treatments (L1, LB, LSH, and L4) (Figures 10, 11, 13) but increased in the two limited food treatments which had partial partitions across the baskets (LP1 and LP2) (Figure 12). No increase in aggressiveness

occurred in XF when food was supplied (Figure 10), and in NF aggressive actions were at steady level throughout the day (Figure 11).

In treatments L1 and L4 the limited food was scattered evenly on the surface of the water. Neither the large nor the small fish defended any specific area. When food was present the large fish fed rapidly but stopped feeding at frequent intervals and swam around in the basket. While swimming throughout the basket the large fish often encountered the small fish, nipped it, and chased it into a corner or to the bottom. The large fish resumed feeding only to repeat the sequence 10-20 seconds later. The small fish began feeding during the periods when the large fish was feeding, but was usually disturbed too frequently to eat many pellets.

In LB the localized food supply was placed in a dish on the bottom. The large fish defended the food dish only when food was present (Figure 11). During this period the small fish would continually attempt to enter the dish but would be chased away by the large fish. This continued for 2 or 3 hours after food was introduced, even though all the food appeared to be gone 5 or 10 minutes after it was supplied. The large fish stayed in the dish except when chasing the small fish away. About 3 hours after a feeding time the large fish left the dish, and the small fish moved into the dish and searched for food (Figure 11). About 2 hours later the small fish also left the dish, and neither fish occupied it until food was presented on the following day (Figure 11).

In LP1 the food was concentrated on the right side of a partial partition and floated on the surface. The large fish tended to inhabit the half of the basket in which the food was placed during the 5 hours before and the 3 hours after food was supplied (Figure 12). After discovering the food the large fish remained in the food area except when chasing away the small fish

which continually re-entered the food area. The small fish also was aggressive and attempted to chase the large fish from the food area but these attempts ended in failure. As in LB above, the large fish left the feeding area about 3 hours after food was introduced and the small fish then remained in the food area (Figure 12).

In LP2 the food was simultaneously placed on both sides of a partial partition. Both fish were aggressive but did not defend specific areas. The large fish moved freely from one side of the partition to the other, but each time the large fish changed sides the small fish immediately swam to the opposite side (Figure 12). At feeding time this behavior left each fish alone with one-half of the food supply even though they alternated sides many times while food was present.

In LSH the basket was only 2.5 cm deep and the two fish seemed to interfere with each other. Both the large and small fish were inactive, and when they did swim it was only for short distances. The large fish did not respond to the food with a sudden increase of feeding activity and aggression, but rather fed slowly for several hours after food was introduced (Figure 13). By this time most of the pellets had sunk, and the large fish tended to defend the pellets for long periods without eating any.

#### Relations Between Growth and Behavior

Aggressive behavior provided large fish with a competitive advantage when food supply was limited, but not when food was absent or in excess. In NF the large fish was socially dominant (Figure 8) but no food was present, and the dominant and subordinate fish lost weight at the same rates (Figure 5). The large fish was more aggressive when a limited food supply was added (L1) and grew better than the subordinate (Figure 5). Aggressive actions by the large fish were most frequent immediately after food was added

and usually prevented the subordinate from eating many pellets. With the introduction of excess food (XF) the social hierarchy disappeared, neither the large nor the small fish was aggressive when food was added, and they grew equally well (Figures 5, 8).

Aggressiveness was associated with the internal state of "hunger," and the external factors of food stimuli and other medaka. The aggressiveness of a particular medaka was high if the other fish was smaller, but was low if the other fish was larger. Aggressive actions among immature medaka were most frequent when the fish had a limited food supply, food stimuli were present, and another smaller medaka was near; for example, the period just after food was supplied in limited food treatments. Aggressive actions were moderately frequent when no food stimuli were present even though the fish had not been fed for some time and a smaller fish was present (NF). If the fish were fed in excess (XF) the frequency of aggressive actions was only 7.5% of the highest frequency even though food stimuli and smaller medaka were present. Aggressive behavior was a mechanism initiated by the internal state of "hunger," a feeding stimulus, and smaller medaka, which gave a competitive advantage to large fish when food supply was limited.

Evidence indicating that aggressiveness was a competitive mechanism for food and not for space, per se, was provided by a comparison of treatments L1, L4, and XF. Even though L1 environments were one-fourth the size of L4 environments, large fish in L1 and L4 were equally aggressive (Figure 8), and the differences between the growth rates of large and small fish were the same in each sized environment (Figure 5). When the amount of space was the same but the amount of food was limited (L1) rather than in excess (XF) the large fish was more aggressive and the difference in growth rates between large and small fish was greater. The difference in aggressiveness and

growth was evidently due to limited food, not the amount of space.

Even though some of the factors associated with space, such as biological conditioning and abundance of food, were removed in these experiments, there were some factors which remained to produce residual unexplained effects associated with space. The average growth among fish fed 10 pellets per fish per day in 4-liter baskets (CL4, CS4) was significantly greater than among fish fed the same amount in 1-liter baskets (CL1, CS1) (Figure 5). The same was true for the average growth of L4 and L1, although the dominant fish had an equal advantage relative to the subordinate in both sized baskets. Factors associated with space which would produce these effects were not isolated in the present experiment. Other possible explanations which suggest themselves are that a microfauna was on the nylon liners which provided more food in larger baskets; the fish found pellets which sank to the bottom more easily in large baskets because the water column was not as narrow; a water-borne growth inhibitor (Richards, 1958) was a particle and was too large to pass out through the fine meshes of the baskets with the circulating water and would be more concentrated in smaller baskets; or the amount of current flow was less on the average through large baskets than small baskets and less energy was used in swimming. It was apparently not associated with any psychological phenomenon, mediated visually, because differences in density had no effects if food was supplied in excess. It is conceivable that when fish were fed in excess they did not eat any of the fecal material in the container, whereas in the limited food treatments more fecal material would have been eaten. Whatever the cause it was not measured in the experiment.

Spatial distribution of the limited food supply influenced the consequences of competition. When food was localized in one part of the environment as in LP1 and LB, aggressiveness of the large fish was greater than when



food was evenly distributed in the environment as in L1 and LP2 (Figure 8). Likewise the increase in aggressiveness just after food was supplied appeared to be greater in localized food treatments (LP1 and LB) than in dispersed food treatments (L1 and LP2) (Figures 10, 11, 12). There was an indication that large fish had a greater competitive advantage for food in LB than in L1 (Figure 5), and the large fish definitely had a greater competitive advantage in LP1 than in LP2. Localizing the limited food supply increased both the aggressiveness and the competitive advantage of the large socially dominant fish.

If the limited food supply was localized (LB or LP1) the aggressive behavior took the form of territoriality. Whenever the small fish approached the food area, the large fish chased it away. Defense of a specific area disappeared when all the food was eaten. Although aggressive behavior appeared to serve in the defense of an area or space it was actually functioning as a competitive mechanism for food, and as in the cases listed above was initiated by the internal state of "hunger," other smaller medaka, and the presence of food stimuli.

The amount of spatial isolation between competitors when food was evenly distributed influenced the consequences of competition. Control fish (CL1, CS1) represented complete isolation and the removal of all interactions between competitors; LP2 represented a partial isolation, in the form of either distance or obstructions in the environment; and L1 represented no isolation between competitors. All were given the same amount of food, but even so, as the amount of isolation decreased, there was a decrease in average growth rate, an increase in aggressive interchanges between competitors, and an increase in competitive advantage to the large socially dominant fish (Figures 5, 8). Segregation of the environment or spatial

isolation between competitors reduced the influence of competition and decreased the advantage of the large dominant fish if food was evenly distributed.

Aggressiveness not only served as a competitive mechanism for food, but also tended to disperse fish throughout the environment if food was evenly distributed. For example, the fish in LP2 were usually on opposite sides of the partial partition (Figure 12) because the small subordinate always moved to the side farthest from the large dominant fish. This occurred only when food was evenly distributed in the environment. In LP1, which had all the food on the right side of the partial partition, the subordinate fish continually re-entered the side containing both the dominant fish and the food. By continually re-entering this area the subordinate was exposed to more aggressive actions than the subordinate in LP2 which avoided the side containing the dominant fish. Aggressive behavior only resulted in a dispersed distribution of medaka if the necessities of the subordinate fish were found in all subsections of the habitat.

In these experiments, growth and condition were measured to demonstrate the consequences of competition under different environmental conditions, and activity and aggressiveness were measured as potential mechanisms which might mediate the consequences of competition. The association between these two response variables and two potential mediating variables were measured by multiple and partial correlation and regression techniques. Data for days 27;21, 39;33, and 51;45 were averaged for each treatment. Levels of activity and aggressiveness were averaged only for the 5.25 and 7.00 hours, because the two hours after food was presented appeared to be most important in determining the consequences of competition. The average difference between the large and the small fish in each treatment was used for analysis (Table 7),

Table 7. Differences in average growth, condition, aggressiveness, and activity between large and small fish in each treatment averaged for days 27;21, 39;33, and 51;45.

Treat- ment Code	$Y_1$ ( $G_L - G_S$ )	$Y_2$ ( $C_L - C_S$ )	Average Aggressiveness During 2.5 Hours After Feeding			Average Activity During 2.5 Hours After Feeding		
			Large Fish	Small Fish	$x_1$ ( $Agg_L - Agg_S$ )	Large Fish	Small Fish	$x_2$ ( $Act_L - Act_S$ )
CL1 CS1	0.00	0.00	0.00	0.00	0.00	15.9	17.4	-1.5
L1	+1.63	+1.63	6.37	0.33	+6.04	22.6	13.2	+9.4
XF	0.00	0.00	0.23	0.27	-0.04	8.3	7.0	+1.3
NF	+0.07	+0.26	2.98	0.88	+2.10	10.5	10.4	+0.1
LB	+2.47	-0.27	8.43	0.10	+8.33	21.7	17.5	+4.2
LP1	+2.83	+1.67	9.13	2.58	+6.55	15.2	9.0	+6.2
LP2	+0.68	-0.49	5.45	1.82	+3.63	13.8	10.3	+3.5
LSH	+2.64	+0.78	5.50	0.48	+5.02	14.0	14.1	-0.1
CL4 CS4	0.00	0.00	0.00	0.00	0.00	15.9	17.4	-1.5
L4	+2.45	+1.71	9.32	0.37	+8.95	38.4	40.8	-2.4

where  $y_1 = (G_L - G_S)$  or the growth of the large minus the growth of the small fish;  $y_2 = (C_L - C_S)$  or condition of large minus condition of small fish;  $x_1 = (Agg_L - Agg_S)$  or aggressiveness of large minus aggressiveness of small fish at 5.25 and 7.00 hours; and  $x_2 = (Act_L - Act_S)$  or the activity of the large minus the activity of the small fish at 5.25 and 7.00 hours. Simple, partial, and multiple correlation coefficients for these data are presented in Table 8.

Growth differences ( $G_L - G_S$ ) were associated with differences in condition ( $C_L - C_S$ ). Differences in growth and condition between large and small fish are two ways of measuring the same response. Growth differences ( $G_L - G_S$ ) were associated with differences in aggression ( $Agg_L - Agg_S$ ) but not with differences in activity ( $Act_L - Act_S$ ) (Table 8). The simple correlation coefficient between  $y_1$  and  $x_1$  (0.910), the partial correlation coefficient which removed the influence of activity (0.891), and the multiple correlation coefficient which takes into account the influence of activity (0.911), were all virtually the same. Therefore prediction of the growth differences was not improved by considering differences in activity; differences in activity had no influence on the consequences of competition but differences in aggression were highly associated with the growth consequences of competition.

None of the associations between condition differences ( $C_L - C_S$ ) and aggression or activity differences were significant, but the pattern of associations was the same as for the growth differences (Table 8). Condition was not as sensitive a measure of the effects of competition as was growth.

The relation between growth differences ( $G_L - G_S$ ) and aggressive differences ( $Agg_L - Agg_S$ ) was adequately described by the linear regression:

$$(G_L - G_S) = -0.143 + 0.341 (Agg_L - Agg_S)$$

and was presented graphically in Figure 14 (95% C.I.,  $n = 10$ ,

Table 8. Simple, partial, and multiple correlation coefficients for  $y_1 = (G_L - G_S)$ ,  $y_2 = (C_L - C_S)$ ,  $x_1 = (Agg_L - Agg_S)$  and  $x_2 = (Act_L - Act_S)$ . (See text for explanation.)

	Correlation Coefficients	Probability Level p =
<u>Simple Correlation Coefficients</u>		
Growth x Condition	$r_{y_1 y_2} = 0.622$	= 0.05
Growth x Aggression	$r_{y_1 x_1} = 0.910$	< 0.01
Growth x Activity	$r_{y_1 x_2} = 0.414$	> 0.05
Condition x Aggression	$r_{y_2 x_1} = 0.576$	> 0.05
Condition x Activity	$r_{y_2 x_2} = 0.317$	> 0.05
Aggression x Activity	$r_{x_1 x_2} = 0.425$	> 0.05
<u>Partial Correlation Coefficients</u>		
Growth x Aggression (Activity)	$r_{y_1 x_1 \cdot x_2} = 0.891$	< 0.01
Growth x Activity (Aggression)	$r_{y_1 x_2 \cdot x_1} = 0.075$	> 0.05
Condition x Aggression (Activity)	$r_{y_2 x_1 \cdot x_2} = 0.514$	> 0.05
Condition x Activity (Aggression)	$r_{y_2 x_2 \cdot x_1} = 0.098$	> 0.05
<u>Multiple Correlation Coefficients</u>		
Growth x Aggression and Activity	$R_{y_1 x_1 x_2} = 0.911$	< 0.01
Condition x Aggression and Activity	$R_{y_2 x_1 x_2} = 0.581$	> 0.05

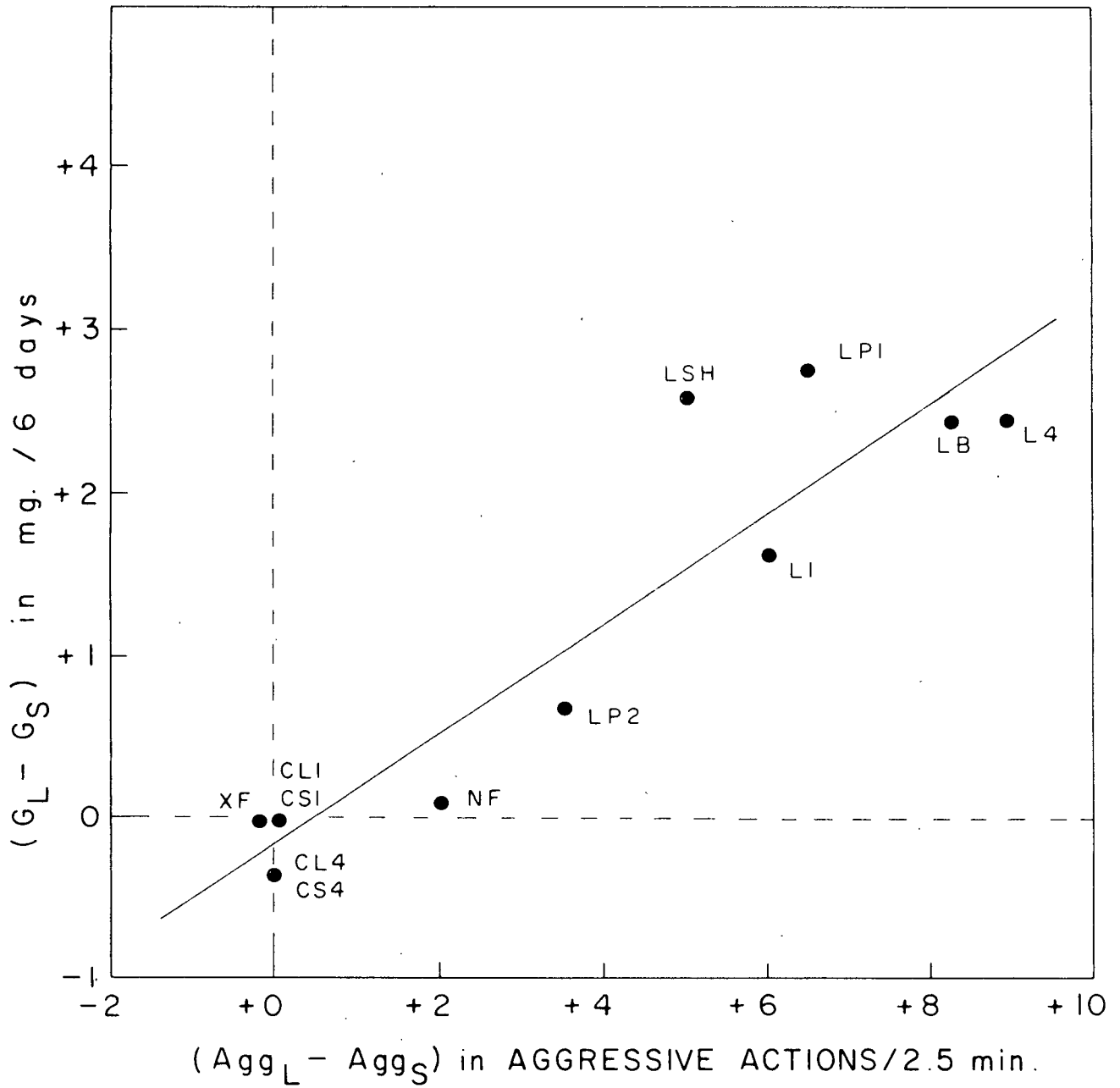


Figure 14. Differences in the growth rates of large and small fish in each treatment plotted against the differences in their aggressiveness during the 2.5 hours after food was presented.

$b = 0.341 \pm 0.117$ , and  $\bar{y}_1 = 1.240 \pm 0.351$ ;  $s_{x_1} = 3.4479$ ,  $s_{y_1 x_1} = 0.5686$ ,  $s_{y_1} = 1.2896$ ). The difference in aggressiveness between the large and small fish was important as a mediating factor or as a mechanism by which the effects of competition were unequally passed on to the large and the small fish. These differences in aggressiveness of the large and small fish varied from treatment to treatment as induced by amount of food, spatial distribution of food, and topography of the habitat. The variables of the environment influenced the growth consequences of competition, but did so through the action of the aggressive behavior in various environments. Detailed analysis of the behavior data discussed previously also supported these conclusions.

Even though differences in aggressiveness between large and small fish had a great influence upon the growth consequences of competition, an aggressive action by the large fish was not equally efficient in different environmental situations. Efficiency of aggression for the large fish was defined as the number of milligrams, per aggressive action, by which the growth of large fish exceeded the growth of small fish, and was calculated by dividing column 1 by column 3 in Table 7. Efficiency of aggression was zero when no food or excess food was provided but was high at intermediate levels of food abundance (Figure 15a). In limited food environments the efficiency of aggression increased as the food became more localized in its spatial distribution (Figure 15b). Efficiency of aggression decreased if the habitat had a dispersed food supply and was subdivided by partial partitions (Figure 15b). Efficiency of aggression decreased as the size of the environment or the amount of space per fish increased (Figure 15c). Environmental features such as the amount of food, spatial distribution of the food, and the topography of the habitat influenced the consequences of competition,

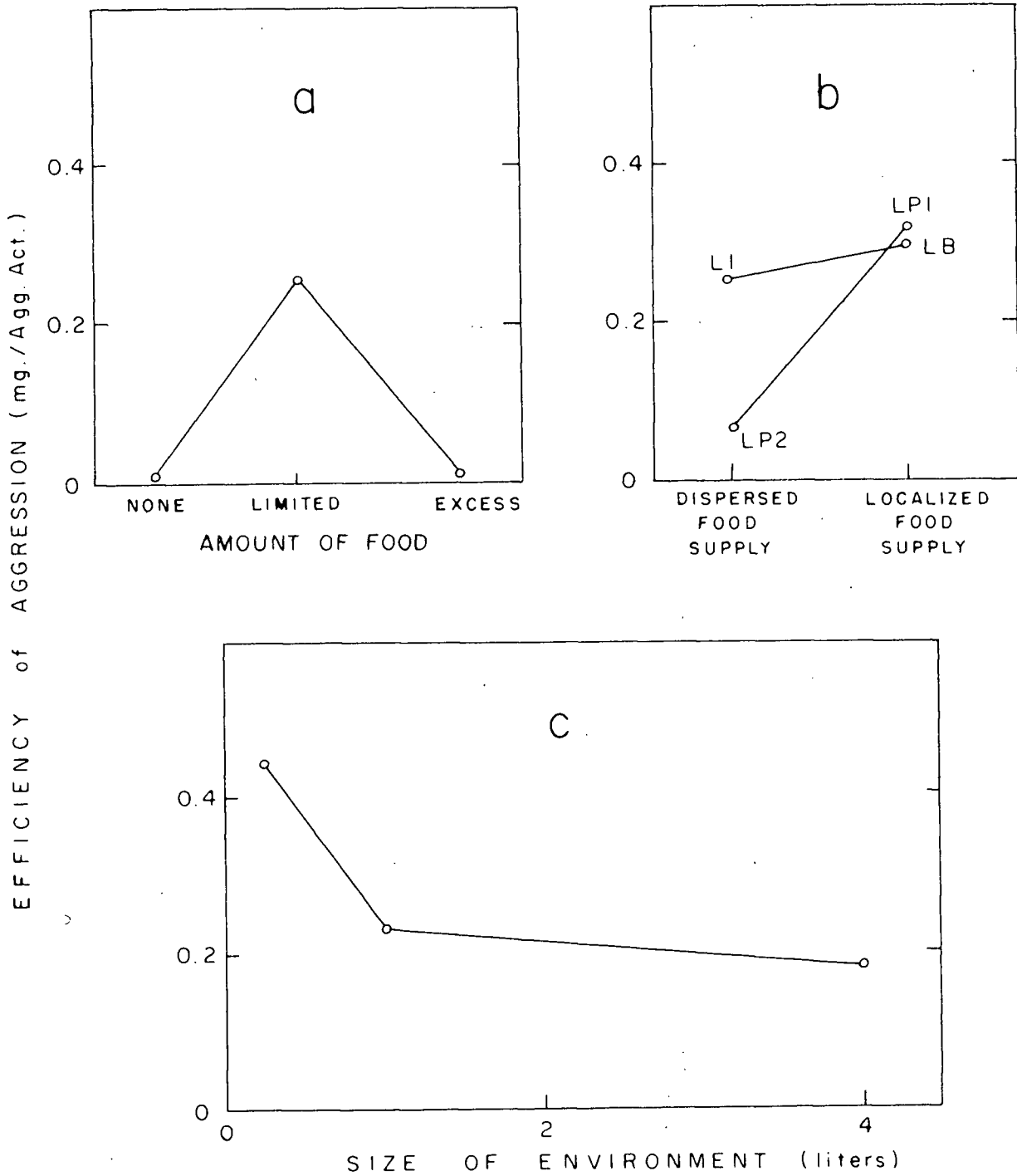


Figure 15. Efficiency of aggression to the large dominant fish as influenced by (a) amount of food, (b) localization of food supply, and (c) size of environment. Efficiency =  $(G_L - G_S) / (\text{Aggressive actions by large fish in 2.5 hours after food was supplied})$



not only by altering the frequency of aggressive actions, but also by altering the efficiency of an aggressive action by the large fish in terms of growth.

#### Summary of Results

Each medaka had the same chance of having genetic potential for becoming an aggressive social dominant, but the large fish always dominated the small fish. The difference between the aggressiveness of a large and small fish was influenced by many environmental factors. An excess food supply resulted in a disintegration of the social hierarchy and a low level of aggression. In limited food treatments the difference between the aggressiveness of large and small fish was greater just after food was presented, increased if the food was spatially concentrated, and decreased if the amount of isolation between competitors was increased. If food was localized, aggressive behavior took the form of territoriality, but the defense of localized areas disappeared several hours after the limited food supply was completely eaten.

Two fish competing for a limited food supply grew slower than two fish grown in isolation on the same amount of food. Differences between the growth of large and small fish from treatment to treatment were closely associated with environmentally induced differences in aggressiveness. The more aggressive the large fish in a treatment the better their growth rates relative to subordinate fish. Aggressive behavior was the mechanism through which the consequences of competition (poor growth) were unequally distributed between large and small fish. Dominant fish had a competitive advantage over small fish in limited food environments unless the environment provided both partial isolation for the subordinate and food in all subsections of the habitat. Social dominance did not confer a competitive

advantage when the food was absent or in excess. Aggressive actions by the dominant large fish were not equally efficient in terms of the competitive advantage they provided as the environmental factors were changed. Efficiency of aggression was zero if there was no food or excess food in the habitat. When food was present but limited in supply the efficiency of aggression decreased as the size of the environment increased, and increased when food was more localized.

## COMPETITION FOR EXCESS FOOD (EXPERIMENT III)

### Introduction and Description of Experiment

The purpose of experiment III was to determine whether large fish had a competitive advantage for an excess food supply which was spatially localized, and whether they would defend the localized area which contained an excess food supply.

Each treatment population was composed of two fish with a 4-day age difference, reared in 4-liter baskets. All fish were fed in excess with brine shrimp nauplii until day 32;28 and thereafter were fed an excess of pellets placed in petri dishes on the bottom. Petri dishes were cleaned and refilled daily. In the dispersed excess food treatment (XD) 2 petri dishes were placed in opposite corners of the basket, and in the localized excess food treatment (XL) 1 petri dish was placed in a corner. Any advantage in competition for the excess spatially localized food could be determined by comparing the growth of large fish in XD and XL and by comparing the growth of small fish in XD and XL. If there were no competitive advantage, the large fish in each treatment would grow at the same rates and the small fish in each treatment would grow at the same rates. Hatching was induced 11 days after fertilization, and the fish from each spawning day were raised as a group until day 32;28 at which time they were randomly allocated to the treatments. Each fish was weighed every 6 days from day 32;28 through 62;58. Both XL and XD were replicated 6 times.

### Results and Conclusions

Size-specific 6-day weight increments were determined graphically for

each fish from a Walford plot (Ricker, 1958) when the small fish were 20 and 30 mg in weight and when the large fish were 25, 35, and 45 mg in weight. Values for the small fish were averaged for 20 and 30 mg and for the large fish they were averaged for 25, 35, and 45 mg. Growth of large fish in XD with a dispersed excess food supply, 8.9 mg/6 days, was not different from growth of large fish in XL with a localized excess food supply, 8.9 mg/6 days ( $t_{25} = 0.02$ ,  $p > 0.25$ ). Small fish also grew equally well in the two treatments, 7.6 mg/6 days in XD and 8.0 mg/6 days in XL ( $t_{17} = 0.72$ ,  $p > 0.25$ ). Large fish did not have a competitive advantage for excess food even though it was locally concentrated.

Although no detailed behavior observations were made on these fish, observations were made on additional baskets with larger populations. As many as 20 medaka, 10-15 mm in total length, would crowd into the 50 mm food dish at one time as long as the amount of food in the dish was maintained in excess. Few aggressive interchanges were observed among them, and large fish did not chase small fish away. As in experiment II, medaka were not aggressive in the presence of food stimuli and smaller medaka as long as food was in excess. Localizing the excess food did not alter this behavior.

#### Summary of Results

Large medaka did not defend localized feeding areas if food was provided in excess. Large and small medaka grew equally well whether the excess food had a dispersed or a localized distribution.

## COMPETITION FOR LIMITED FOOD IN LARGER POPULATIONS (EXPERIMENT IV)

### Introduction

The purpose of experiment IV was to examine the action and consequences of aggressive behavior in larger populations in more complicated environments when food was limited in supply. Spatial distribution of the food and the number of subdivisions in the habitat were varied to clarify the influence of these modifying factors. The influence of biological conditioning of the water was removed as in previous experiments. Experimental animals were selected from many different spawning pairs.

### Description of Experiment

Each population was composed of 8 fish raised in 8-liter baskets, and food was supplied at a rate of 10 pellets per fish per day. Individual fish could not be identified, and differences in growth rates of large and small fish were studied by comparing the variation in sizes observed in different treatments. A description and code number for each treatment are presented in Table 9 and Figure 16. Partial partitions which subdivided some baskets were made from nylon "horsehair" crinoline (10 meshes/cm), and holes through partitions were 3 cm wide and 5 cm deep and were placed with the top edge 3 cm below the water surface. In those treatments not receiving food in every subsection of the habitat, the subsections in which food was placed were evenly spaced after one food location had been chosen at random. Food was placed in the same locations throughout the experiment.

Eggs were selected from many spawning pairs, but were fertilized on the same day. Temperature was varied 10, 11, 12, and 13 days after fertilization

Table 9. Design of experiment IV showing treatments and number of replications with treatment codes and descriptions.

Treatment Code	No. of Replications	Population Size	Basket		Food	
			Size (liters)	No. of Subsections	No. of Pellets Per Day	Location on Surface
1E	3	8	8	1	80	even
4E	3	8	8	4	80	even
8E	3	8	8	8	80	even
8C4	3	8	8	8	80	in 4 sub-sections
8C2	3	8	8	8	80	in 2 sub-sections
8C1	3	8	8	8	80	in 1 sub-section

to induce hatching, and approximately the same number hatched on each of the four days. They were fed "in excess" on brine shrimp nauplii for 15 days after hatching was induced, at which time they were randomly allocated to the treatments under the restriction that each population contained 2 fish from each hatching day. Treatments were randomly allocated to water bath positions under the restrictions that each bath contained only a single replicate from a given treatment, and that no two replicates of a treatment occupied the same position in different baths.

Each fish was weighed every 6 days from 15 through 39 days after hatching was induced. The positions of fish in the habitat and the total number of aggressive actions were recorded for two 2.5-minute periods after food was presented on days 30, 32, 36, and 38. Two replicates from each treatment were observed on each date.

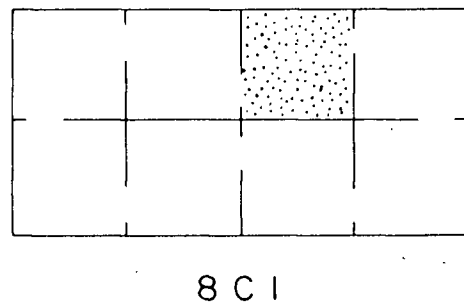
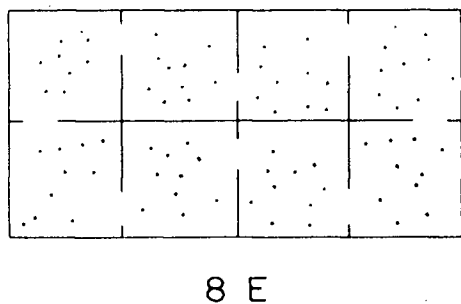
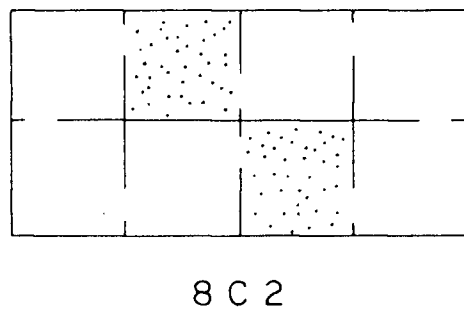
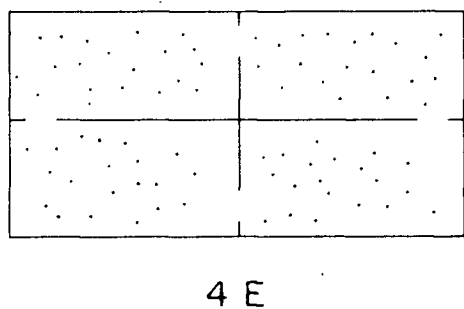
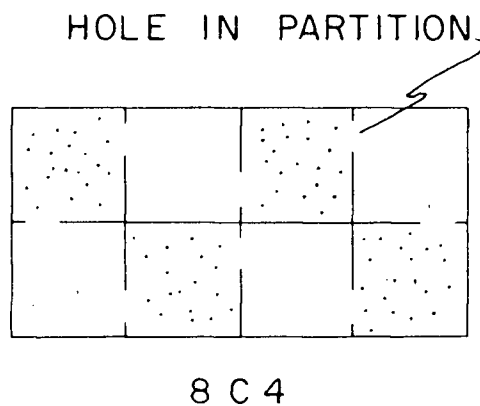
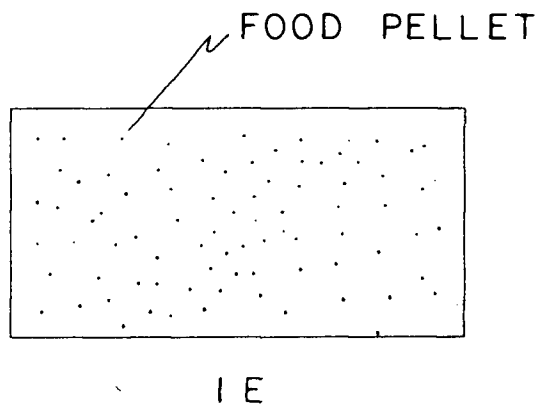


Figure 16. Diagram showing partitions and food locations of the 8-liter baskets used in experiment IV. (top view)

## Results

### Growth Rates

Growth depensation in populations of 8 fish was measured by the increase in the variance of size-frequency distributions during 6-day intervals. Variances of weight distributions within each population were calculated for days 15, 21, 27, 33, and 39, but day 39 was omitted because deaths of small fish were biasing the estimates. A cube root transformation of each variance was used to convert the variances into a normally distributed variable. Increase in variance due to growth differences within a population was expressed as the 6-day increment in the cube root of the variances

$\left[ (s^2_{t+6})^{\frac{1}{3}} - (s^2_t)^{\frac{1}{3}} \right]$ . This measure of growth depensation increases in value as differences between growth rates of large and small fish increase. Growth depensation estimates for the 15-21, 21-27, and 27-39 day intervals were averaged for each treatment (Table 10), and the averages were compared by multiple comparison techniques in Figure 17 (Duncan, 1955; Krammer, 1956).<sup>11/</sup>

Growth depensation was greater when the limited food supply was

Table 10.. The average increase in variability of weight-frequency distributions during a 6-day period due to differences in growth rate in populations of 8 fish.

Treatment Code	1E	4E	8E	8C4	8C2	8C1
Mean increase in variability $\left[ (s^2_{t+6})^{\frac{1}{3}} - (s^2_t)^{\frac{1}{3}} \right]$	+0.40	+0.44	+0.24	+0.31	+0.42	+0.49

<sup>11/</sup> Pooled variance used in multiple comparisons was equal to 0.2213 with 46 degrees of freedom. Time intervals were used as a blocking variable.



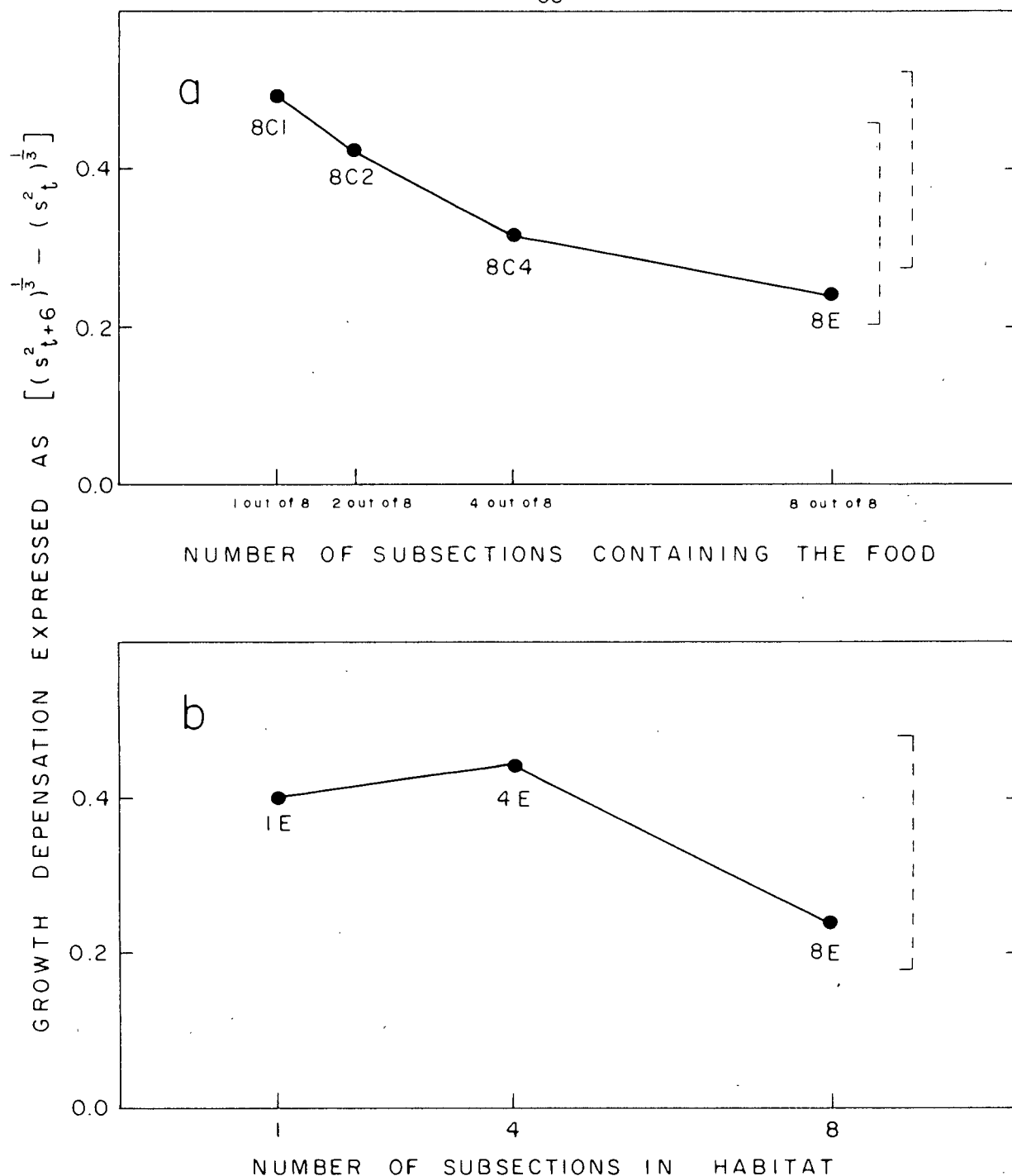


Figure 17. Relation between growth depensation  $\left[ (s_{t+6}^2)^{\frac{1}{3}} - (s_t^2)^{\frac{1}{3}} \right]$  and (a) the spatial distribution of limited food in a subdivided habitat and (b) the extent to which the habitat is subdivided. (Brackets enclose means which do not differ at  $p \leq 0.05$ )

spatially concentrated than when it was evenly distributed (Figure 17a).

Much of the growth depensation in the spatially concentrated food treatments resulted from slow growth of one or two individuals rather than from extremely fast growth of one or two individuals.

In treatments with an evenly distributed food supply, growth depensation appeared to be least if there was one subdivision per fish, intermediate if there were no subdivisions, and greatest if there was one subdivision for every 2 fish (Figure 17b).

### Behavior

Average number of aggressive actions/2.5 min during the 5-minute period after food was presented was calculated for each treatment (Table 11). Each mean is based on sixteen 2.5-minute observations and is the total number of aggressive actions by all 8 fish during the 2.5-minute period. These

Table 11. Frequency of aggressive actions/2.5 min by 8 fish and the coefficient of variation (%) resulting from differences in frequency of aggression on different days of observation during the 5 minutes after food was provided.

Treatment Code	1E	4E	8E	8C4	8C2	8C1
Frequency of Aggressive Acts/ 2.5 Minutes	9.0	43.9	51.4	81.8	36.9	24.8
Coefficient of Variation	76.2	37.4	113.0	56.3	62.7	39.8
$C = (100 \frac{s}{\bar{x}})$						

data are compared by multiple comparisons in Figure 18 (Duncan, 1955; Krammer, 1956).<sup>12/</sup>

The highest level of aggression occurred when food was placed in one out of every two subsections of the habitat (8C4) (Figure 18a). Aggressiveness was less in treatments with a greater localization of the food supply and appeared to be less in treatment 8E with an evenly distributed food supply. Frequency of aggressive actions was more variable from day to day in 8E which had 10 pellets of food in each of the 8 subsections (coefficient of variation = 113%) than in treatments with contagiously distributed (bunched, clustered or spatially localized) food (8C4, 8C2, and 8C1) (coefficient of variation = 56, 63, and 40% respectively) (Table 11). The frequency of aggressive actions varied between 2 and 198 per 2.5 min in 8E. In the case with 198 aggressive actions, 190 were from the aggressive interchanges between a single pair which happened to be in the same subsection at feeding time. If fish in 8E were evenly distributed at feeding time, the level of aggression was very low.

In treatments with an even distribution of food, aggressive actions were more frequent if the habitat had more subdivisions (Figure 18b). The least number of aggressive actions was observed when there were no partial partitions (1E) in the 8-liter baskets. The aggressiveness in 1E usually occurred 4-5 minutes after the food was introduced at which time almost all the food had been eaten, and fish were concentrated near single pellets which had sunk to the bottom. As mentioned above, the high level of aggression in 8E which

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<sup>12/</sup> The  $\log_{10}$  transformation was used to achieve homogeneous variance. Pooled variance of the logarithms of aggressiveness used for multiple comparisons between 1E and 8E versus any other treatment was 0.08132 with 42 degrees of freedom, and for comparisons among 4E, 8C4, 8C2, and 8C1 was 0.04084 with 28 degrees of freedom.

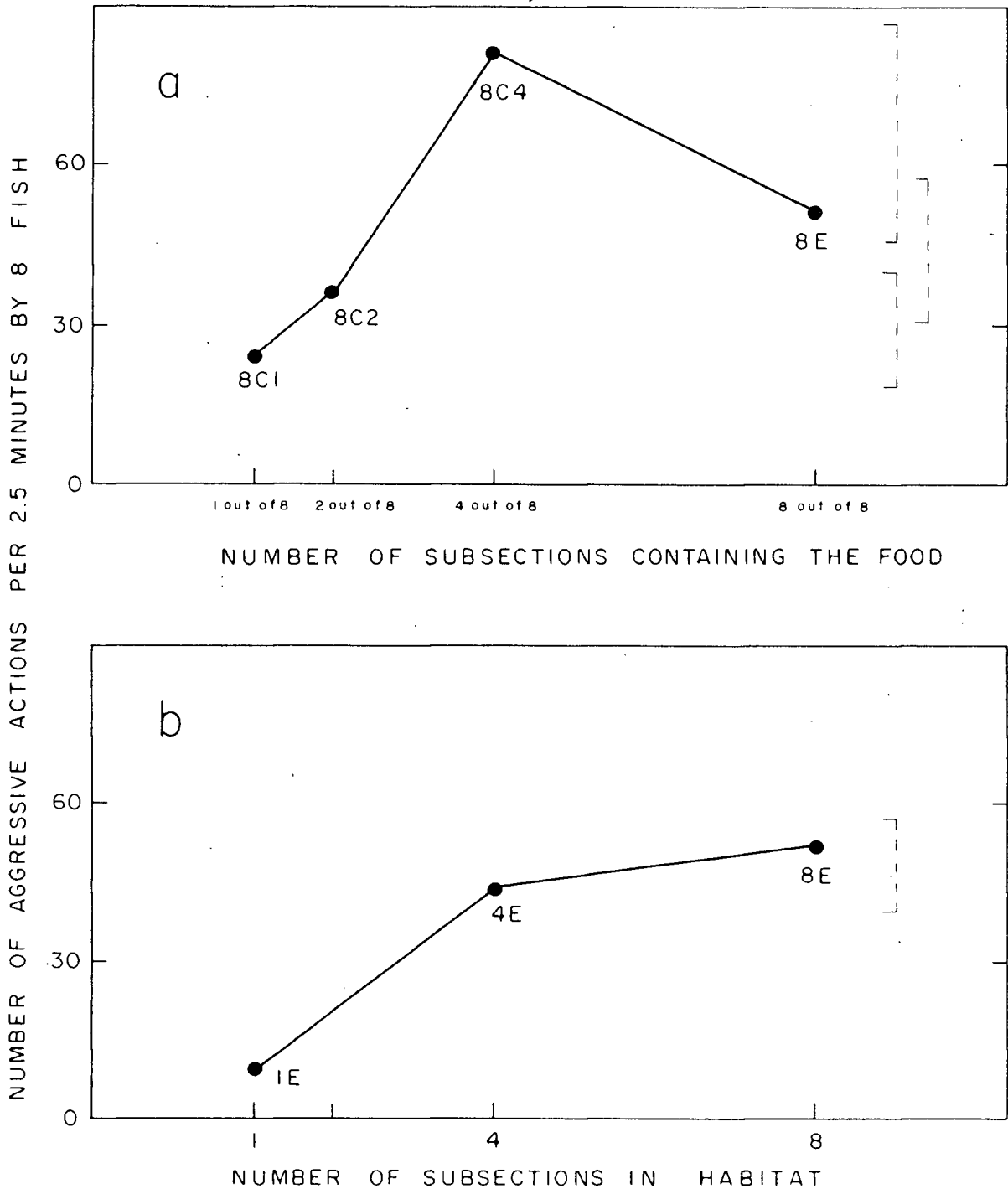
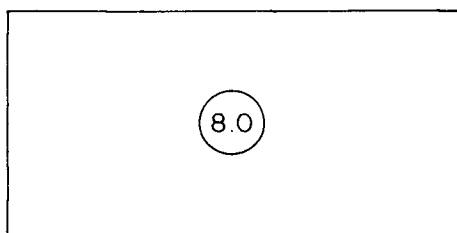


Figure 18. Relation between frequency of aggressive actions in populations of 8 fish and (a) the spatial distribution of limited food in a subdivided habitat and (b) the extent to which the habitat is subdivided in evenly distributed food treatments. (Brackets enclose those means which are not different at  $p \leq 0.05$ )

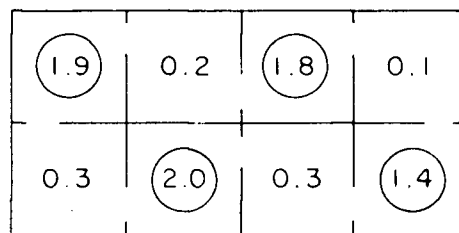
had 8 subsections resulted from the chance occurrence of more than one fish in a subsection at the time of feeding.

While food was present in the environment, the distribution of fish was primarily determined by the location of the food (Figure 19). In the treatments with an even spatial distribution of food (1E, 4E, and 8E) the fish were dispersed over the whole environment, but in treatments with contagiously distributed food (8C4, 8C2, and 8C1) fish were concentrated in feeding areas. The number of fish moving into a single subsection increased as the contagion of the food supply increased; for example, when food was placed in one-half the subsections (8C4), approximately 2 fish crowded into each food area, but when food was placed in one-eighth of the subsections (8C1), 4.8 fish crowded into the food subsection to feed. Even though concentrations of 7 fish were occasionally found in a single subsection, the average percentage of fish in subsections with food decreased as the food supply was more localized. One hundred percent of the medaka were in subsections with food when it was evenly distributed (8E), 90% when it was in one-half of the subsections (8C4), 70% when it was in one-fourth of the subsections (8C2), and 60% when it was in one-eighth of the subsections (8C1).

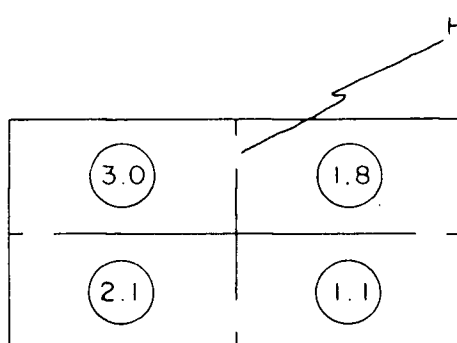
Often one, two, or three fish found the food subsection a minute or more before the remainder did, and much of the food was eaten by these few individuals. Large fish did not appear to set up territories in the food sections, but occasionally a fish would be in the container when the food was introduced. As the contagion of the food supply increased, the contagion of the fish distribution also increased after the food was introduced. Yet the contagion of the fish distribution was not proportional to that of the food, and a lower percentage of fish were in food subsections in those treatments with a greater localization of food.



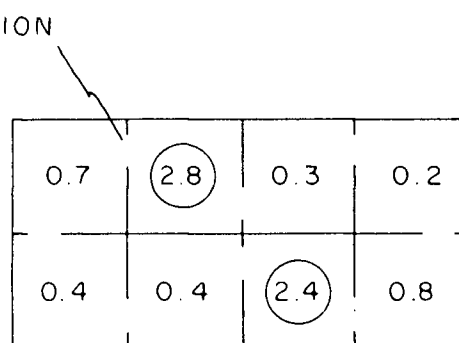
1 E



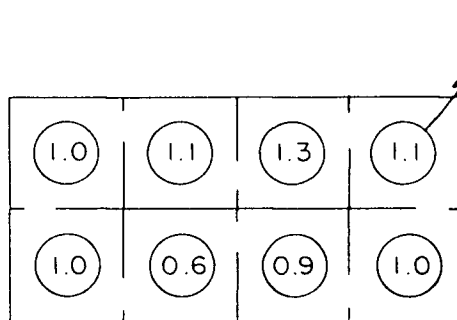
8 C 4



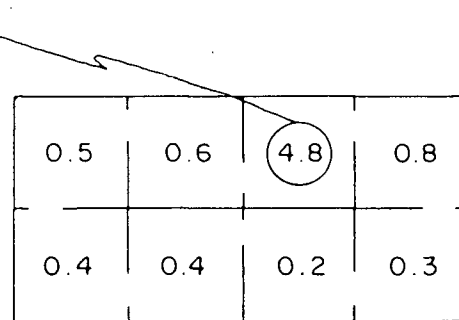
4 E



8 C 2



8 E



8 C 1

Figure 19. Average number of fish in subsections during the 5 minutes after food was introduced.

Fish learned to recognize the single subsection which received food in 8C1, but in treatments receiving food in 2 (8C2) or 4 (8C4) subsections, they did not learn to recognize subsections which received food. Before food was introduced the fish in 8C2 and 8C4 were swimming throughout the basket. When food was introduced they swam from section to section until they located the food. Locating the subsections containing food appeared to be a matter of chance in the latter 2 treatments. Often 4 or 5 fish would concentrate in a single subsection while another containing food was empty. A dominant fish would often chase a smaller fish out of one subsection and then not return to the subsection which contained the food.

#### Relation between Growth and Behavior

The modifying influence of the spatial distribution of food was studied in those treatments which were divided into 8 subsections by partial partitions. Growth depensation was greatest when all the food was placed in one subsection, and it was least when the food was evenly distributed (Figure 17a). Although dominant large fish apparently had a greater competitive advantage when food was spatially concentrated, the data indicated that other factors were also involved. First, frequency of aggression was at a low level when food was placed in only one subsection, while it was at a higher level when food was placed in every second subsection or even in every subsection. As many as 6 fish would move into a single subsection to feed when food was contagiously distributed and only 10-40 aggressive actions/2.5 min resulted, while in other treatments the presence of two fish in one subsection resulted in as many as 190 aggressive actions/2.5 min. A large fish was not able to defend the food area from the other 7 fish, and the presence of more than 1 smaller fish lowered the aggressiveness of large fish. Second, locating the food section was primarily a matter of chance. In treatments which had only

1 or 2 subsections with food, a fish not finding a food section in the first 2-5 days was left far behind those which located and learned to feed on the pelleted food at the start of the experiment. After the food was found, it was rapidly eaten, and the time during which it was available was short. At the end of the experiments, populations in treatments with a contagious food distribution (8C2 and 8C1) had one or two very small fish which did not even enter the food subsections, while the other fish entered a food subsection as soon as they found it even if there were larger fish there first. These small fish may have been chased from the food section at the start of the experiment, or perhaps they never learned to search for the food immediately after it was introduced.

In conclusion, if food was localized in only a few subsections of the habitat, high growth depensation resulted either because the smallest fish were chased from the food areas early in the experiment, the small fish, due to chance distribution, never had the opportunity to learn to locate and feed on the localized food pellets, or because smaller fish were slower and had less chance of locating the food subsection during the short periods while food was present.

When food was placed in every second subsection (8C2) aggressiveness was high and fighting occurred between the two fish which entered each subsection containing food. Growth depensation in this treatment was more likely a product of the social hierarchy than chance. Fish seldom failed to find a subsection containing food, but often chased a second fish out of a food area.

Aggressive behavior did not result in a dispersed distribution of medaka unless food was present in every subsection of the habitat. In this case (8E) fighting was very intense if a fish happened to find itself in a subsection with both food and another medaka.



Effects of partial isolation between competitors were studied in treatments which received an even spatial distribution of food but had no subsections (1E), 4 subsections (4E), or 8 subsections (8E) separated by partial partitions. The data indicated that growth depensation decreased when the environment was subdivided so that each fish had a subsection containing food (Figure 17a). It is doubtful that aggressive behavior provided the large fish with a significant competitive advantage when no subsections were in the environment (1E). Aggressive actions were least frequent in the treatment with no partial partitions, although definite social hierarchies were established. Large fish appeared to eat more rapidly and ate more because they could graze effectively over the whole environment. Food particles on the far side of the environment were never temporarily inaccessible due to a maze of subsections such as were present in other treatments. The advantage to the large fish in terms of rate of feeding was noted especially in the consumption of larger food particles. Large fish swallowed these particles with apparent ease, while smaller fish usually made several nips at the larger particles and then rejected them in preference to a smaller particle nearby. Partial partitions provided partial isolation between the competitors. In treatments with subsections, the food supply of the small fish was protected, and the rate of feeding was not as important a factor in determining the total amount of food eaten by a fish.

In the environment with 4 subsections or 2 fish per subsection (4E), aggressive behavior again appeared to be more important in determining which fish ate the pellets. Aggressive behavior apparently served better as a competitive mechanism in those situations in which competition was primarily isolated as an interaction between two fish. When more than two fish were involved a medaka was not able to defend the food area from all intruders,

and both the frequency of aggression and the growth advantage it gave the dominant appeared to decrease.

#### Summary of Results

Growth depensation increased if the food was more contagiously distributed, but aggressiveness was most intense when a subsection of the environment contained food for every two fish. If food was concentrated in only one-eighth or one-fourth of the habitat, growth depensation resulted apparently because some fish, due to lack of opportunity, never learned to feed on the pellets. They did not learn to eat the pellets either because the large fish chased them from the food areas before small fish became conditioned to the pellets or because chance phenomenon early in the experiment resulted in some fish not finding the food during the short time it was available. A large medaka was not able to defend the food areas from the 4 to 5 other fish which also entered and fed on the pellets, but a smaller proportion of fish were in food areas when food was contagiously distributed. The high level of aggression in a treatment with food distributed in all subsections resulted from fights between two fish which were situated by chance in the same subsection at feeding time. A dispersed distribution of medaka due to aggressive behavior was not observed unless necessities of the subordinates were found in all subsections of the habitat.

If food was evenly distributed in the environment, growth depensation was less if there was one subsection in the habitat for each fish. Growth depensation in treatments with a subsection for every two fish resulted from the consequences of aggressive behavior. When there were no subsections, growth depensation resulted because large fish could eat the larger food particles more rapidly than small fish could, and the rate of feeding during

the short time in which food was present determined the amount of food eaten per fish. Aggressive behavior in the latter treatment was at a low level. As mentioned above, aggressiveness was high when there was 1 subsection for each fish due to the chance distribution of more than one fish in a subsection at feeding time.

Aggressive behavior appeared to be more functional as a competitive mechanism for limited food when competition was primarily isolated to interactions between two fish. If population size increased or if more than two fish competed for the food in one subsection, additional factors such as rate of feeding, chance, learning, etc. had a great influence upon the growth consequences of competition. When food was evenly distributed and there was a subsection of the habitat for each fish, aggressive behavior dispersed the fish. In this case the subordinate was no longer at a competitive disadvantage.

## DISCUSSION

Competing animals can influence each other in at least two ways in terms of growth consequences of competition. First, if they share a limited resource in such a way that no genotypic or phenotypic character provides one fish with a priority for the resource, poor growth consequences of competition will be equally distributed among all members of the population. Second, if any fish has a characteristic which gives it first choice or access to the resource, detrimental growth consequences of competition will be unequally distributed among members of the population. A gradation might exist, from equal sharing of the resource to complete possession of the resource by one or few individuals. Situations in which the resource is not shared have been called "contest," and situations in which the resource is shared have been called "scramble" by Nicholson (1954).

Aggressive behavior is a mechanism which might provide certain animals (those which win) with a competitive advantage, and they would get more than their share of the resource in question. If the acquisition of the resource had any effect upon the growth of the animal, competitive situations in which aggressive behavior was important might be characterized by a wide variation in growth rates among members of the population. Many other factors producing the same effects must be accounted for or eliminated before the role of an aggressive behavior mechanism and growth consequences of competition can be determined.

Even if animals shared the resource with no class distinction, genetic differences in the growth potential would result in growth depensation (an expanding size distribution due to differences in growth rate). Some workers

(Brown, 1946; Allee et al. 1948) neglected to compare the variability in growth among fish in populations with the variability among those which were raised in isolation. By doing this, these investigators assume that none of the genetic differences in growth rate were large enough to bias their conclusions. A considerable amount of growth depensation, however, is observed among the offspring of a single pair of medaka from a highly inbred domestic stock even when they are raised in isolation under "identical" environmental conditions.

Allee et al. (1948) publish data which indicate that genetic differences should not have been neglected. They raised immature green sunfish both in isolation and in populations of 4 and noted that growth of individual fish in populations was positively associated with social rank of the fish. The implication is that social rank resulted in observed differences in growth rate. Yet in their Table 2 (page 7) the variability in growth rates observed in populations of 4 fish is identical to the variability observed among the same number of isolated fish. This demonstrates that the same variability existed even in the absence of social interactions. Probably the relative size of each fish was associated with its rate of growth, and in addition the relative size determined the position of the fish in the social hierarchy, but there was no causal relationship between rate of growth and position in the social hierarchy. Greenberg (1947) demonstrated that relative size is important in determining the social rank of an individual green sunfish.

A number of other factors known to result in growth depensation must also be removed to isolate effects of aggressive behavior in competition. The accumulation of excreted substances results in growth inhibition. Rose (1959, 1960) demonstrates that these water-borne inhibitors have a greater influence on smaller members of a population and result in growth depensation.

In addition growth depensation occurs among immature carp, Cyprinus carpio, if the size of the food particle is large and its abundance is low (Nakamura and Kasahara, 1956). Extreme growth depensation was observed among young-of-the-year smallmouth bass, Micropterus dolomieu Lacépède, resulting from cannibalism of the smallest by the largest members of the population (Langlois, 1936).

To the best of the author's knowledge all of the above factors resulting in growth depensation have been removed or accounted for in the design and analysis of the present experiments (see materials and methods, and description of experiments) though there may be other unknown factors which have been neglected.

To study competition, the particular resource for which competition is occurring should be determined, and its abundance or availability should be varied. The two resources of the environment considered in these studies were food and space.

Space is a more tenuous "resource" than food. Living space or Lebensraum has long been considered important as an ecological factor (see Allee et al. 1949, p.22; Larkin, 1956), and many hypotheses were put forward to explain slower growth of aquatic vertebrates and invertebrates which were reared in smaller volumes of water or at higher population densities. Among Rana pipiens tadpoles, the hypotheses that surface area, restricted movement, or collisions between individuals inhibited growth at higher population densities were found to be unnecessary by Richards (1958). She was able to explain most of these results by the presence of a growth inhibitory substance in the feces which accumulated at higher concentrations in smaller more crowded containers. Growth inhibition resulting from ammonia excretions was also demonstrated in trout (Brockway, 1950) and in carp (Kawamoto, 1961). The

need for space, per se, in aquatic animals is primarily a consequence of accumulating waste products if food is supplied in excess. Whether space in this context can be considered as a resource is a matter of opinion and definition. Other aspects of space as it is involved in competition will be discussed in conjunction with competition for food.

Food is easily visualized as a resource but some confusion arises when attempts are made to supply it "in excess." Food can be limited in amount, not only spatially, but also temporally. In addition some foods are more stimulating and are eaten in greater amounts. If a food is present "in excess" for only short periods of time, fish will not always be feeding to satiation. Brown (1946, 1951, 1957), for example, fed an excess of minced liver twice a day to brown trout fry, but observed that the liver was only eaten while suspended in the water. Consequently the fish would have no food available as soon as all particles fell to the bottom. Medaka feed to satiation on brine shrimp nauplii, but within one or two hours begin to search for food again. Two meals per day can not be considered as "excess"; instead palatable food should be present at all times. If food is not highly stimulating to fish, it is debatable whether fish can be fed in excess except in relative terms. Medaka would feed on living brine shrimp nauplii after they ceased to feed on pellets or frozen brine shrimp. Care must be taken in interpreting results when it is assumed that food is supplied in excess, especially when the excess is present only during short periods of time or the food is not very stimulating to the fish in terms of initiating feeding behavior.

When the abundance of individual resources is varied, the action of aggressive behavior is observed, and care is taken to remove extraneous factors influencing growth, then both the growth consequences of competition

for a specific resource and the action of the aggressive behavior mechanism can be studied.

In the present experiments the amount of space was varied by raising equal numbers of fish in containers of different sizes and by raising different numbers of fish in containers of the same sizes. In both cases food was provided "in excess," and accumulation of water-borne growth inhibitors was prevented. In these situations, limiting the amount of space did not reduce growth rates nor cause growth depensation. Aggressive behavior was not more common when space was most limited. The lowest frequency of aggression was observed when the least space was supplied. Aggressive behavior did not in this case function as a competitive mechanism for space, and, in fact, competition for space was apparently not taking place in medaka at densities up to 16 fish per liter.

Neither a general depression in growth rate nor growth depensation was observed in medaka populations relative to isolates if food was supplied "in excess." The presence of one animal did not lower the growth rate of all other members of the population, nor did any fish have a competitive advantage for food over any other fish. Aggressive behavior was at a very low level, and both large and small members of the population were equally aggressive. The resource was present "in excess" amounts both spatially and temporally, the aggressive behavior mechanism was not operating, and evidently there was no competition of any sort occurring in these populations. Yet when food was limited in supply a social hierarchy was established in which large fish dominated small fish. In addition, average growth rates of all fish reared in populations were less than among isolated fish fed the same amount of food, and growth depensation occurred. Small fish did not show any reluctance to feed but did not get many food particles because



large dominant fish kept chasing them away from food. Competition for food was taking place, and the aggressive behavior mechanism was operating in a way which resulted in the large fish getting a greater share of the limited supply of food. Nakamura and Kasahara (1956, 1957) observed that the amount of growth depensation in carp decreased when more food was supplied and that little growth depensation occurred among fish grown in isolation. Immature carp were not observed to be aggressive.<sup>13/</sup> Brown (1946, 1951, 1957) observed that larger socially dominant brown trout inhibited the growth of smaller ones even when food was supplied "in excess" and a good circulation of water was provided. It is difficult to evaluate her conclusions because she assumes that the fish were fed "in excess" even though they were given minced liver only twice each day. Since Brown assumed that food was supplied "in excess," the social hierarchies which she observed could not be considered in terms of competition for food. She postulated that the very presence of the large fish in some way, possibly "stress," resulted in slower growth among small brown trout. In medaka, small fish in the presence of large fish grew as well as isolated controls when food was "in excess." Also when medaka were not fed at all, both fish did equally poorly even though the large fish was quite aggressive towards the small fish. Only when food supply was limited did dominant large fish have a competitive advantage over small fish in terms of growth. Evidently any "stress" provided by the presence of large fish was not important, but access to limited food augmented by social dominance was important.

Aggressiveness of medaka was in part initiated by food stimuli. Frequency of aggressive actions increased when food was added in all limited

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<sup>13/</sup> Behavior observations reported to the author in a letter dated May 18, 1961, to Mr. Taizo Miura from Mr. Kenji Chiba, Freshwater Fishery Research Laboratory, Miya, Hino Machi, Minamitamagun, Tokyo, Japan.

food treatments but did not increase in excess food treatments. An increase in aggression after food is presented has been observed among the fishes in immature Dolly Varden (Salvelinus malma [Walbaum]), cutthroat trout (Salmo clarki Richardson), coho salmon (Oncorhynchus kisutch [Walbaum]) (M. Newman, 1960); rainbow trout (Salmo gairdneri Richardson) and brook trout (Salvelinus fontinalis [Mitchell]) (M. Newman, 1956); brown trout and Atlantic salmon (Salmo salar Linnaeus) (Kalleberg, 1958); Iowa darter (Etheostoma exile [Girard]) and fantail darter (Etheostoma flabellare Rafinesque) (Winn, 1958); and in mature white cloud mountainfish (Tanichthys albonubes Lin) (unpublished observations by the author). This relation between food and aggressiveness is probably a common phenomenon in many species of fish and, as in medaka, could function to reserve a larger portion of food for dominant fish. Aggressive behavior of immature medaka can be thought of as a mechanism which potentially provides dominant fish with a competitive advantage and which is initiated by the internal state of "hunger," and the presence of food stimuli and smaller medaka.

Additional factors other than the amount of food and a fish's position in the social hierarchy influence growth consequences of competition for food. The extent to which the food supply is shared and also the extent to which the overall growth rate is depressed due to limited food supply depends in part upon modifying influences of many environmental factors as discussed below.

First, the modifying influence of the spatial distribution of food is considered. Medaka concentrate in the parts of the environment containing food. In populations of two fish the socially dominant medaka defends and occupies the food area while food is present and for several hours after it is all eaten. Aggressive actions in this case are more efficient in

in reserving the food for the dominant than when food is scattered through the environment. If excess food is spatially localized in the environment, however, the two fish share the food with no differential access.

The same conditions (internal state of "hunger," food stimuli, and smaller medaka) initiate aggression when food is either spatially concentrated or evenly distributed, but the localization of food added site attachment to the behavior pattern. Noble (1939) defined a territory as "any defended area," and Tinbergen (1957) defined it as a combination of intra-specific hostility and site attachment. In terms of these two general definitions, the localization of the food supply was sufficient to change a social hierarchical society into a territorial society in the medaka.

Both Hinde (1956) and Tinbergen (1957) have discussed the variety of objects which animals (primarily birds) defend in territorial behavior. Tinbergen points out that "hostility without site attachment may serve the purpose of reserving vital objects just as well as the two tendencies combined -- it all depends upon the nature of the defended object." The present study indicates that (i) the nature of the defended object (its spatial distribution and mobility) brings out the expression of site attachment, (ii) the defense of the object is more efficient if it is spatially localized, and (iii) aggression only functions to reserve the food if the supply is limited.

Dependence of site attachment upon the nature of the resource or object defended is probably quite common in fishes. The stationary nests built by male ten-spined sticklebacks, Pygosteus pungitius Linnaeus (Morris, 1958), and the pits dug by some cichlid fishes during the reproductive period (Baerends and Baerends-van Roon, 1950) form the center of their territories. Morris (1958) argues that the center of the territory is more stable than the

periphery. In the bitterling, Rhodeus amarus Linnaeus, if the "nest site" moves, the male fish's territory moves also (Boeseman et al. 1938; as cited in Tinbergen, 1951). Bitterlings deposit their eggs in the mantle cavity of a freshwater clam, and the male defends the clam as a moving territory. Winn (1958) observed that certain darters, subfamily Etheostominae, defended a reproductive territory if eggs were on the rock, but lost interest in the rock if eggs were removed. Likewise the male moved from rock to rock defending each for only a short time if no eggs were laid on a rock which it defended. Other species of darters have a territory which moves about with the female. Winn (1958) also observed that those species of darters which laid their eggs in one spot and had well developed territorial defense were less fecund than darters which did not have this behavior as highly developed. Evidently egg defense in territorial situations is more efficient.

In summary, there is often some object in the territory about which defense is centered. In immature medaka this object is food. Spatial distribution of the food determines not only whether territories or social hierarchies will be formed, but also the efficiency of aggressive action in terms of the competitive advantage to the dominant.

A second peculiarity of the environment influencing the action of the aggressive behavior mechanism and the growth consequences of competition is the amount of isolation between competitors. In the present experiments partitions with and without holes through them were used to provide partial and complete isolation between competitors. The partitions can be thought of as a stylized form of obstruction provided by rocks, vegetation, turbidity or distance in nature. This aspect of the environment must always be considered in conjunction with the spatial distribution of food.

If food is evenly distributed, complete isolation prevents all

interaction between the competitors, and the two fish share the food resource equally. Sharing in this case is induced entirely by characteristics of the habitat. As the amount of isolation decreases, aggressive interactions between competitors increase, and the dominant gets an increasing proportion of the limited food. In a complicated environment, however, the dominant can defend and reserve the food in one area, but the subordinate is left to feed unmolested in another part of the environment. This occurs only when there is a partially isolated area of the environment for each fish. This partial isolation need only be present while food is actually in the environment. Medaka move from one area to another, but the dominant can only be effective in one area at a time. The small fish avoids the area in which the dominant is feeding and is for the most part at no competitive disadvantage even though it is socially subordinate and food supply is limited. When all isolating barriers are removed from the environment, the dominant medaka is able to prevent the subordinate from feeding by chasing it away from food.

Among other species which defend more permanent territories than medaka, there are many cases in which topography of the habitat either influences the size or the borders of the territory. Kalleberg (1958) observed in Atlantic salmon fry that territories were more closely packed if the topography of the substrate was interrupted by larger rocks, and that territories were smaller in turbid water. Greenberg (1947) noted that more territories were formed among green sunfish if partial partitions were placed in the aquaria. Vegetation can be used to demarcate and to increase the potential number of breeding territories in male Colisa labia, (Forselius, 1957), and Fabricius (1950) demonstrated that the size and shape of reproductive territories were in part determined by the substrate and the presence and density of vegetation in male white cloud mountainfish and in the bream, Abramis brama.

In summary, the topography of the habitat or the visual isolation between competitors determines both the number of fish that can occupy a given area and the extent to which food distributed evenly in that area will be shared. The more visual isolation in the environment the smaller effect aggressive behavior mechanism has in reserving a larger proportion of the food supply for the dominant.

The above is true only when food is evenly distributed. If food is contagiously distributed aggressive behavior does not disperse the medaka throughout the habitat. They concentrate in the food areas. In this situation the amount of visual isolation also influences the number of fish in a given area and the extent to which the food is shared. In contrast to the evenly distributed food, if food is contagiously distributed the more visual isolation in the environment the greater effect aggressive behavior mechanism has in reserving a larger proportion of the food supply for the dominant.

A third complication develops in relation to spatial distribution of food and topography of the habitat if populations are large. Aggressive behavior is most effective in the defense of a resource if competition is occurring between only two fish at one time. A large dominant medaka could defend the food from one smaller medaka but not from several smaller medaka at the same time. The same phenomenon was observed (Swingle and Smith, 1943) in largemouth bass, Micropterus salmoides (Lacépède), while they defend their nest from egg predation by bluegills, Lepomis macrochirus Rafinesque. Bass egg survival was very low at high densities of bluegills because while the male bass chased one bluegill from the nest area, several others would dart in from the other side. There is at least one case in fishes (Berwein, 1941) in which groups of Phoxinus actively drive off smaller or larger individuals or another group. These situations may be rare among the fishes, but even

where they do occur it is likely that present considerations would apply because the group at least temporarily would be acting as an individual.

In medaka, not only was aggression ineffectual in reserving the resource when there were many subordinates, but also aggressive actions of the dominant were less frequent. Among green sunfish the highest frequency of aggression occurs at intermediate densities (Greenberg, 1947). Evidently at low densities the fish do not come into contact (spatial isolation) as frequently, and at high densities aggressiveness is in some way inhibited. It is doubtful that the dominant medaka "decided" it would not be able to chase all the fish away and had better eat as much as possible. Instead the presence of multiple stimuli probably had an inhibiting or confusing effect on the directed attacks of the dominant.

Ayu, Plecoglossus altivelis Temminck and Schlegel, defend feeding territories if population density is low, and those defending territories seem to grow faster than those which are not able to maintain territories and form schools (Kawanabe, 1958). At high densities none of the fish are able to defend territories, and territorial behavior breaks up into a schooling society. Kalleberg (1958) observed that in large populations of young trout in hatchery troughs no territories are established; at intermediate densities the population forms two factions, territory holders and non-territory holders, and at lower densities site attachment is maintained by all individuals. Anabantid fishes (Forselius, 1957) would not form reproductive territories at high densities, but when the density was reduced would almost immediately begin to set up breeding territories. In a theoretical mathematical analysis of social hierarchies, Landau (1951) demonstrated that a social bias (for example relative size, prior residence, etc.) is less effective in establishing hierarchies in large populations than in small populations.

In summary, aggressive behavior even with site attachment is only effective as a competitive mechanism to the dominant if the number of subordinates contacted at any one time is small. It is a competitive mechanism functioning primarily at the level of the individual.

A fourth consideration is that not only the abundance of food, but also the relation between size of food particle and size of a fish's mouth is important in determining the amount of food available to a particular fish. Even if the food is small enough to be eaten by the smallest fish the size of the food particle is important in that it determines the rate at which a fish can eat the food. Smaller medaka can not eat the larger particles as fast as the large fish can. In a "scramble" type of competition in which all fish have equal access to the food, the time involved in eating an individual food item is important. If food is present only for a short time the small fish does not get as much food as the large fish. Even if the food were available for long periods of time but scarce and widely scattered, the time spent eating each particle a fish found would reduce the amount of time it had for searching. The importance of this latter aspect is emphasized by Holling (1959) who develops a mathematical model for predation in which a decreased searching time is available for a predator at high prey densities due to the increased proportion of time spent actually devouring the prey.

Hartman (1958) observed that rainbow trout could swallow smaller stonefly nymphs (Plecoptera) but often rejected larger nymphs even though they fitted into the mouth because the stonefly would anchor itself to the nose of the fish and attempt to crawl out. He observed also that smaller fry rejected smaller stonefly nymphs than did larger trout. The same relationship was observed if caddis fly larvae (Trichoptera) with the cases removed were used for food. This time spent attempting to eat an insect but finally



rejecting it would reduce hunting time. The studies by Nakamura and Kasahara (1956) demonstrate that growth depensation is greater if the food particle size is larger but decreases if increased amounts of this food is provided. These data all indicate that if food is limited in supply either temporally or spatially, the rate of feeding may be an important factor determining the growth consequences of competition.

In this respect a species feeding on small food particles would be more likely to share the food than fish feeding upon large food particles. If there are 20 small particles two fish would "scramble" for the resource, but if there is one large particle it would be impossible to share the resource in the fish world. Assuming that the particle could be swallowed intact, only one fish could eat it.

In summary, the size of the food particle is important in determining the extent to which limited food is shared because the size determines the scarcity of food particles, the rate a fish can eat the food, and whether the particle can be eaten at all.

The action and consequences of aggressive behavior described in the present investigation function in laboratory populations of immature medaka, but it is difficult to determine to what extent the findings can be generalized.

Some fishes have not been observed to demonstrate aggressive behavior, and among these fishes the mechanism would not function. Other fish are only aggressive in the breeding season and are territorial only in terms of procuring a mate or defending the eggs and young. Yet as observations on behavior of immature fish accumulate in the literature it becomes increasingly obvious that many species defend territories or are aggressive during the sexually immature period of their life. Aggressive behavior among juveniles

has been observed in green sunfish, (Greenberg, 1947); medaka; ayu, (Kawanabe, 1958); in many of the salmonids (Hoar, 1954; Stringer and Hoar, 1955; Kalleberg, 1958; M. Newman, 1956; Lindroth, 1955; and others); and in several marine species as cited by Kalleberg (1958). In many of these species and in the adults of additional species aggressive behavior is associated with feeding, as mentioned previously. Evidently the mechanism described here is potentially available for observation in many other species.

Evidence indicates that the aggressive mechanism would function for a wide variety of species under the right environmental conditions. Medaka (Kawabata, 1954, 1960), for example, tend to be a schooling fish in nature but in confined conditions demonstrate both social hierarchy and territoriality. Young sockeye salmon also school in nature but in the laboratory form hierarchies (H. Newman, 1959). It can be argued that aggressive behavior may be only a laboratory phenomenon which would not function in nature. Individuals of a species demonstrating this behavior in confinement, however, do possess the genetic potential to respond as a social dominant. Those species demonstrating aggressive behavior in the laboratory would also be expected to demonstrate the same type of behavior if similar conditions were found in nature.

Care must be taken in any attempt at generalization from one species to another because aggressive behavior differs even in closely related species. Winn (1958) organized the phylogeny of the Etheostominae in part on the differences in their reproductive territoriality. Some species were not territorial but demonstrated hierarchies, others demonstrated moving territories, and others had definite territories with site attachment. The same could be expected in food competition among immature fishes. Lake trout, Salvelinus namaycush (Walbaum), are not aggressive as immatures even at

feeding time (M. Newman, 1960), even though many of its close relatives are aggressive. It is also difficult to generalize even among fish that are known to be aggressive because there are a large number of alternative functions which aggressive behavior might serve in different species. For example, Carpenter (1958) lists 32 functions of territorial behavior which have been postulated for animals. Cichlid fishes in a territorial mosaic pay no attention to territories if food is placed in the environment; and they all rush into the food area (Baerends and Baerends-van Roon, 1950). Kalleberg (1958) demonstrates that the feeding territories of immature Atlantic salmon break up into a schooling society if the water velocity is reduced to zero. Diebschlag (1941) observed in pigeons that one chased other pigeons from its territory in which food was placed only after it had fed to satiation. Medaka, on the other hand, only chased fish from the food area if they were not satiated. Apparently aggressive behavior and territoriality have many different functions which operate in some cases quite distinctly. The function in food competition, as depicted by these experiments, is just one of the functions aggressive behavior might be expected to serve in other species.

As pointed out in the present study, a detailed consideration of the environment is necessary to determine the action of aggressive behavior and the growth consequences of competition for food. The aggressive behavior mechanism is not rigid and stereotyped; rather it is within limits adaptable to the environmental situation. In fishes this adaptability would appear to arise from a plastic expression of the genetic tendency to aggressive behavior in different situations. Although learning can not be disregarded it is probably of minor importance.

Aggressive behavior expressed as social hierarchy or territoriality is a competitive mechanism which potentially provides a competitive advantage to

the dominant by augmenting access to the food supply. It is by its nature a mechanism which would be expected to result in an unequal distribution of the food resource among the population. Even though social dominance provides a potential advantage, the extent to which food is shared depends upon

(i) spatial distribution of the food, (ii) visual isolation provided by the habitat, (iii) population density, (iv) size of environment, (v) abundance of food, (vi) size of the food particles. The fluctuation of these environmental factors can alter the competitive advantage derived from social dominance from complete sharing to complete hoarding of the food. The distinction, made by Nicholson (1954) and Birch (1957), that "contest" occurs for resources which can not be consumed and that "scramble" occurs for resources which are consumed seems unwarranted. Competition for food among medaka can lead either to a "contest" or to a "scramble." Which one occurs depends upon environmental factors.

Competition in the form of "scramble" would be expected to result in large fluctuations in population size (Nicholson, 1954), whereas in the form of "contest" would be expected to result in small fluctuations in population size. If aggression or territoriality is to dampen fluctuations in population size it should prevent sharing of food when food is abundant and when population size is large. In medaka as the abundance of food increases or as population density increases aggressiveness and territoriality are less efficient in reserving food for the dominant. The "contest" occurring at low population densities or at low food abundance changes to "scramble" at high densities or high food abundance. The aggressive behavior mechanism is too flexible to stabilize fluctuations in medaka populations, and natural populations of medaka would be expected to demonstrate large fluctuations associated with any fluctuations in food abundance. Aggressive behavior in

juvenile medaka would be expected to help maintain a portion of the population in periods of low food abundance, but would not check rapid population growth under more favorable food conditions.

Territories may be more rigid in other species. For example, Forselius (1957) observed that Anabantid fishes would not set up reproductive territories at high densities, and Miller (1958) observed that trout introduced into an unfamiliar section of stream inhabited by other trout were displaced downstream by the territorial residents. Reproductive territories of birds are probably more stable and fixed in size than feeding territories of medaka and may limit the number of reproducing pairs in a given area (Hinde, 1957; Lack, 1954; MacArthur, 1958). However, the aggressive behavior mechanism in juvenile medaka and perhaps in juvenile ayu (Kawanabe, 1958) is too flexible to limit density.

In general, aggressive behavior is a competitive mechanism in immature medaka which can provide the dominant animal with a competitive food advantage when food is limited in supply. The mechanism is more effective in reserving food for the dominant if the food is spatially localized, the number of challengers is low, and the environment is small. If food is evenly distributed in space, increasing the visual isolation in the environment reduces the effect of the mechanism, but if food is contagiously distributed, increasing the visual isolation in the environment increases the effect of the mechanism. Aggressive behavior will disperse the competitors throughout the habitat only if food is found in all areas. The phenomena described in the present study would be expected to occur among fish which exhibit aggressive behavior in connection with food, in habitats containing contagiously distributed food limited in supply, and among fishes which live near the substrate or among aquatic vegetation.

## SUMMARY OF RESULTS

1. Growth depensation occurs among medaka sibs grown in isolation under the same environmental conditions.
2. Medaka raised in smaller containers or at higher population densities do not grow slower than medaka with more space per fish, provided that other factors usually associated with space are supplied in excess (food) or eliminated (conditioning of environment).
3. Growth depensation is no greater in populations at densities up to 16 fish per liter than it is among sibs raised in isolation under the same conditions (food in excess, conditioning of environment removed).
4. Aggressive behavior is not greatest at the highest population densities, but seems to be highest at an intermediate density.
5. If food is limited in supply, a social hierarchy develops in which larger medaka are dominant and grow faster than subordinates; the dominant has no advantage if no food or excess food is supplied.
6. Aggressiveness is initiated in juvenile medaka by the internal state of "hunger" and the presence of food stimuli and smaller medaka; frequency of aggressive actions is highest just after limited food is placed in the environment, is intermediate if the environment contains no food, and lowest if the environment contains excess food.
7. When limited food is spatially localized, the dominant defends the food area as a territory and the growth advantage of social dominance is higher than if food is evenly distributed.
8. If an excess amount of food is localized the fish share it with no differential access.

9. In a large population the dominant can not defend the concentrations of limited food from all subordinates, and both the growth advantage of social dominance and the frequency of aggression by the dominant fish decrease.
10. As the amount of environmental isolation between competitors is decreased, aggressive interactions between them increase; general growth rate of the population decreases even though the same amount of food is provided, and the competitive advantage of social dominance increases.
11. If there is one semi-isolated subsection in the environment for each fish and limited food is evenly distributed, both the dominant and subordinate grow equally well.
12. Aggressive behavior disperses medaka throughout the environment if food is evenly distributed, but does not result in a dispersed distribution of medaka if food is contagiously distributed.
13. Increasing the visual isolation in the environment increases the competitive advantage to the dominant if food is contagiously distributed, but decreases the advantage if food is evenly distributed.
14. If the population is very small and food is evenly distributed, the advantage of social dominance increases if the size of the environment is decreased.
15. If all fish have equal access to a limited food supply, the rate at which they can eat is important in determining their growth rates; small medaka can not eat pellets as rapidly as can large medaka.
16. In medaka aggressive behavior is evidently not a mechanism used in competition for space, per se, but is a mechanism which reserves a greater portion of a limited food supply for the dominant under certain environmental conditions.

17. Competition for food mediated by aggressive behavior can be altered from "scramble" to "contest" and all gradations between by changing environmental factors such as (i) amount of food, (ii) size of food particle, (iii) spatial distribution of food, (iv) visual isolation in the environment, (v) population size, and (vi) population density.



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## APPENDIX

In experiment II relative condition was expressed as the difference between weight of a fish and weight of an isolate control fish of the same length ( $W - \hat{W}$ ). This measure of condition was 2.45 times more variable for large fish (pooled  $s^2_x = 3.985$ , d.f. = 183) than it was for small fish (pooled  $s^2_x = 1.627$ , d.f. = 179). If this is true among individual fish, it is possible that it would also be true for the mean effects of various treatments; the expectation is that large fish in the same environmental situation as small fish would have a greater mean deviation from the controls. Ideally, the variance in the condition values should be homogeneous for comparisons of large fish with small fish.

A logarithmic transformation ( $\log_{10}W - \widehat{\log_{10}W}$ ) was used in an attempt to achieve homogeneity. Yet in this case the measure of condition was 2.58 times more variable for small fish (pooled  $s^2_x = 0.0029071$ , d.f. = 161) than for large fish (pooled  $s^2_x = 0.0011247$ , d.f. = 165). The difference between the variances was just as large for the ( $W - \hat{W}$ ) and ( $\log_{10}W - \widehat{\log_{10}W}$ ) values, but was in the reverse direction.

Since neither method resulted in homogeneous variance another criterion was used for selection. The large and small controls (CL1, CS1) by definition have the same value of condition (0.00) which would be expected since they were raised in isolation and no growth differences due to competition would occur. Likewise both the large and small fish raised in isolation in 4-liter baskets (CL4, CS4) should have the same condition when measured as deviations from the CL1 and CS1 controls since they also had no competitive interactions. In the transformed data, difference between the isolates in

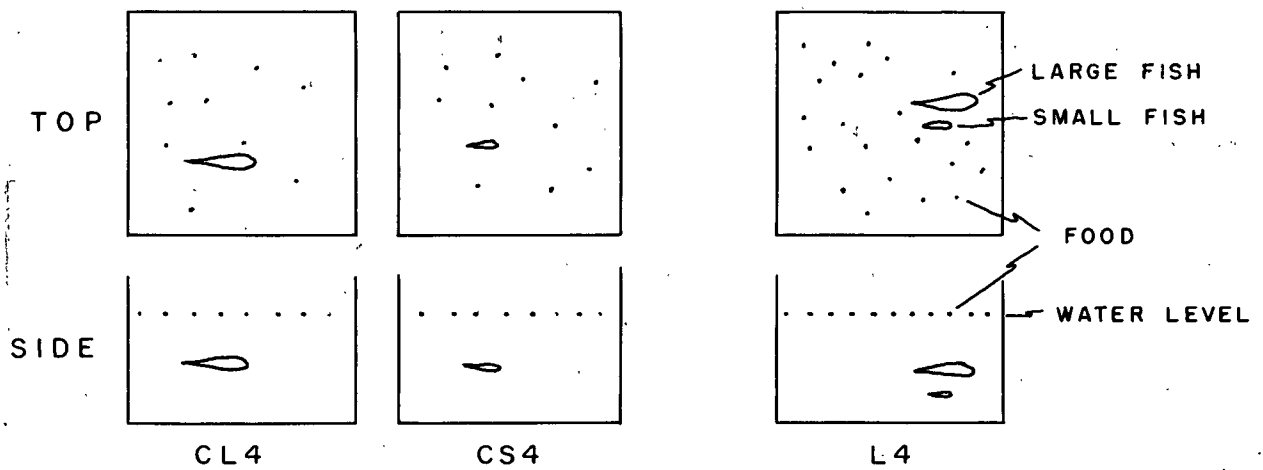
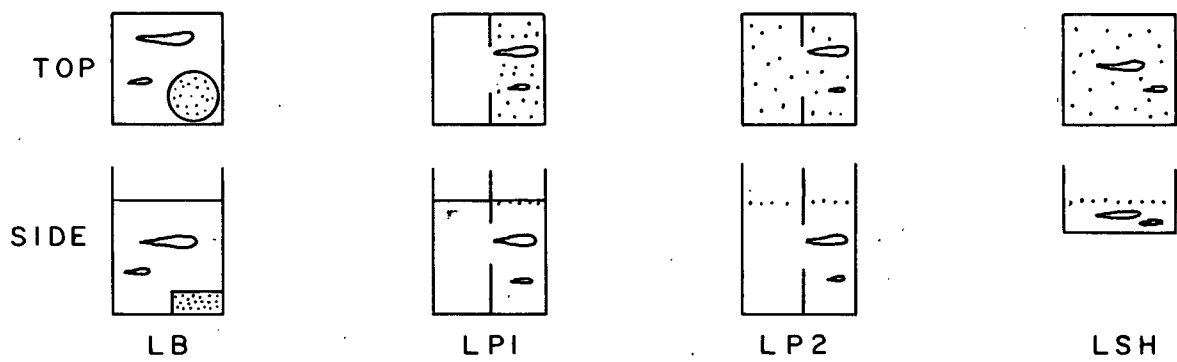
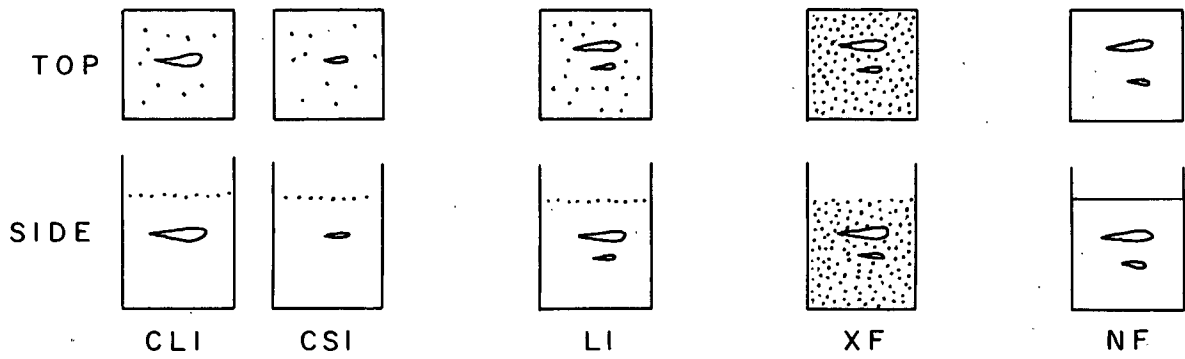
4-liter containers (CL4, CS4) was 0.0215 or 34% of the greatest mean difference (0.0634) between large and small fish in a treatment observed in L1. On the other hand, in the untransformed data the difference between large and small isolates in 4-liter baskets was 0.07 or 4% of the greatest mean difference (1.71) between large and small fish in a treatment observed in L4. These comparisons indicate that the log transformations were not as valid as the untransformed data for comparing large and small fish which were in the same environmental situation. In general, the log transformation resulted in a greater difference between the small fish in a treatment and the isolate controls of the same length than did the untransformed data. This occurred both when the small fish in a treatment had a positive condition (CS4) and when the small fish had a negative condition (NF and L1).

Untransformed data ( $W - \hat{W}$ ) were chosen for presentation primarily because large and small fish grown in isolation in 4-liter baskets had more similar values of ( $W - \hat{W}$ ) than they did values of ( $\log_{10} W - \widehat{\log_{10} W}$ ). The mean values of ( $W - \hat{W}$ ) and ( $\log_{10} W - \widehat{\log_{10} W}$ ) for each treatment are presented in the appendix table.

Appendix Table. Mean values of relative condition for large and small fish in each treatment, except XF, expressed as  $(W-\hat{W})$  and  $(\log_{10}W - \widehat{\log_{10}W})$ .

Treatment Code	Fish Size	$(W-\hat{W})$	$(\log_{10}W - \widehat{\log_{10}W})$
CL1	Large	0.00	0.0000
CS1	Small	0.00	0.0000
	Difference	0.00	0.0000
L1	Large	+0.93	+0.0118
	Small	-0.70	-0.0516
	Difference	+1.63	+0.0634
NF	Large	-0.53	-0.0154
	Small	-0.79	-0.0436
	Difference	+0.26	-0.0282
LB	Large	+0.08	+0.0023
	Small	+0.35	+0.0067
	Difference	-0.27	-0.0044
LP1	Large	+1.15	+0.0200
	Small	-0.52	-0.0173
	Difference	+1.67	+0.0373
LP2	Large	-0.03	+0.0042
	Small	+0.46	+0.0174
	Difference	-0.49	-0.0132
LSH	Large	-0.08	-0.0016
	Small	-0.86	-0.0276
	Difference	+0.78	-0.0260
CL4	Large	+2.52	+0.0300
CS4	Small	+2.59	+0.0515
	Difference	-0.07	-0.0215
L4	Large	+1.86	+0.0222
	Small	+0.15	+0.0001
	Difference	+1.71	+0.0221

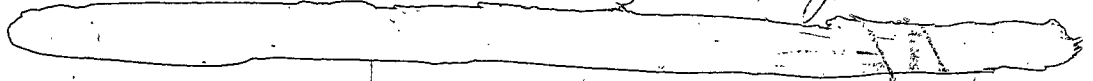


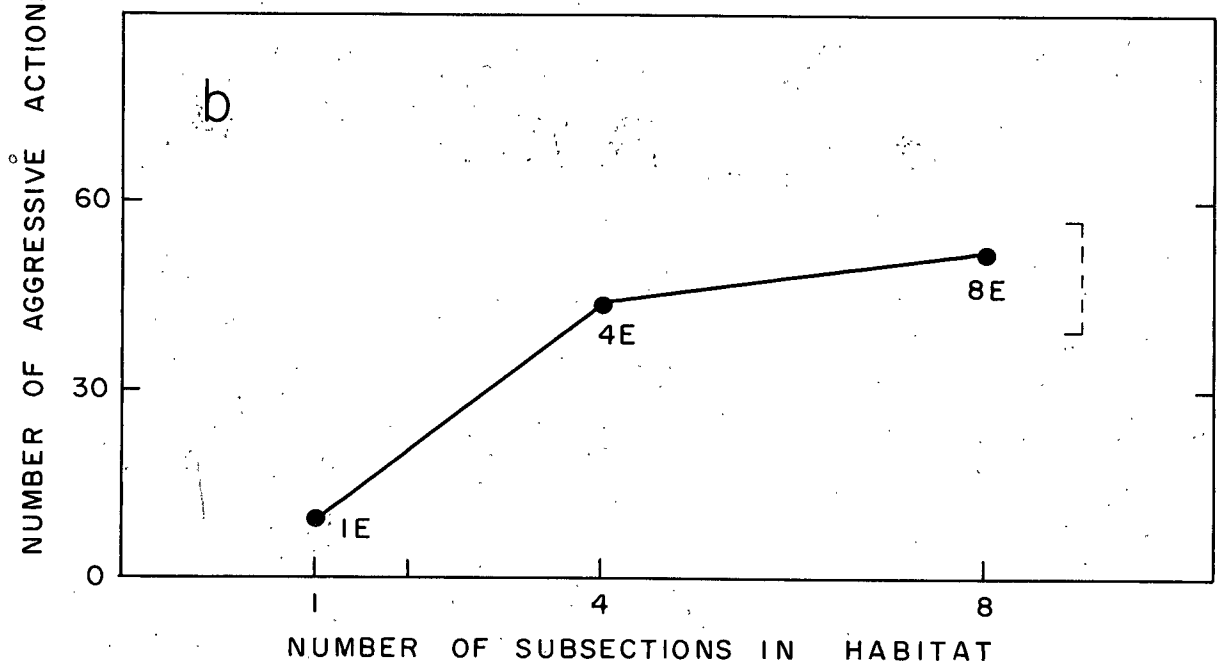
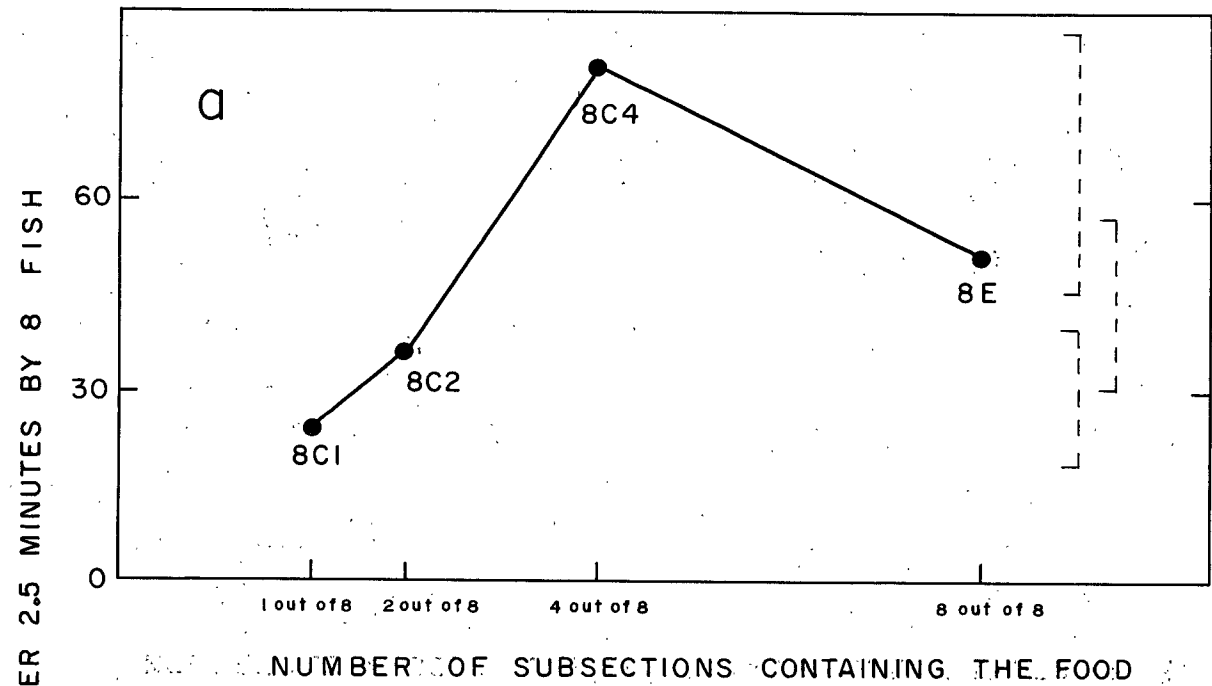


← 4 inches →

#1986

Magnuson  
361-84 Jan (2)



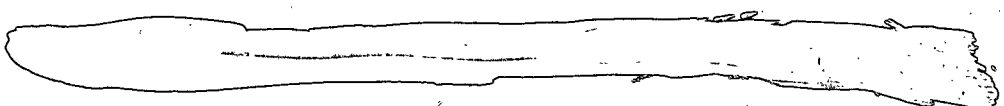


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1986

Magnuson  
361-84 Jan (17)

645



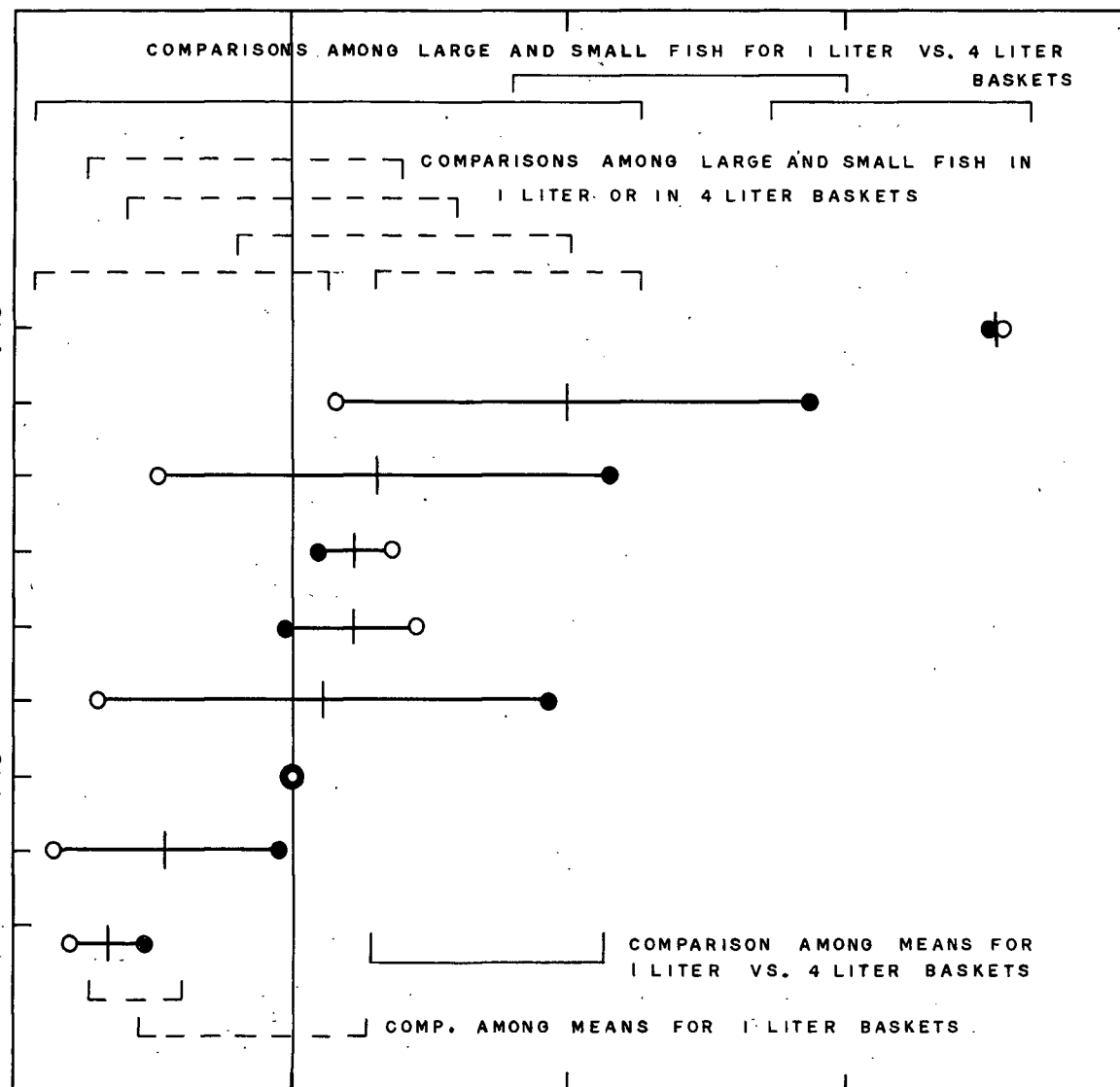
CONDITION RELATIVE TO CONTROLS ( $W_i - \hat{W}_i$ ) in mg

-1 0 +1 +2 +3

COMPARISONS AMONG LARGE AND SMALL FISH FOR 1 LITER VS. 4 LITER BASKETS

COMPARISONS AMONG LARGE AND SMALL FISH IN 1 LITER OR IN 4 LITER BASKETS

TREATMENT CODE  
CL4 L4 LP1 LB LP2 LI CL1 LSH NF



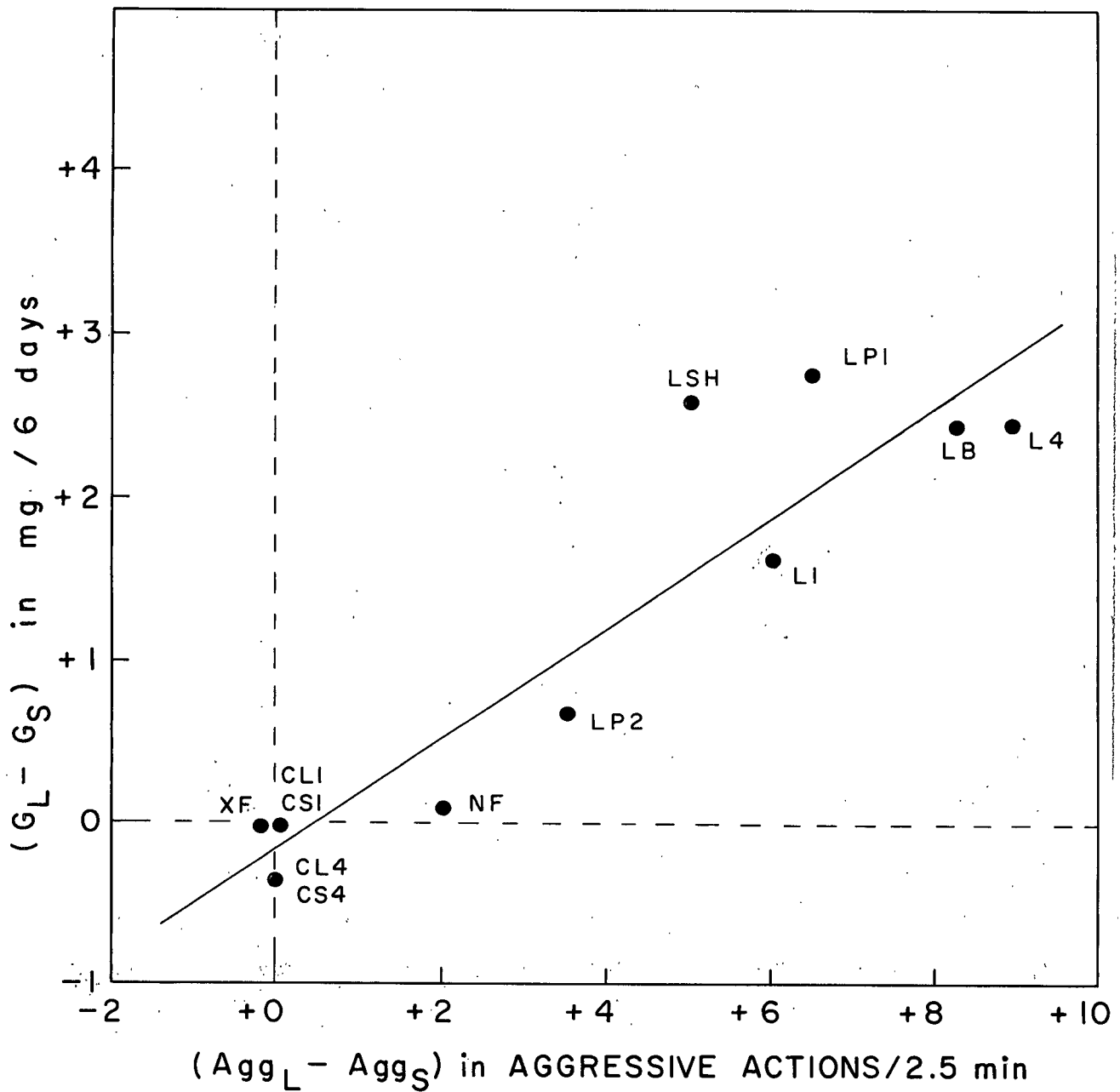
4 inches →

Magnified  
36x Jan. 5

#1986

624





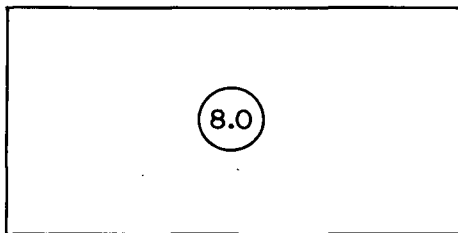
← 3 inches →

44.6

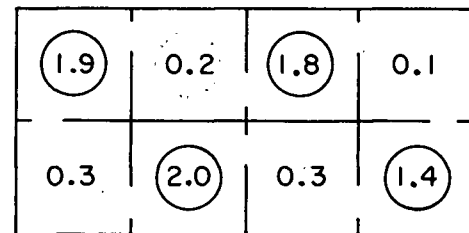
Magnuson  
361-84 Jan.

1985

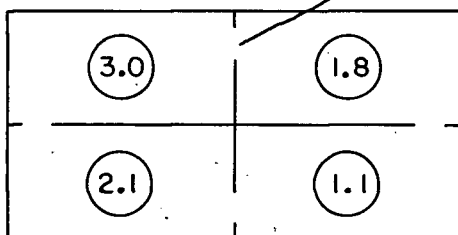
13



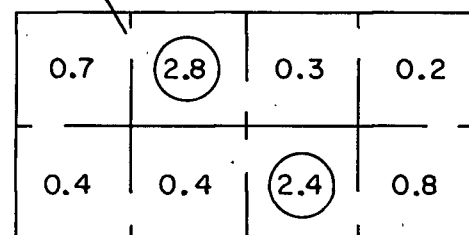
1 E



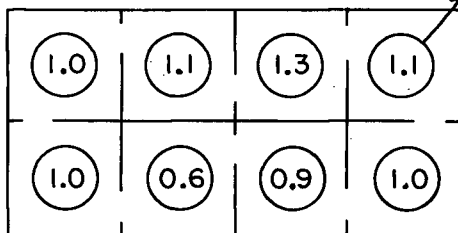
8 C 4



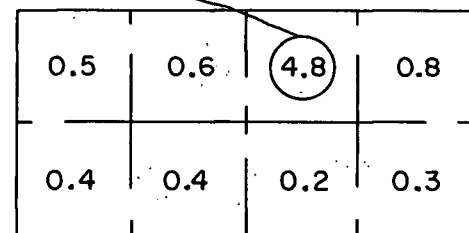
4 E



8 C 2



8 E



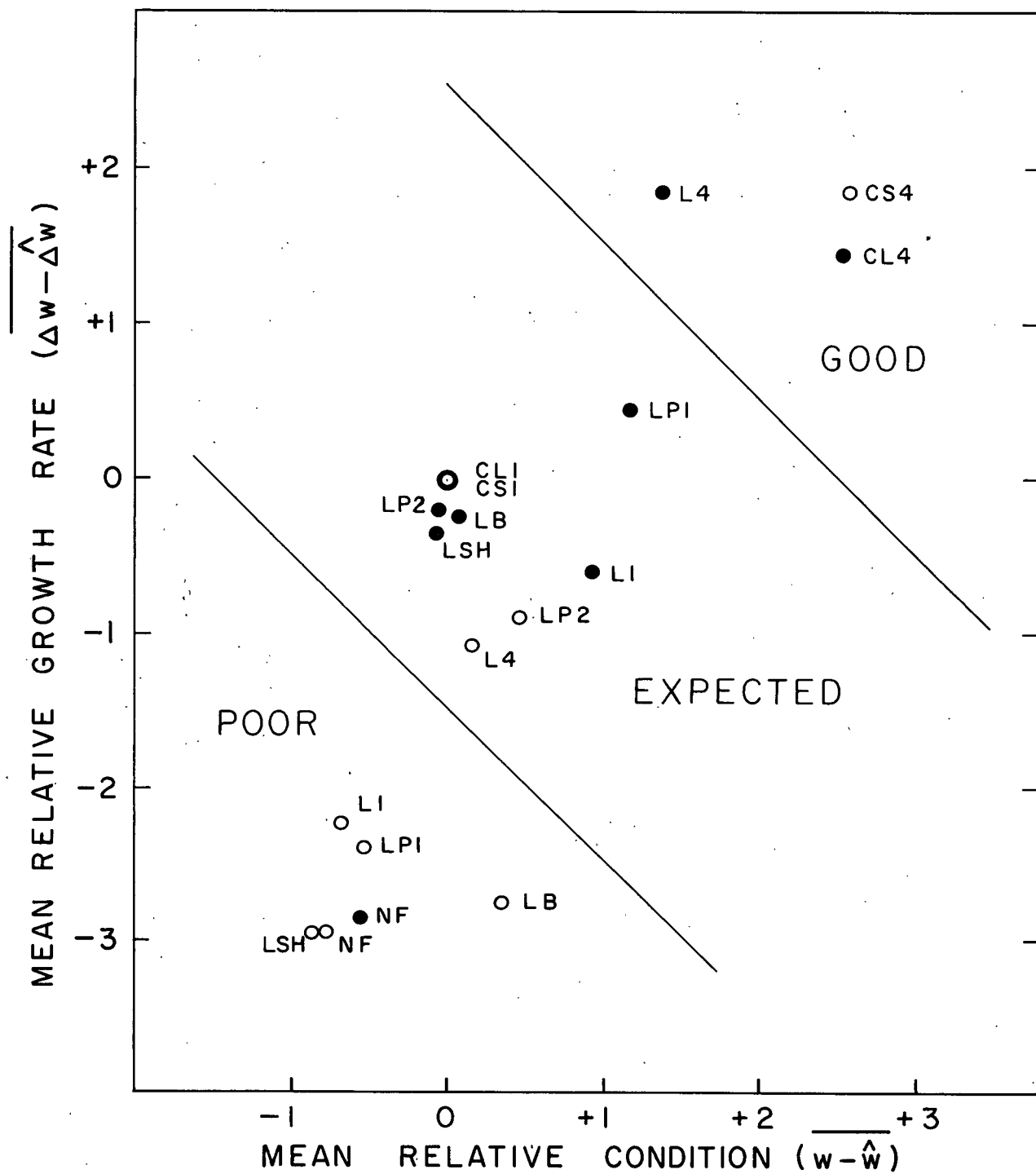
8 C 1

← 4 inches →

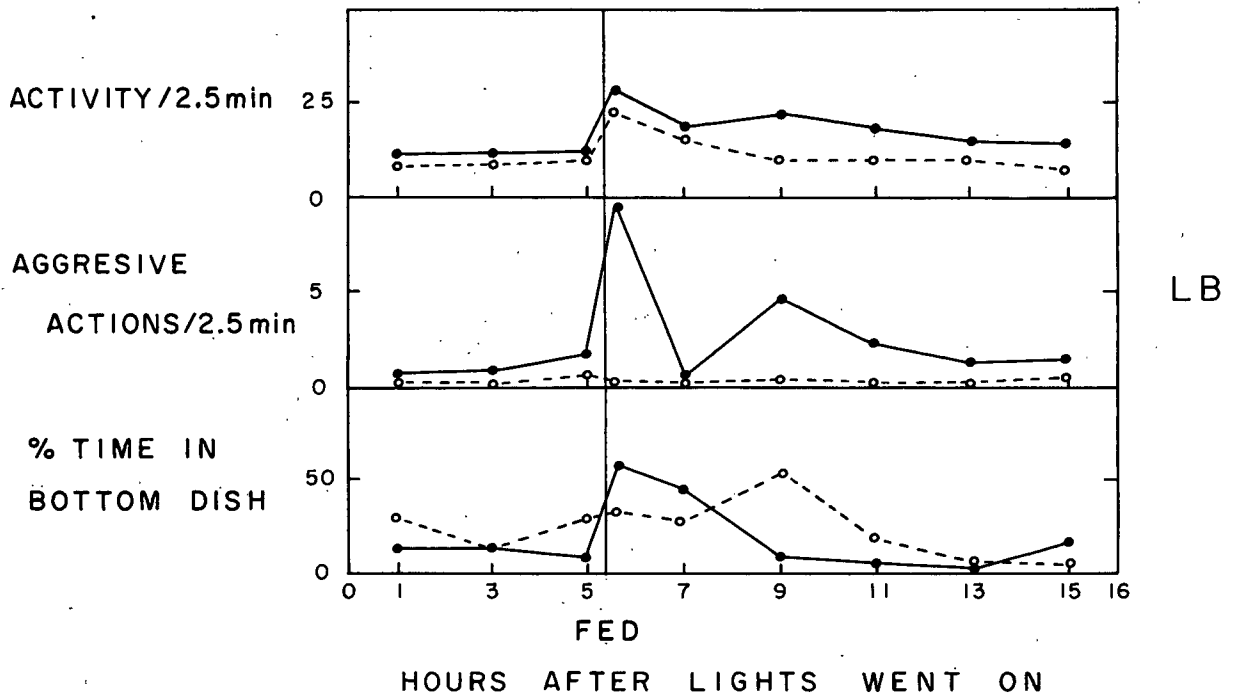
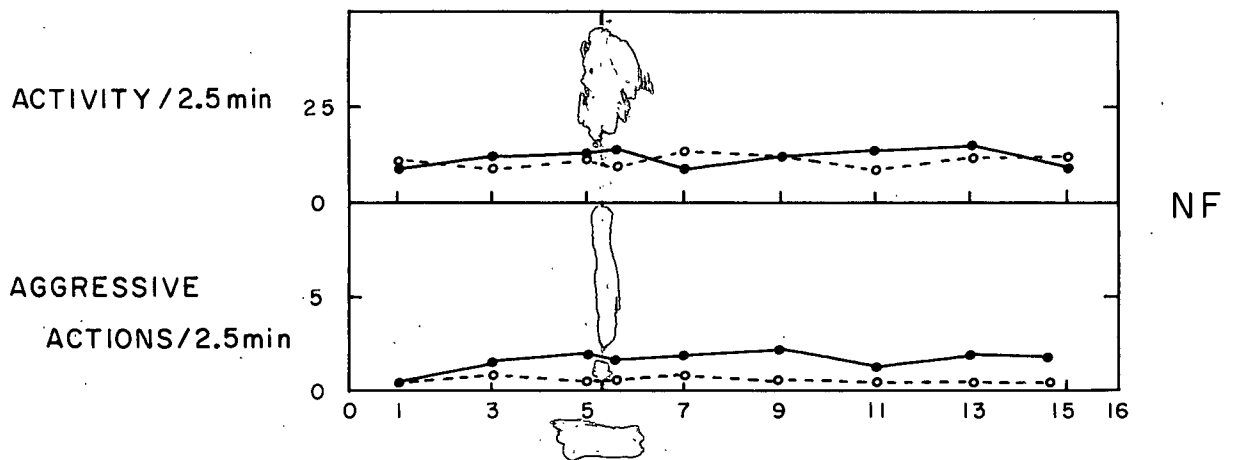
#1986

Magnuson  
361-84 Jan 18

64



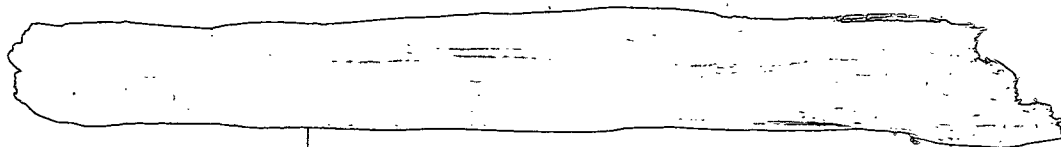
458  
 1986  
 ← 3 inches →  
 Magnuson  
 361-84 Jan. (6)

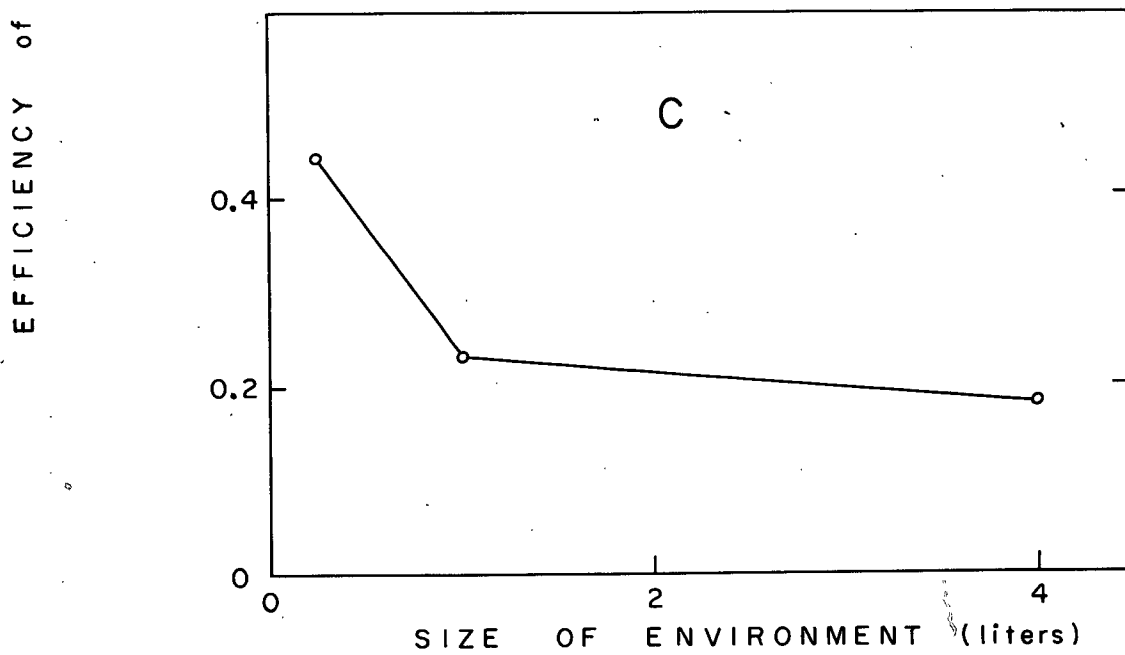
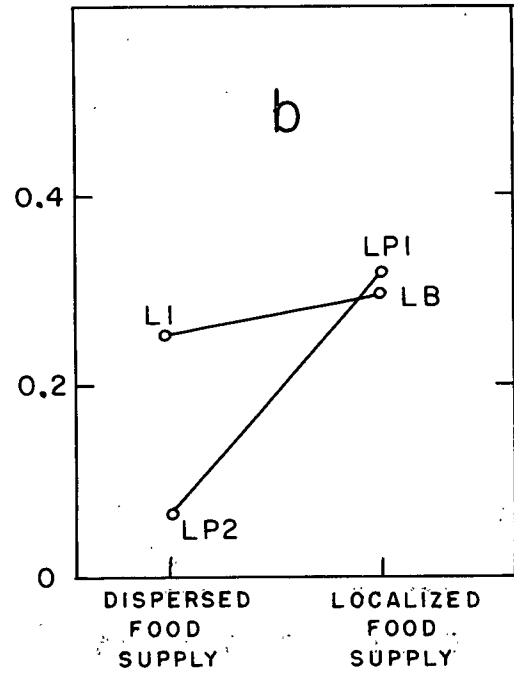
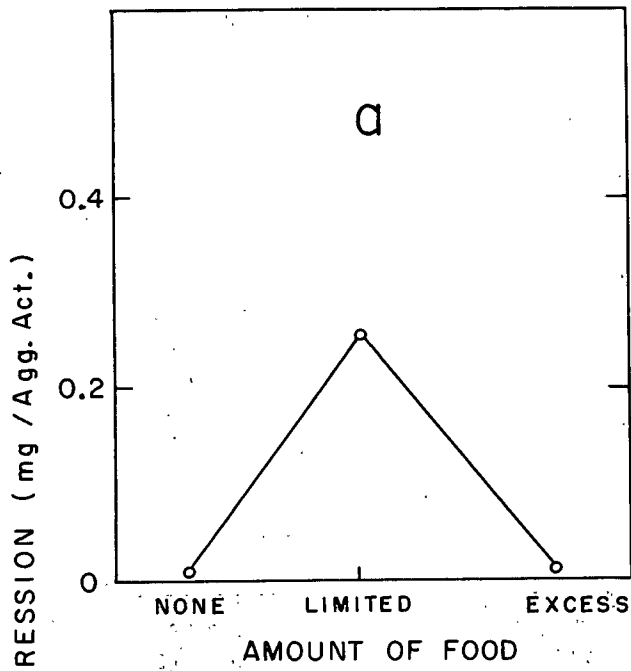


← Finches →

Magnuson #1986  
361-84 Jan. 10

GH





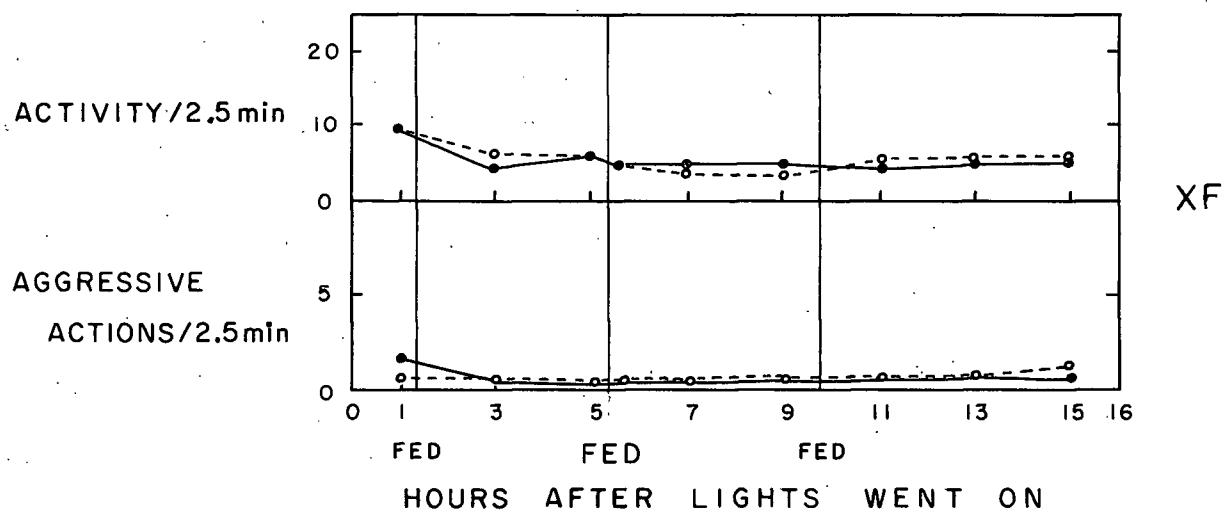
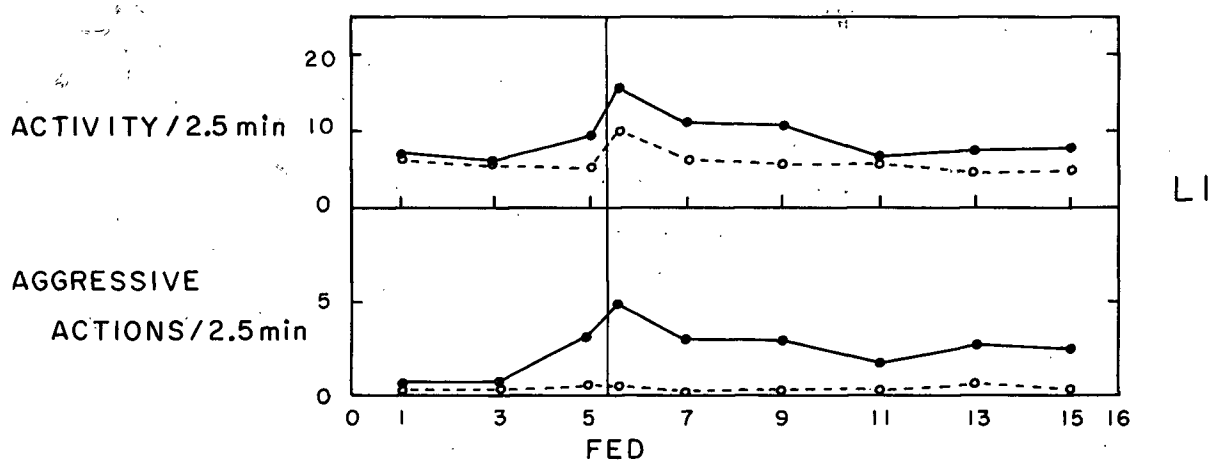
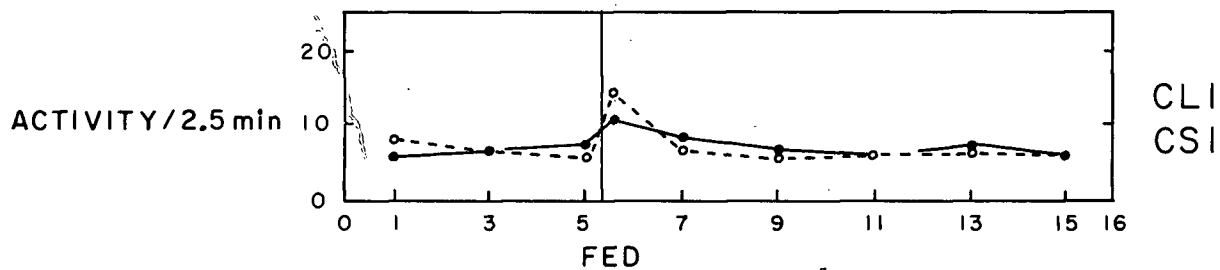
← 4 inches →

# 1986

63.5

Magnuson  
361-84 Jan. (14)



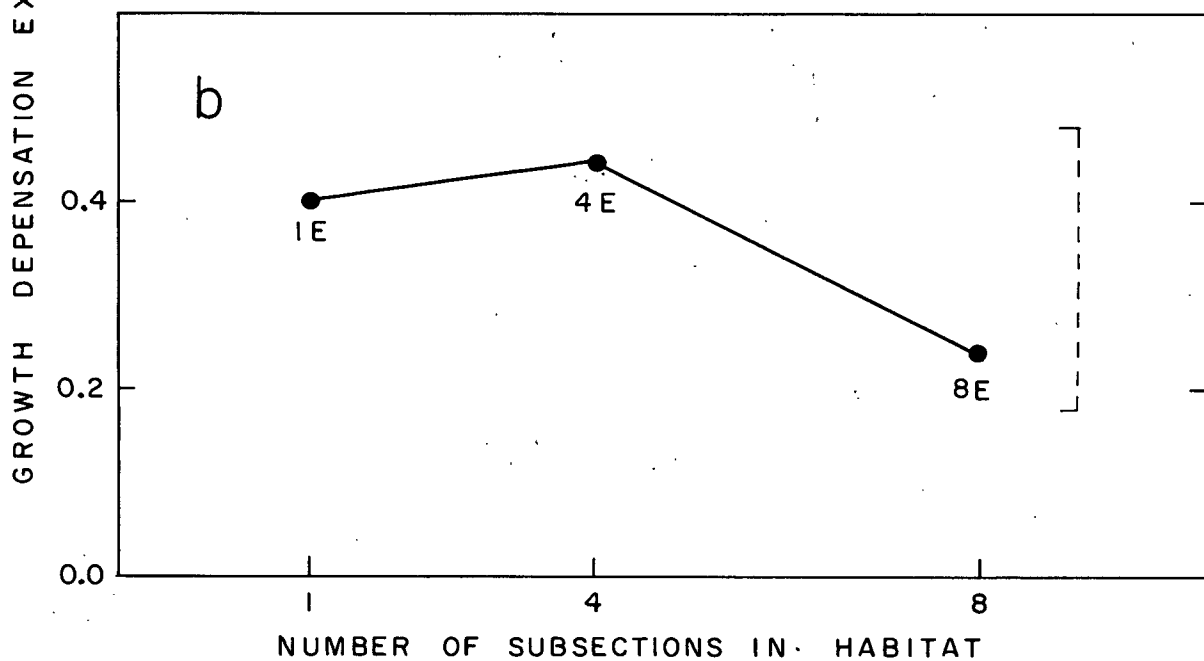
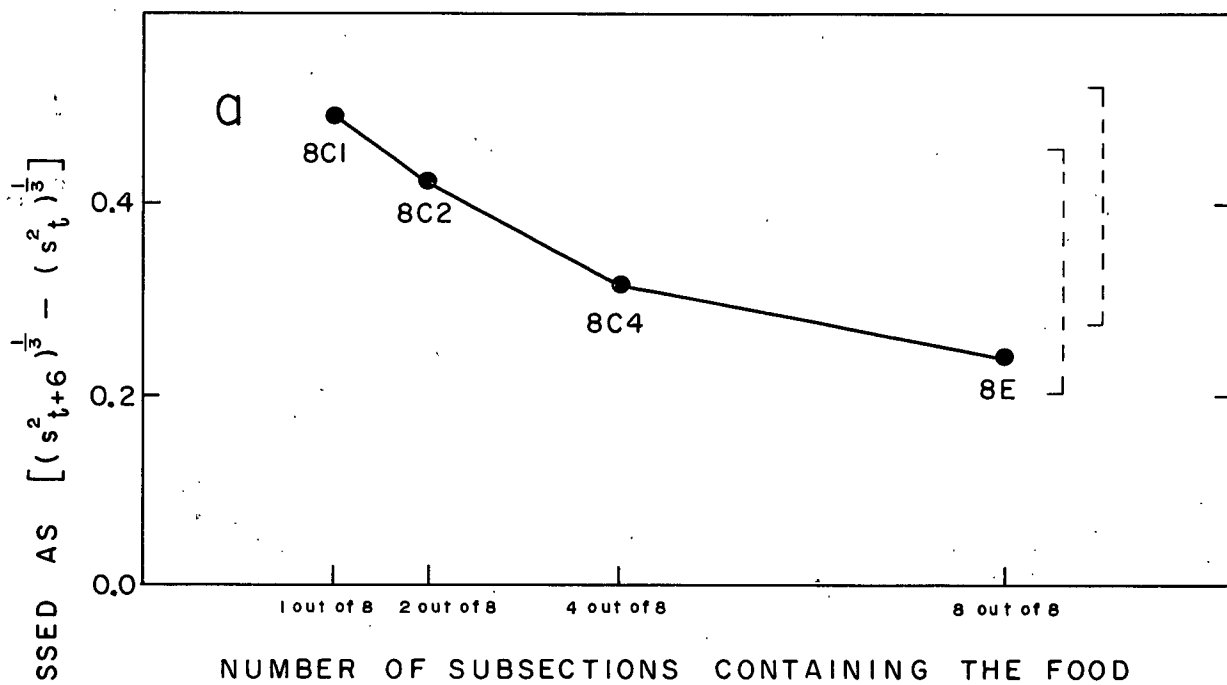


← 4 inches →

#1986

Magnuson  
361-84 Jan 9

645

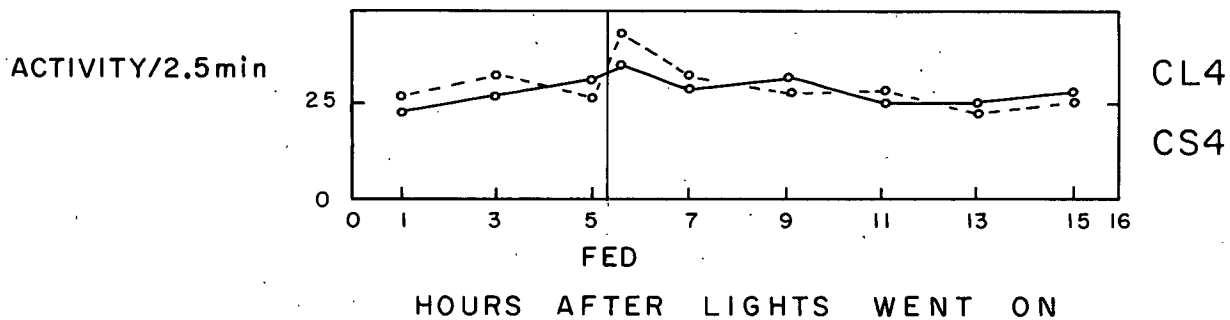
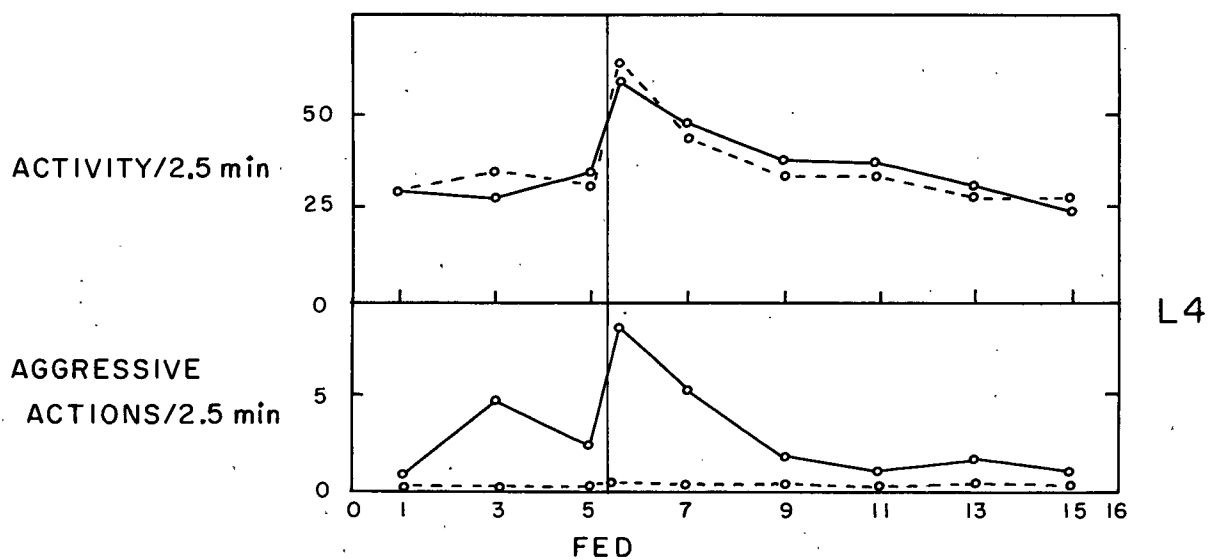
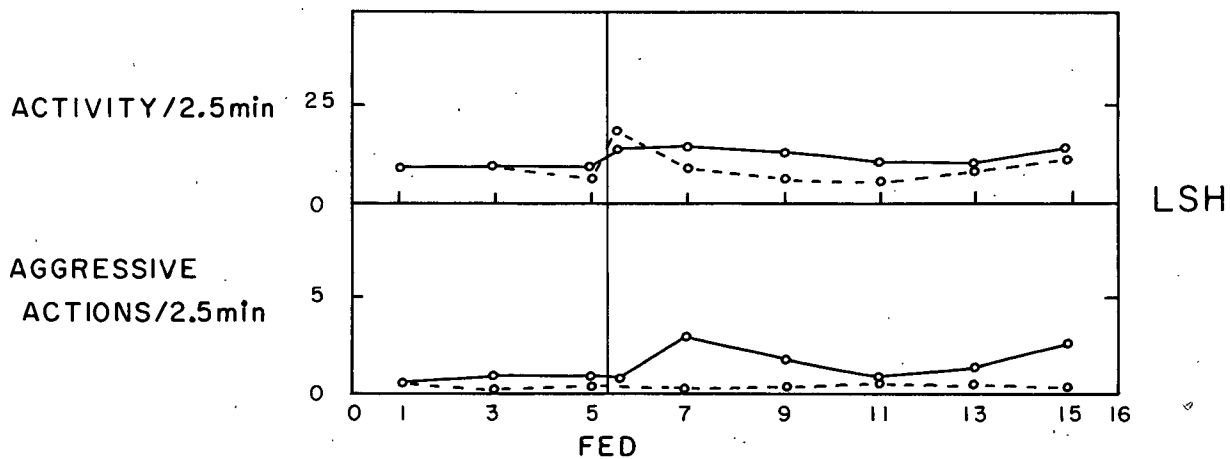


← 4 inches →

#1986

Magnuson  
361-84 Jan. 16

63

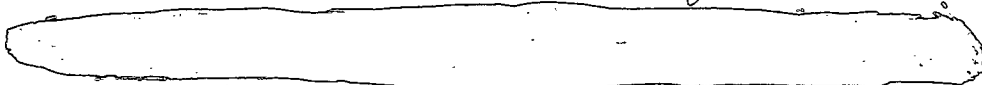


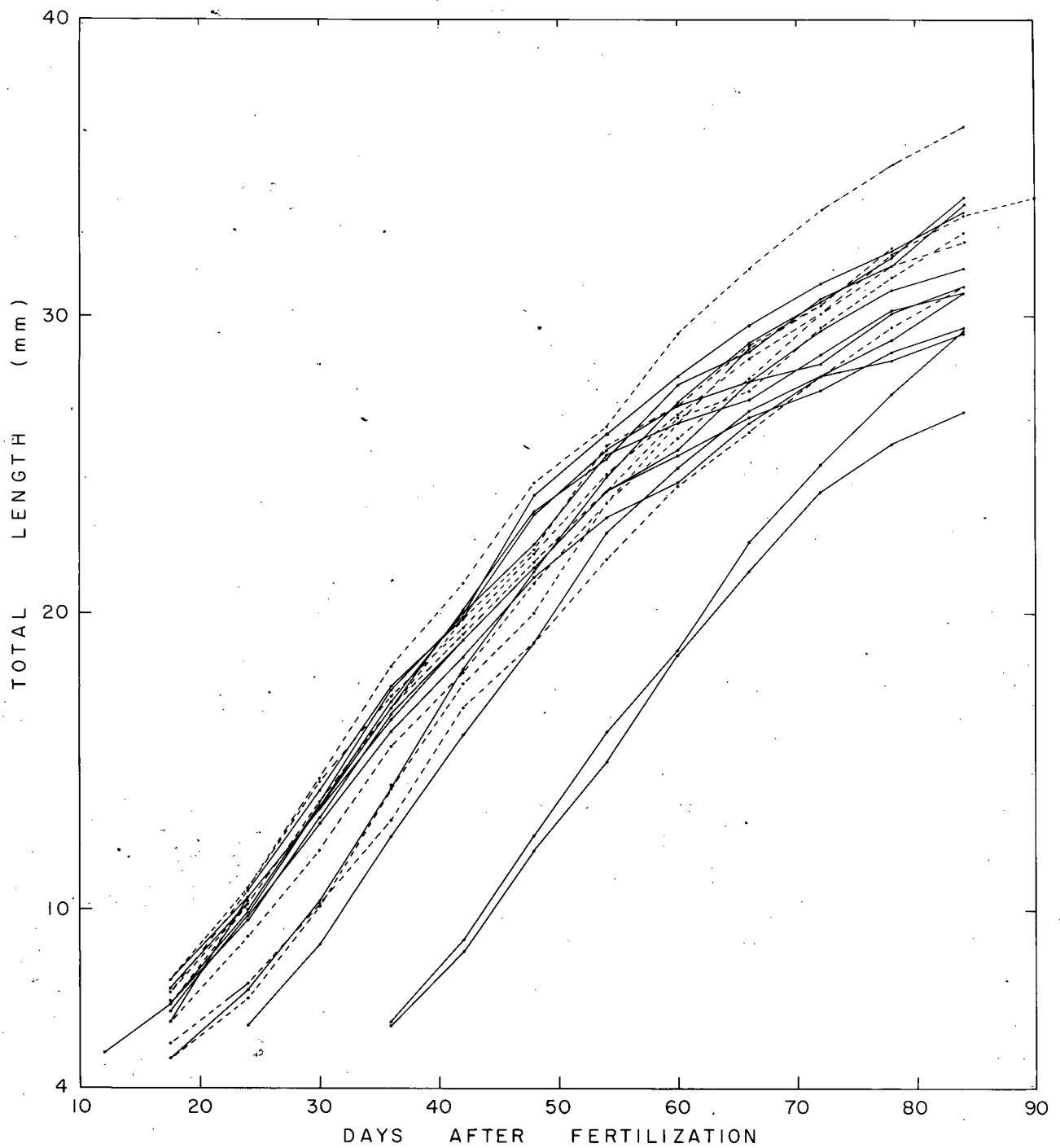
← 4 inches →

# 1986

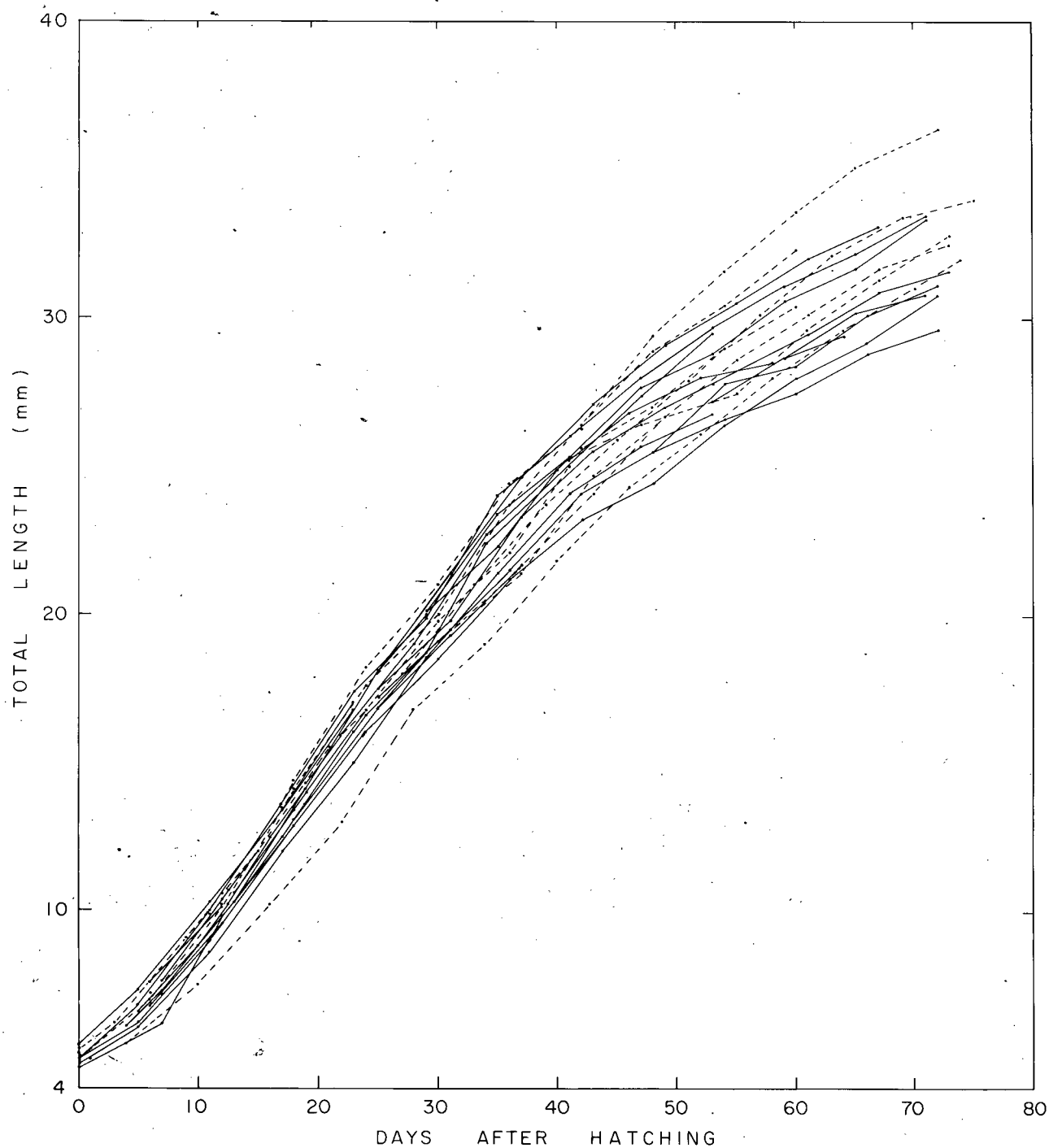
63.5

Magnuson  
361-84 Jan (12)



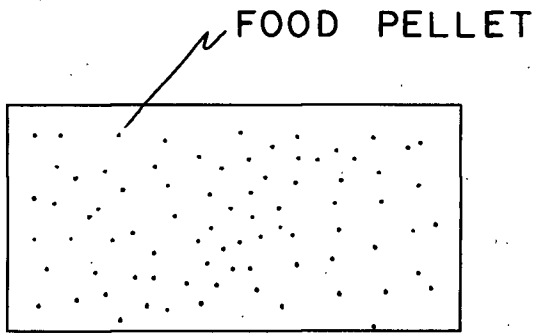


←  $4\frac{3}{4}$  inches → #1986 (123)  
 Magnusson  
 361-84 Jan ①  
 Fig-1

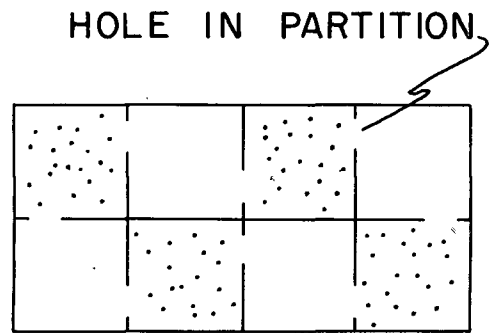


← 4 <sup>3</sup>/<sub>4</sub> inches →

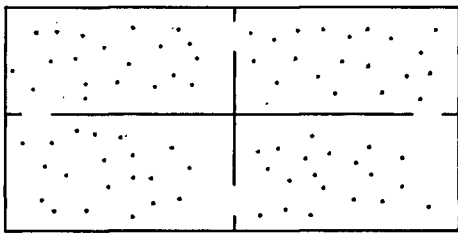
Magnuson  
361-84 Jan. (2)  
Fig. 2



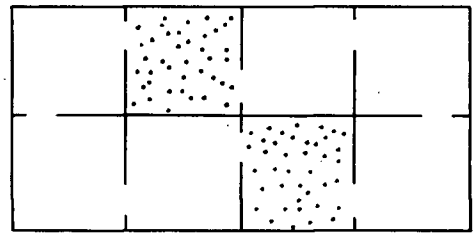
1 E



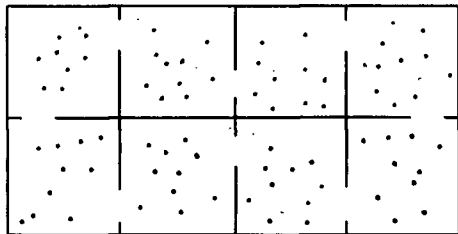
8 C 4



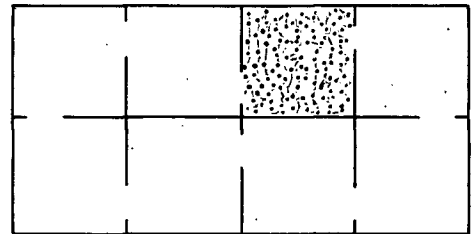
4 E



8 C 2



8 E



8 C 1

627

← 4 inches →

4/1986

Magnuson

361-84 Jan

15

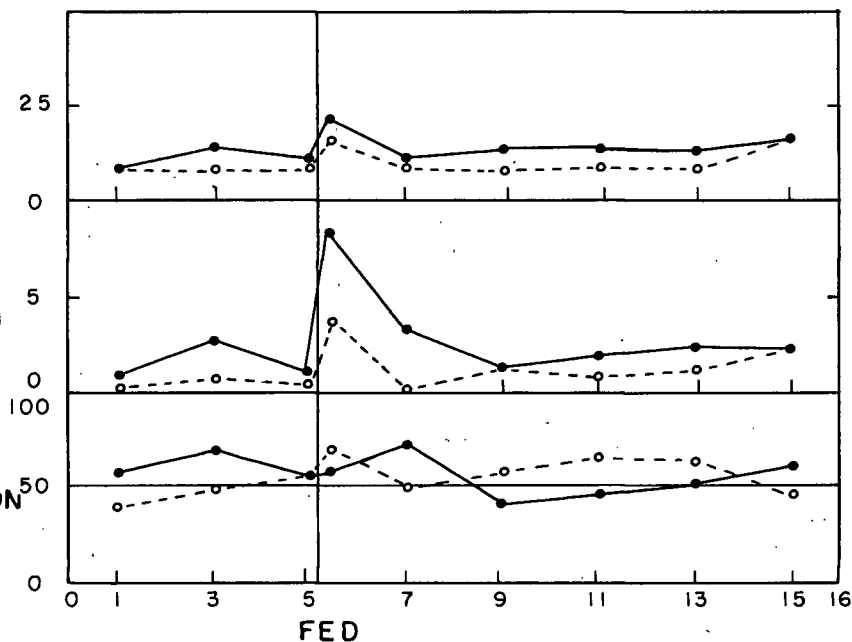
ACTIVITY/2.5 min

AGGRESSIVE

ACTIONS/2.5 min

% TIME ON FOOD

SIDE OF PARTITION



LPI

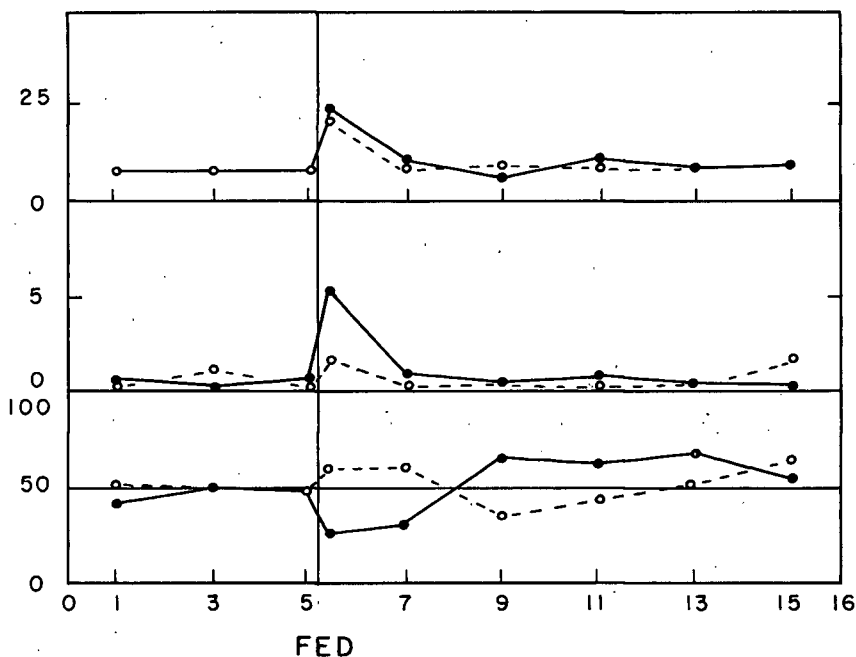
ACTIVITY/2.5 min

AGGRESSIVE

ACTIONS/2.5 min

% TIME ON RIGHT

SIDE OF PARTITION



LP2

HOURS AFTER LIGHTS WENT ON

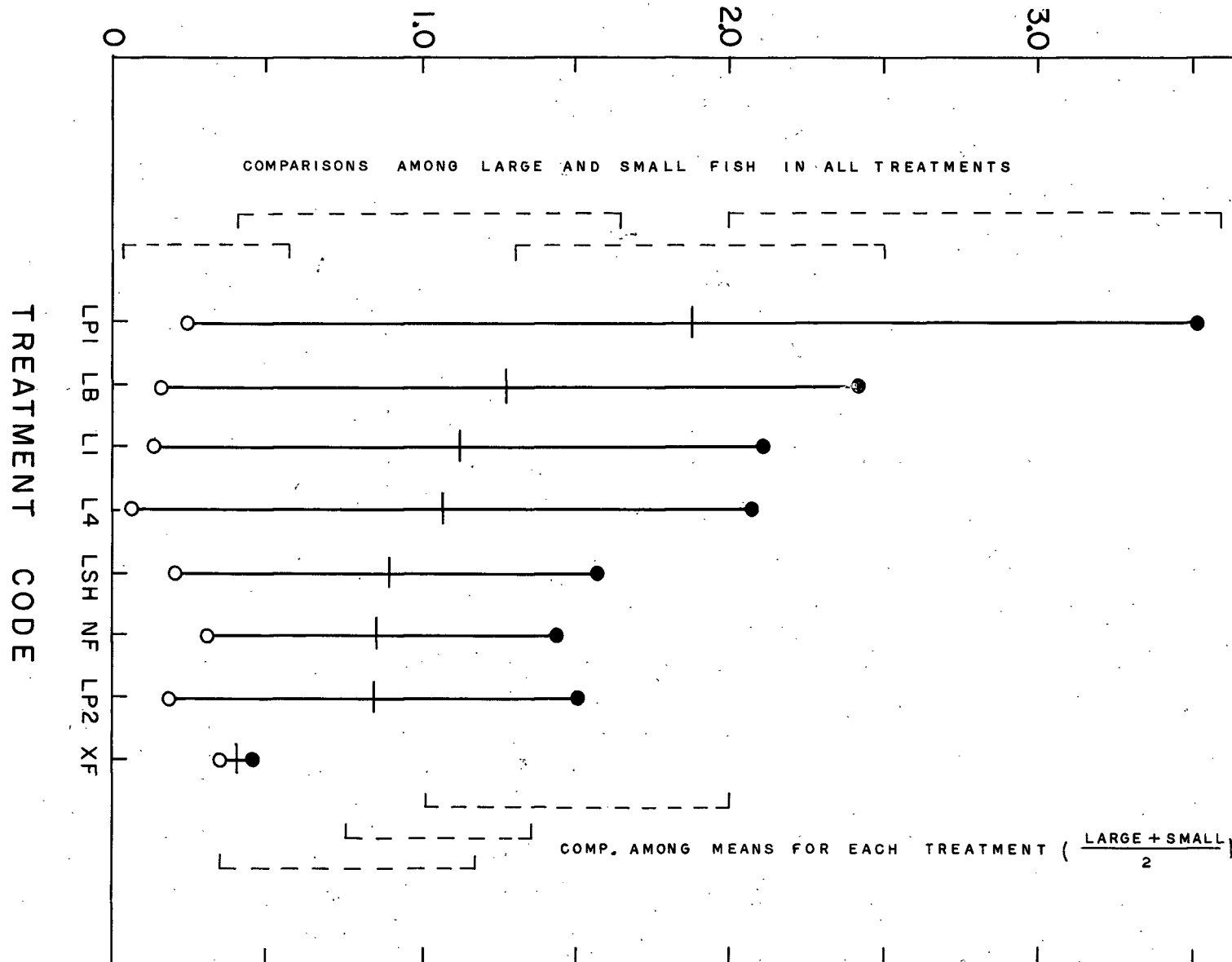
(61)

← 4 inches →

# 1986

Magnuson  
361-84 Jan. 11

# AGGRESSIVENESS (Agg. Act. / 2.5 min.)



TREATMENT CODE

LPI LB LI L4 LSH NF LP2 XF

59.1

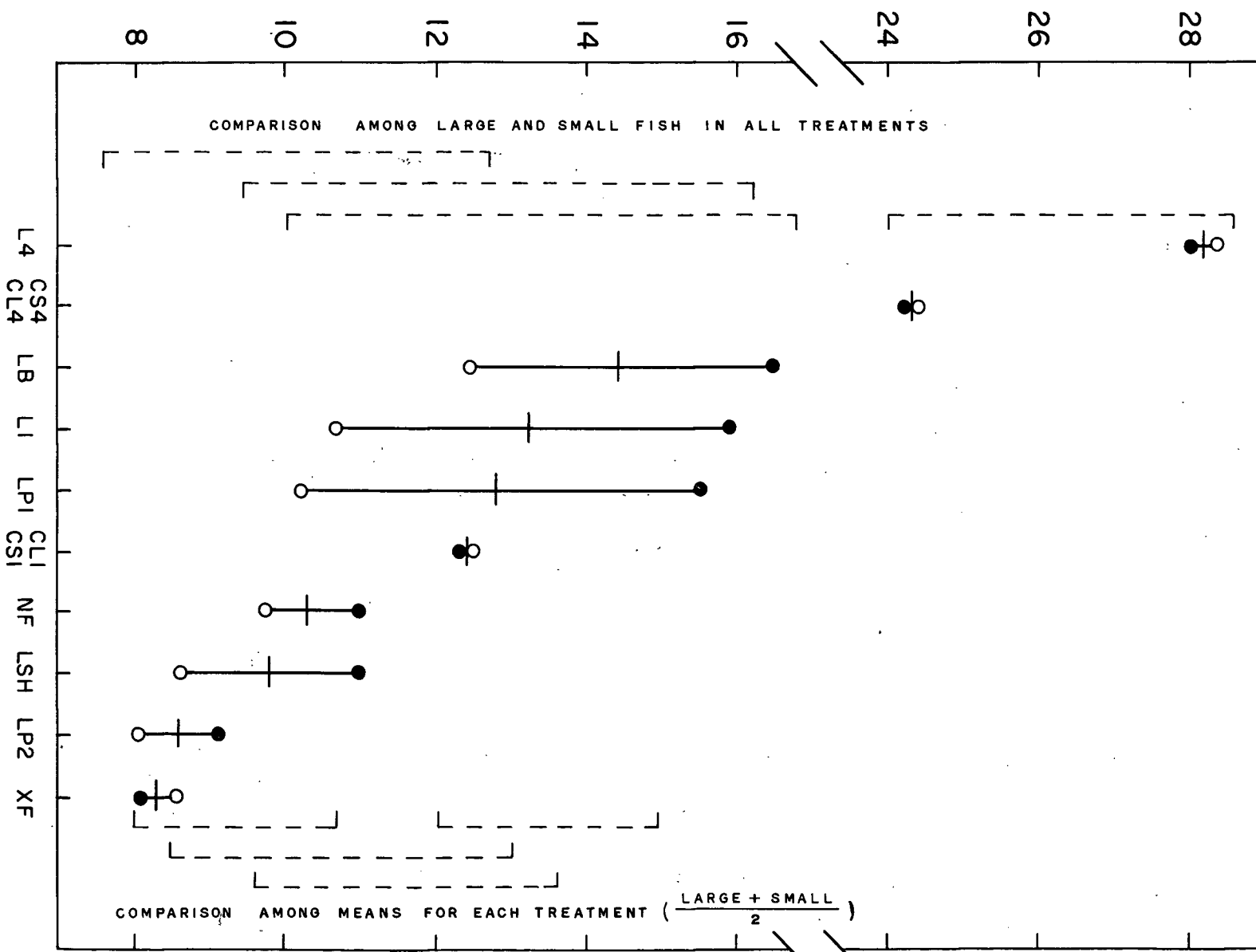
← 3 3/4 inches →

Magnuson  
30-84 Jan 7

1986



# ACTIVITY (COUNTS/2.5 min)



5-7.5

←

3 3/4 mches

→

1986

Magnesian ⑧  
341-54

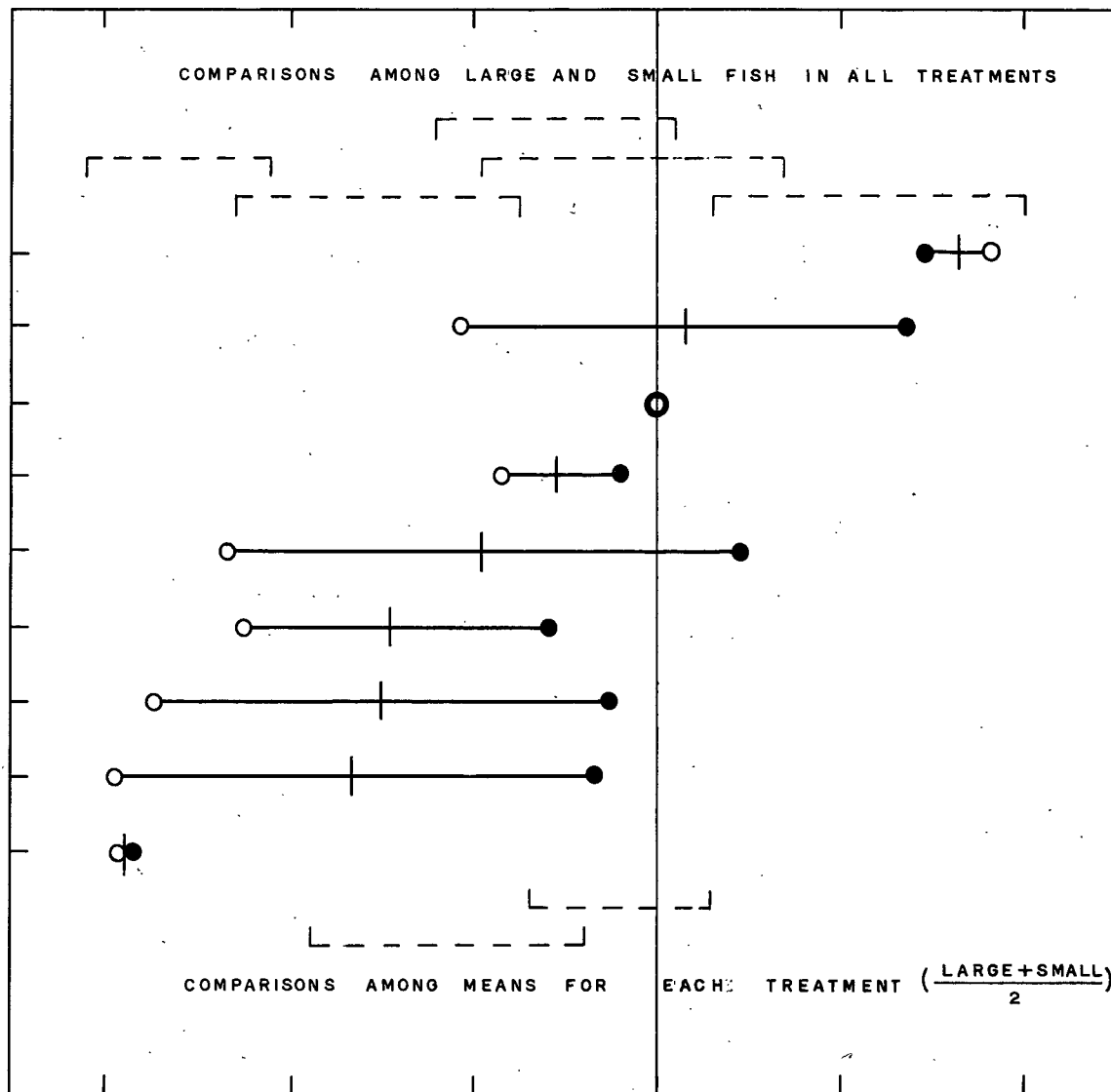
SIZE - SPECIFIC GROWTH RELATIVE TO CONTROLS ( $\Delta W - \Delta \hat{W}$ ) in mg

-3 -2 -1 0 +1 +2

COMPARISONS AMONG LARGE AND SMALL FISH IN ALL TREATMENTS

TREATMENT CODE  
CS4 L4 CS1 LP2 LP1 LI LB LSH NF

COMPARISONS AMONG MEANS FOR EACH TREATMENT ( $\frac{\text{LARGE} + \text{SMALL}}{2}$ )



← 4 weeks →

#1986

Magnuson  
30/84 Jan. (4)

62