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Temperature induced changes in the territorial dynamics of Cyprinodon macularius Baird and Girard

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TEMPERATURE INDUCED CHANGES

IN THE TERRITORIAL DYNAMICS OF

CYPRINODON MACULARIUS BAIRD AND GIRARD

A Thesis

Presented to the Faculty of the Graduate School

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By

Don Victor Plantz, Jr.

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This thesis, written and submitted by

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INTRODUCTION

The pupfishes, Cyprinodon Lacepede are widely distributed across North America (Miller, 1956). The genus probably arose in shallow coastal waters and salt marshes -- a habitat like that of the present-day North American east coast form, Cyprinodon variegatus Lacepede (Raney et al., 1953). Pupfish have evolved characteristic behavioral and physiological adaptations in order to cope with the extreme conditions of their shallow water habitat. Their simple but flexable and variable behavioral repertoire allows appropriate response to a wide variety of conditions that might prove fatal to a less generally adapted form.

The adaptive trend in Cyprinodon, then, is exploitation of widely fluctuating niches. Pupfish have been found in waters as hot as 41°C, "... the highest valid temperature yet recorded for voluntary fish activity in the field" (Lowe and Heath, 1969: 57). They have been observed moving from fresh water into waters with salinities exceeding that of sea water (personal observation and Barlow, 1958a). Additional ecological information on the genus is provided by Liu (1969).

Ethology

One of the earliest descriptions of the reproductive behavior of a pupfish was that of Newman (1907). Since that time there have been many studies describing in general the social behavior of various members of the genus (Nicols and

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Breder, 1927; Liu, 1965; Cox, 1966; Fanara, 1966; Foster, 1967; Kaill, 1967; Minckley and Itzkowitz, 1967; Itzkowitz, 1968; Echelle, 1970).

The Desert Pupfish

Cyprinodon macularius Baird and Girard is one of several species commonly referred to as desert pupfishes. It is distributed throughout the lower Colorado River drainage, with a large population in the Salton Sea and its contiguous shore pools and agricultural drainage canals (Miller, 1943; Barlow, 1958b). The behavior of C. macularius at Salton Sea was described by Cowles (1934) and Barlow (1958b, 1961). Lowe and Heath (1969) discuss thermal tolerance and behavioral thermoregulation in desert pupfish. Recent interest in the genus has been stimulated by the threatened extinction of certain pupfish inhabiting desert drainages (Pister, 1970).

Temperature Effects

Increasing concern is being shown about the effects of heated effluents in the aquatic environment. Some of the effects of temperature on aquatic organisms are well established, such as direct effects of temperature on the bodily functions of fishes. Maintenance of body temperature, growth and development, breathing rate, heartbeat, osmoregulatory function and the spermatogenic cycle, for example, are all

influenced by temperature (Hoar and Randall, 1969). Temperature may also indirectly affect aquatic organisms through a number of environmental characteristics such as pH and dissolved oxygen concentration. Temperature may also increase the effects of pollutants present in the water (Hoak, 1961). The problems associated with thermal pollution and its assessment are complex. This complexity is reflected in the diverse literature dealing with the many facets of thermal pollution (Raney and Menzel, 1967; Kennedy and Mihursky, 1967).

With seasonal changes in photoperiod and temperature, the immediate water temperature is among the most important factors governing the behavior of C. macularius populations. Studies on the effects of temperature upon fishes have tended to focus upon extreme temperatures. Barlow (1961) conducted field studies to determine the role high temperatures ($38^{o}C$) play in the regulation of territory size. He suggests that at $38^{o}C$ the metabolic demands of pupfish compel them to seek food continuously and accordingly the intensity of their territorial defense is low. At low temperatures ($10^{o}C$), males abandon their territories altogether and school with the females. Between these extremes, males occupy and pugnaciously defend territories varying in size from 1 to 6 square meters, depending upon the size of the fish, the time of year, population density and other factors. The mechanisms by which temperature influences territoriality and other sexual behavior

in lower vertebrates are not well understood (Aronson, 1965).

Behavior is qualitatively and quantitatively modified by the environment. Thus, any consideration of behavior must take into consideration the environmental conditions present. The present study evaluates the interelationship between one environmental condition (temperature) and a measureable behavioral phenomenon (territoriality).

MATERIALS AND METHODS

Test fish were acclimated in nine aquaria, three
each at 22, 27 and 32°C, arranged in a 3 X 3 latin square
design (Figure 1). The aquaria measured 30.65 cm X 30.65 cm
X 61 cm with volumes of approximately 47 liters. Each was
equipped with a subgravel filtration system and an airstone.
At bottom-center of each aquarium was located a synthetic
yarn "spawning mop," a central reference point about which
the males invariably established their territories. A plastic
flower pot in a consistent rear position provided refuge for
the females (Figure 2). The salinity was adjusted to 5-6
parts per thousand and the aquaria were fitted with glass
lids to prevent water loss and temperature changes by evap-
oration. Water temperatures were maintained to within ± 1°C
by means of aquarium heaters. Fluorescent 40 Watt lamps
mounted over the aquaria were controlled by electrical timers
to produce a fourteen hour light period (8:00 A.M. - 10:00
P.M., PST).

The C. macularius used in this study were collected
from a pool on the western shore of the Salton Sea, Imperial
County, California, near Avenue 82. A description of the
physical and chemical characteristics of similar shore pools
surrounding the Salton Sea may be found in Barlow (1958b).
Specimens used were young of the year of similar size (25-
32 mm). Each test aquarium contained one male and two female

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pupfish.

Data Collection

Eibl-Eibesfeldt (1970: 11) discusses the advantages

of motion-picture photography in behavioral research:

> On film the behavior patterns become fixed and can
> be preserved for later comparison. In addition, fast
> and slow motion allow for the analysis of data that
> would not normally be accessible to direct observation.
> The slow motion technique has frequently been used to
> make visible for the human eye events that run off too
> quickly to be perceived. The value of the speeding-up
> (Zeitraffer) technique has hardly been recognized in
> ethology.

Distributional patterns of the fish over time at

each of the three test temperatures were recorded with time

lapse photography. Position of the fish within the aquaria

were photographed once each minute during the lighted per-

iod by means of a motion-picture camera equipped with an

intervalometer. The order in which the aquaria were filmed

was determined from a random numbers table. Each of the nine

aquaria was filmed for one fourteen-hour period, with the

resulting nine-day filming "run" repeated nine times. The

order of filming was randomized for each run. Filming time

for the entire study was forty-five days. A few days were

usually allowed between nine-day runs to facilitate aqua-

rium maintenance. Processed films were projected frame-by-

frame onto a screen gridded into eight areas, so that half

of the aquarium was covered by the grid (Figure 3). Only

half of the aquarium was considered in order to simplify

analysis of the films. Right and left halves of the aqua-

ria were compared and no differences were found to exist in

the distributional patterns. The number of fish appearing

in each area of the screen during each hour was recorded.

Distributional patterns for males and females were analyzed

separately.

The total and mean numbers of observations for each

of the grid zones was determined for both sexes for each

replication (Table 1). These data were then compared for

each of the three temperatures using the Brandt-Snedecor

formula for χ_s^2 , a modification of χ^2 for the analysis of

2 X n contingency tables (Keeping, 1962) (Table 2). The

distributional patterns for the females differed signi-

ficantly ($0.01 < P < 0.02$) between 22°C and the other two

test temperatures. No significant differences between the

27°C and 32°C pattern were indicated. Differences among the

distributional patterns of the males were not indicated.

Behavioral differences at the three temperatures do exist,

however, and are discussed in another section. The distribu-

tional patterns of the males differed significantly from

the corresponding patterns for the females. In each case,

pairwise comparisons between patterns were made.

Figures 4, 5 and 6 represent the distributional

patterns of males and females at each of the three experi-

mental temperatures. The male's territorial center is at the

origin with increasing distance from the territorial center

on the vertical axis. In Figure 7, a smooth curve composite

of the graphs in the preceding three figures, the relation-

ships between these patterns become evident. The greater di-

vergence between patterns of females as compared to those of

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males may be seen.

At 22°C, there were greater numbers of observations of females in the upper regions of the aquarium and fewer near the male's territorial center than at the other two temperatures. With increasing temperature, females are more frequently observed in lower zones. The 32°C curve shows the fewest number of observations in the upper regions and the greatest number in the lower zones. The curve for 27°C is intermediate between that for 22°C and that for 32°C (Figure 7).

The total number of observations for any replication was the same, barring those instances when the fish were out of the camera's view (i.e., behind the flower pot or spawning mop). An increase in the total number of observations in one zone will result in a decrease in the number of observations in one or more of the remaining zones. This produces the observed effect of a pivoting curve (Figure 7).

DISCUSSION

Warner et al. (1966: 225) provide a rationale for the selection of behavior as an indicator of effects caused by environmental change:

(1) The behavior (or activities) of an organism represents the final integrated result of a diversity of biochemical and physiological processes. Thus, a single behavioral parameter is generally more comprehensive than a physiological or biochemical parameter.

(2) Behavior patterns are known to be highly sensitive to changes in the steady state of an organism. This sensitivity is one of the key values for its use in exploring sublethal toxication.

(3) Behavioral measurements can usually be made without direct physical harm to the organism. With aquatic organisms especially, implantation of detectors introduces problems of considerable complexity. Behavior mesurements can avoid this difficulty.

In addition, behavior is especially suitable as an environmental indicator in that it is often quickly responsive to fluctuations and may allow time to correct a natural situation before irreversible changes have occurred.

Territoriality is strongly developed in Cyprinodon males (Cowles, 1934; Raney et al., 1953). Males defend their territories by means of incessant rapid and vigorous patrolling movements, darting back and forth across their territories and occasionally leaving them to chase an intruding fish. Males spend most of their time either patrolling or posting (maintaining a more or less stationary position near the center of the territory). Females, however, are thought

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to defend territories only sporadically if, indeed, territoriality exists in the females (Barlow, 1958b). It is the female that chooses the spawning partner and initiates and ends reproductive behavior. Spawning and courtship behavior in the male is therefore dependent upon the reproductive activities of the female.

The data indicate that temperature differentially affects the distributional patterns of males and females. The distributional pattern of the male is apparently independent of temperature within the range of this experiment. Qualitative observations show that at 22°C the male has assumed its territorial station. This is consistent with the distributional data, which indicate that the male spends in the order of 60% of his time in grid zones (A and B) adjacent to the territorial center. Apparently, then, 22°C is above the lower threshold for establishment of territoriality in Cyprinodon macularius males. This agrees with field observations by Barlow (1961). The experimental temperatures also appeared to be below that at which territoriality is inhibited. No changes in spatial orientation over time were noted for the male between the high and low temperature limits of this study. Qualitative observations show that territoriality is still very much in evidence at 32°C.

The distributional pattern of the female, on the other hand, appears to be temperature dependent. Females

were observed in lower areas of the aquaria at the two higher
temperatures than at the lower test temperature. In order to
initiate courtship activities, the female must leave the re-
gion in which she spends most of her time (the upper part of
the aquarium) and approach the male. The increased frequency
with which the female was observed in lower regions at higher
temperatures may, then, be the result of greater numbers of
reproductive overtures. If this is the case, the lower thresh-
old temperature for reproductive behavior in the female
would appear to occur between 22°C and 27°C. At 22°C, the
female is seen only rarely in the lower regions of the aqua-
rium. Apparently, then, she makes few attempts to initiate
courtship at 22°C. At 27°C and 32°C, the female is observed
with much greater frequency in lower areas, suggesting an in-
creased number of attempts to initiate spawning (i.e., the
threshold for reproductive behavior in the female has been
exceeded).

Courtship and spawning occurs within the male's
territory. He need not move from one region of the aquarium
to another in order to engage in reproductive activities.
The female, on the other hand, must leave the upper part of
the aquarium and enter the male's territory. A shift from
noncourtship to courtship behavior would therefore affect
the distributional patterns of males and females differently.

The pattern of the male would be expected to show little change, since both courtship and noncourtship behavior occur in the same area. The pattern for the female, however, should be altered since these two types of behavior take place in two different regions. A shift from virtually noncourtship activities towards courtship and spawning activities could, therefore, account for the greater divergence in the distributional patterns of the females as compared to those of the males.

Although no changes in the distributional patterns of the males appeared to have occurred as a function of temperature, filmed behavioral sequences at each of the test temperatures show that behavioral differences did occur. Data from the analysis of these filmed sequences indicate that changes in the type of behavior exhibited by the male were apparently in response to increased numbers of attempts by the female to initiate courtship (W.M. Kaill, personal communication).

SUMMARY

Cinematographic methods were employed for the quantification of temperature induced changes in the distributional patterns of Cyprinodon macularius, the desert pupfish. The patterns for males did not differ significantly between $22^{\circ}C$, $27^{\circ}C$ and $32^{\circ}C$. The patterns for the females differed significantly between $22^{\circ}C$ and $27^{\circ}C$, and between $22^{\circ}C$ and $32^{\circ}C$. The patterns for the females did not differ significantly between $27^{\circ}C$ and $32^{\circ}C$. The data from the distributional analysis coupled with information from filmed behavioral sequences lead to the conclusion that the lower threshold temperature for courtship activities is below $22^{\circ}C$ for the male and between $22^{\circ}C$ and $27^{\circ}C$ for the female. Thus, a behavioral phenomenon is described in which for the two sexes, not only are different patterns seen, but with different thresholds as well. Therefore, generalizations cannot be made for the species as a whole, and males and females must be considered as separate cases.

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APPENDIX

Mean Numbers of Observations

Grid Zone	22°C		27°C		32°C	
	Male	Female	Male	Female	Male	Female
A	9.7	0	9.1	0.5	9.5	0.3
A'	2.4	0.1	2.3	1.1	2.0	2.0
B	4.7	0.1	3.2	1.0	4.9	1.0
B'	1.5	0.2	1.3	3.4	1.8	1.5
C	2.4	1.7	3.6	5.1	2.6	4.9
C'	1.2	1.4	1.9	5.2	1.8	7.3
D	1.2	19.2	1.8	13.6	1.2	14.6
D'	1.2	22.1	1.0	15.0	0.7	13.2

Table 1. Mean numbers of observations in each of the grid zones for male and female _Cyprinodon macularius_ at each of the three experimental temperatures. Each mean is based on 210 observations.

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The χ_s^2 value for a sample with frequencies as given below is:

$$\chi_s^2 = \frac{N^2}{r_1 r_2} \left(\sum_j \frac{a_j^2}{c_j} - \frac{r_1^2}{N} \right)$$

Aquarium Grid Zones

Y_1	Y_2	Y_3	$\cdots$	Y_n		
a_1	a_2	a_3	$\cdots$	a_n	r_1	X_1
b_1	b_2	b_3	$\cdots$	b_n	r_2	X_2
c_1	c_2	c_3	$\cdots$	c_n	N	

Temperatures

a_j = number of hourly observations in each grid zone at temperature X_1

b_j = number of hourly observations in each grid zone at temperature X_2

$c_j = a_j + b_j$ $\qquad$ $r_1 = \sum_j a_j$ $\qquad$ $r_2 = \sum_j b_j$ $\qquad$ $N = r_1 + r_2$

Table 2. Explanation of terms employed in the general Brandt-Snedecor Formula for χ_s^2.

Figure 1. Physical arrangement of experimental aquaria.
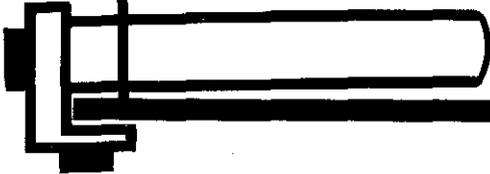
32°C

22°C

27°C

27°C

32°C

22°C

22°C

27°C

32°C
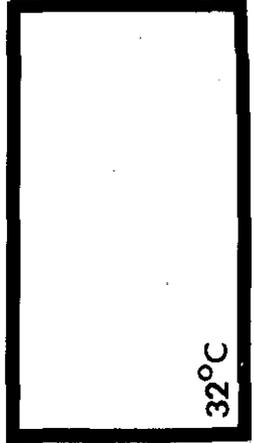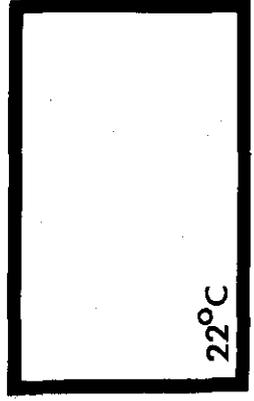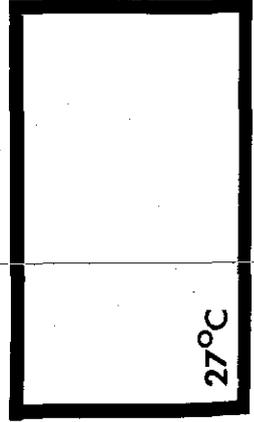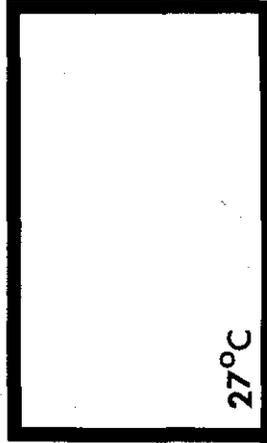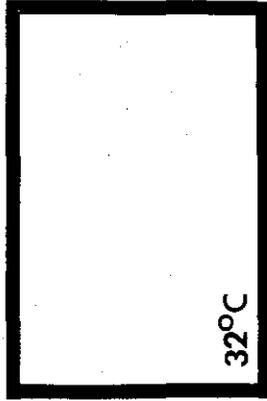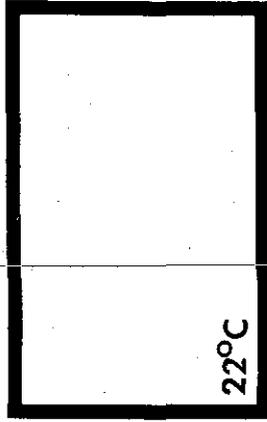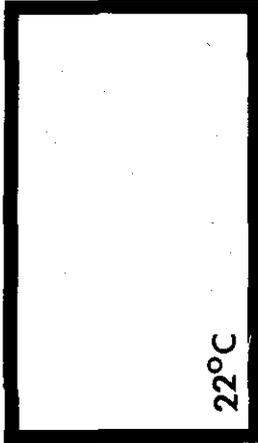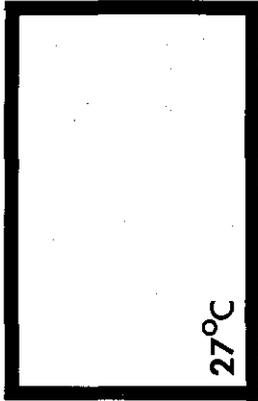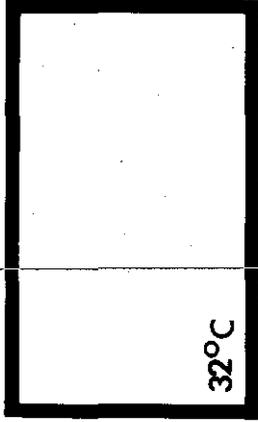
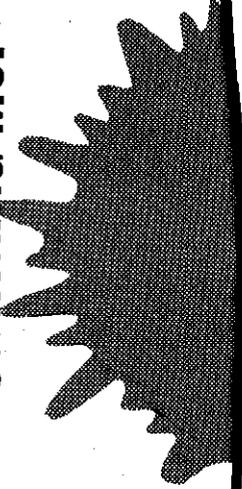Figure 2. Diagramatic representation of a single experimental aquarium.

HEATER

SPAWNING MOP

FLOWER
POT

FILTER

Figure 3. Zones into which each aquarium was divided for
the purposes of data analysis.

Figure 4. Distributional patterns of male and female
Cyprinodon macularius at 32°C.

32°C

GRID ZONES (y-axis)

D/D'
C/C'
B/B'
A/A'
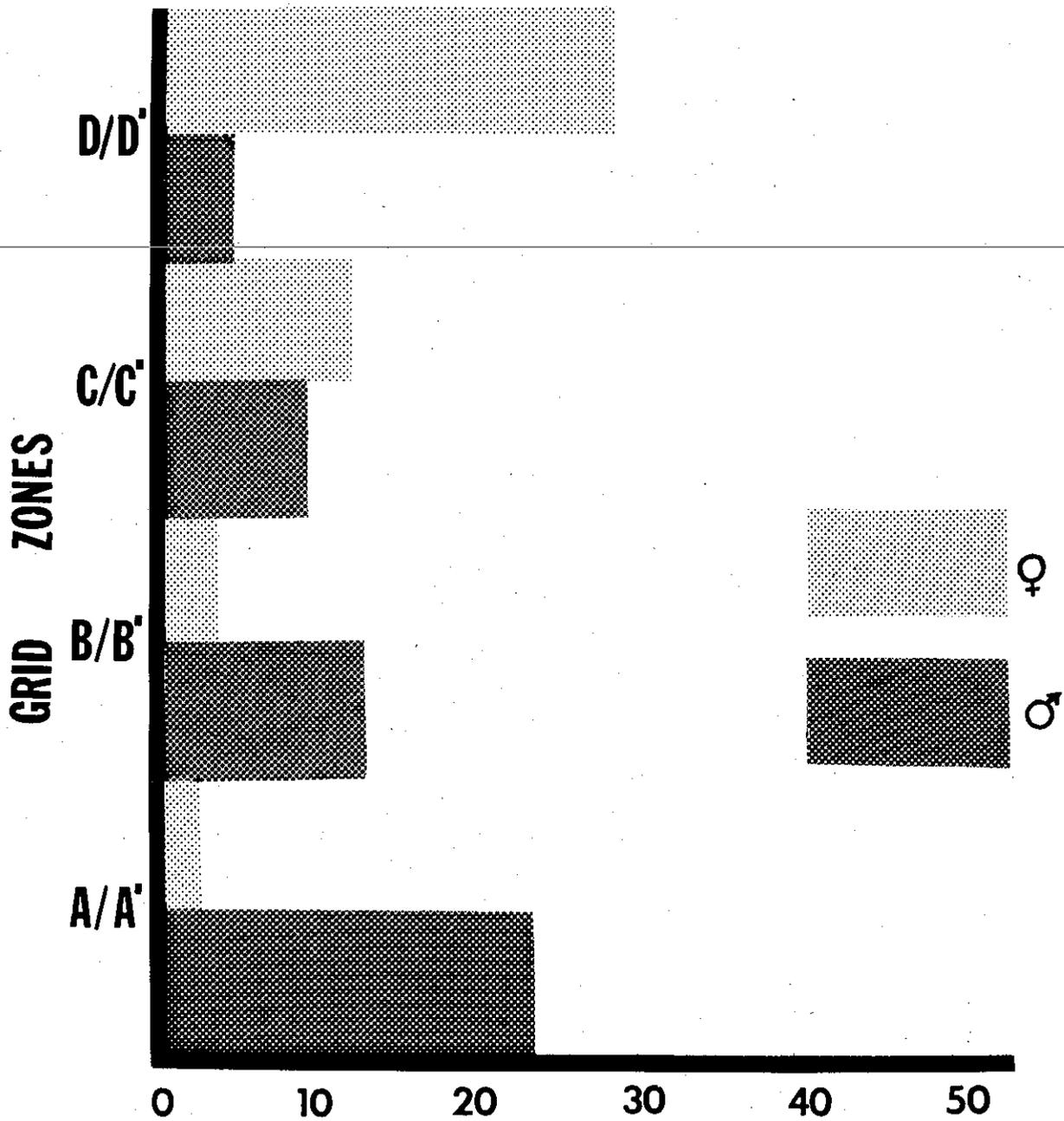
MEAN NUMBER OF HOURLY OBSERVATIONS (x-axis: 0, 10, 20, 30, 40, 50)

♀

♂

Figure 5. Distributional patterns of male and female
Cyprinodon macularius at 27°C.

27°C
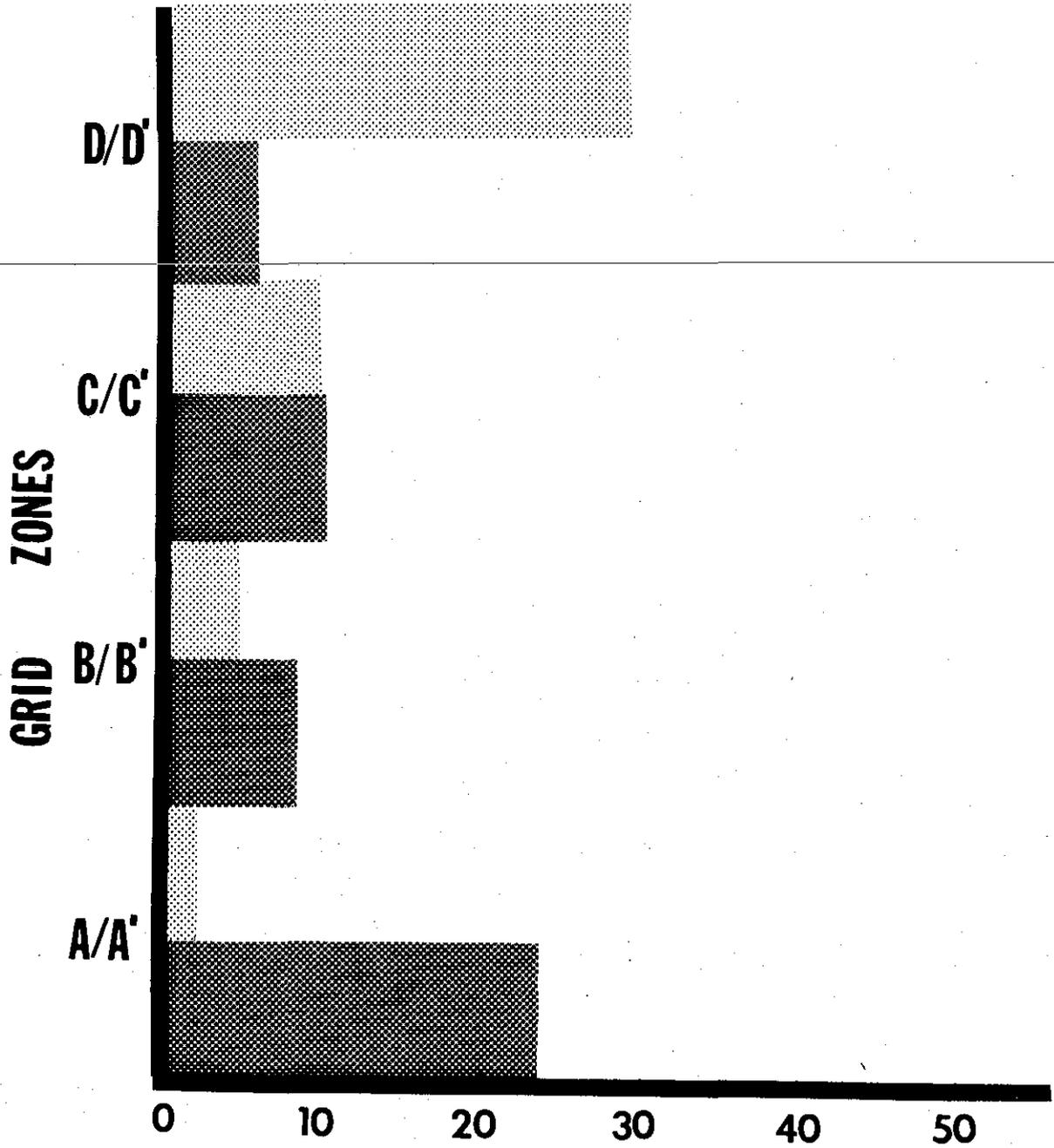
Figure 6. Distributional patterns of male and female
Cyprinodon macularius at 22°C.
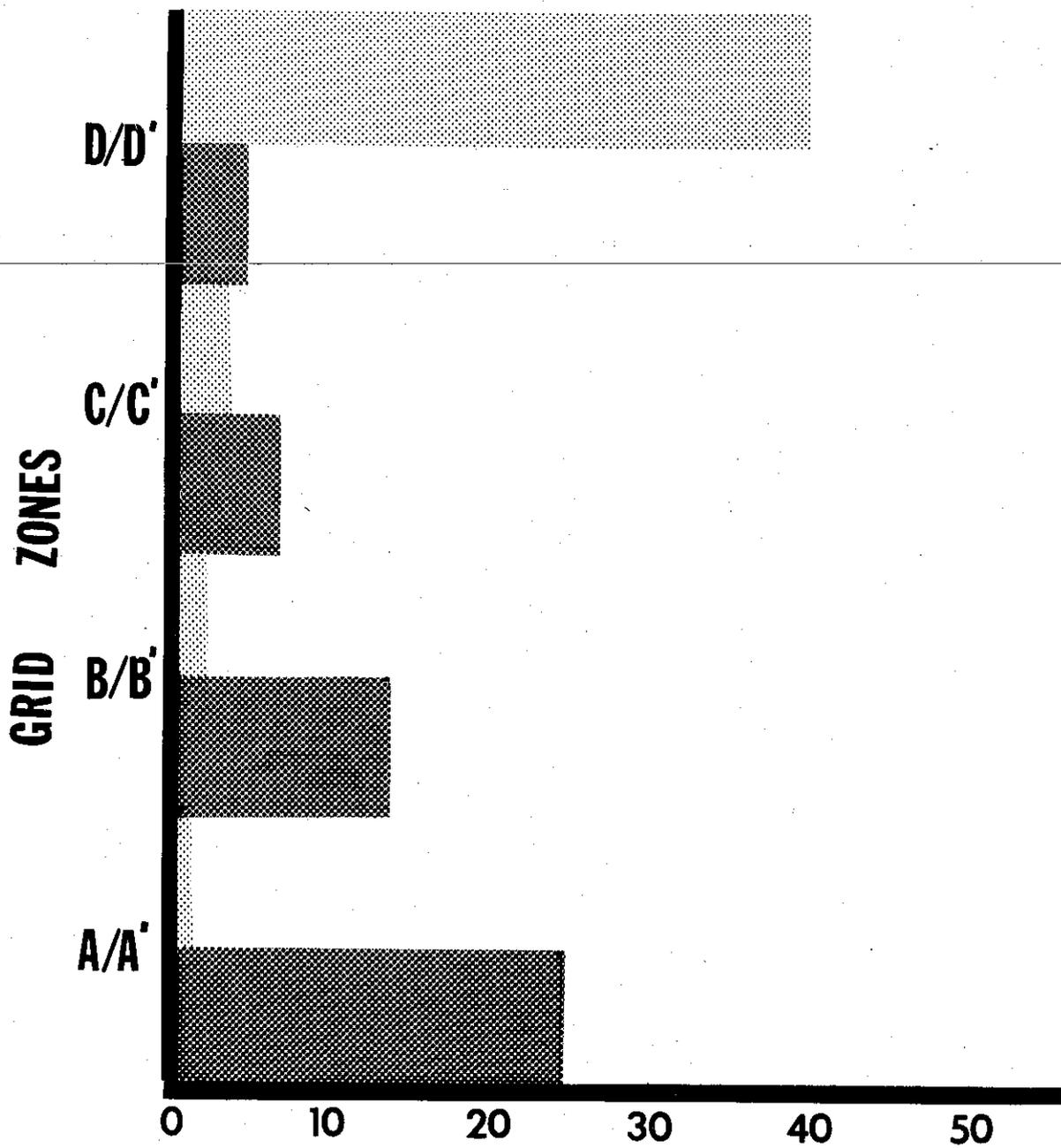
Figure 7. Smooth curve representation of distributional patterns of male and female Cyprinodon macularius, fitted by eye, for each of the three experimental temperatures.
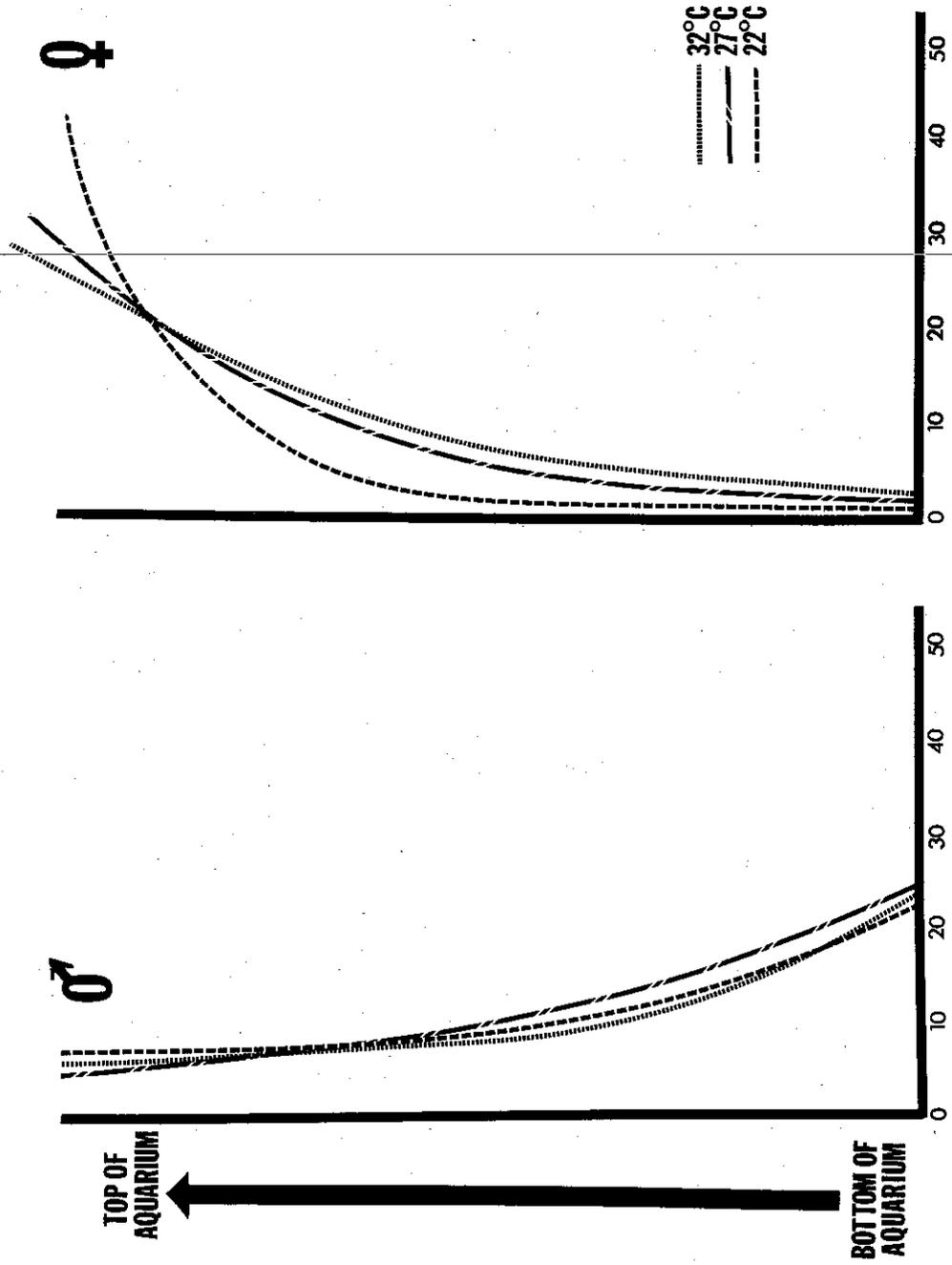
MEAN NUMBERS OF
HOURLY OBSERVATIONS

♀

♂

TOP OF
AQUARIUM

BOTTOM OF
AQUARIUM

32°C
27°C
22°C