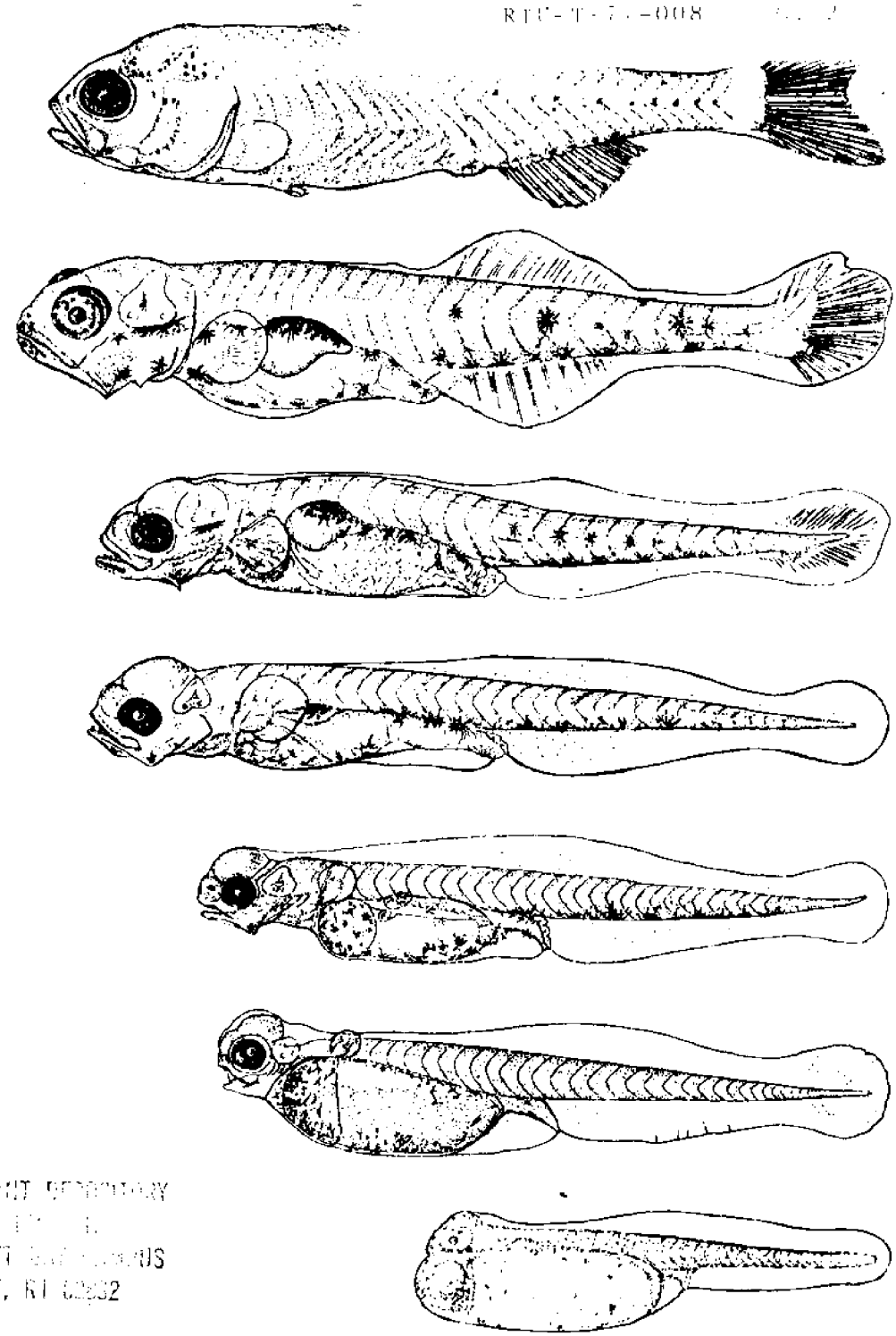

Life Stage Duration Studies on Hudson River Striped Bass

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Applied Marine Research Group
NOAA Sea Grant
University of Rhode Island
Marine Technical Report No. 31

Life Stage Duration Studies on Hudson River Striped Bass, *Morone saxatilis* (Walbaum)

by

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ABSTRACT

Laboratory experiments were undertaken to determine the effect of rearing temperature on the time duration of the egg, yolk sac, and post-yolk sac larval stages of the striped bass, Morone saxitilis. Five fixed test temperatures were used between 12° and 24°C. In all the stages examined, stage duration was reduced at higher temperatures within this range, which spans that normally encountered by developing striped bass in their natural environment. The time from fertilization through hatching was related to temperature by:

$$\text{time to hatching (hours)} = 258.5\ e^{-0.934(\text{Temp.}^\circ\text{C})}$$

The yolk sac stage ranged from 3.8 days at 24°C to 9 days at 12°C. The larval stage, from yolk absorption to metamorphosis, ranged from 26.5 days at 24°C to 40.5 days at 18°C and an estimated 76 days at 15°C.

Evidence supporting the occurrence of a temperature optimum for development within each stage was presented.

Nutritional factors were found to be at least as important as temperature in determining stage duration among feeding larvae. The relationship between the laboratory stage duration estimates presented here and those used by previous authors in predicting power plant entrainment losses were discussed, as well as some of the reservations which may apply to larval age estimates based on length frequency distributions obtained from field collections.

ACKNOWLEDGMENTS

This study would not have been possible without the kind cooperation of Texas Instruments, Inc., which supplied us with striped bass eggs and larvae from their hatchery operation in Verplank, New York. We greatly appreciate the consideration shown us by their hatchery staff throughout our stay in Verplank.

We wish to thank Steve Clements, John Hartley and Lisa Pearce for their able assistance in maintaining the larval cultures and in measuring numerous preserved samples. Special thanks are given to Jan Steele for typing this manuscript. All of the figures were drafted by Stephanine Gall, Marion McHugh and Margret Leonard.

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INTRODUCTION

This study was undertaken to provide experimental information on the effect of water temperature on the rate of growth and development of the early life stages of the striped bass, Morone saxatilis (Walbaum) as an aid in assessing the effect of water-cooled electric power plant operations on the population dynamics of this important commercial species.

A number of simulation models have been devised for the hydrography of the Hudson River. In recent years these have achieved a high degree of reliability in describing the hydrodynamics of the lower Hudson and its estuary (Lawler et al., 1974). The value of hydrodynamic models in predicting the spatial and temporal distribution of the planktonic early life stages of estuarine fish can be improved by incorporating relevant information on the natural history, behavior, and developmental physiology of the species involved (Wallace, 1975).

Although growth is a continuous process from fertilization through adulthood, it is convenient to divide the early life history of fishes into a series of stages, based on the degree of structural development and the mode of larval nutrition (Hubbs, 1943). Because each of these stages defines a sequential part of the developing ability of the young fish to avoid power plant entrainment, modellers have applied different avoidance factors to each stage. Within this context, stage duration defines the rate at which the young fish are growing toward a size at which they will be able to avoid entrainment.

Knowledge of water movements, avoidance abilities of fish at each stage, rates of egg production through the spawning season and some

measure of the duration of each life stage permits development of life history models. These, in turn, may accurately predict the extent of losses attributable to both power plant entrainment and to the complex of events that constitutes natural mortality.

To date, estimates of life stage duration have been made empirically. That is, the time and duration of the appearance of various stages in plankton and beach seine collections have been observed following striped bass spawning. Although this approach has provided estimates of stage duration under natural conditions, experimental studies provide a better means of isolating the effect of a single given environmental factor from the many conditions that affect stage duration in the river. The study of larval fish biology is still in its infancy. Nevertheless, it is clear that the pattern of growth seen in the increasing modal size of larvae taken in plankton collections represents a result of the interaction of a variety of factors, including some not yet properly identified. Factors that have been identified as affecting the success and rate of embryonic and larval development include: temperature, salinity, dissolved oxygen, water-borne toxicants, food type, food abundance, density of individuals, and disease. Although it is impossible to take all these factors into account, some can be systematically varied and the results observed. This experimental approach permits the evaluation of particular factors, but introduces a measure of simplicity which does not exist in nature, because of elimination of the influence of other factors and factor interactions. This approach is useful, however, in identifying which factors are important and which are not.

In this study attention is limited to the role of temperature on the rate of development. From studies on other species there is reason to expect that temperature plays a dominant role in determining the rate of development in striped bass eggs and prolarvae. It is also an important determinant of the rate of growth of feeding larvae and juveniles. Yolk is the only source of nutrition for the developing egg and prolarva. Since temperature affects the maintenance energy requirements of the embryo, the efficiency of conversion of yolk to embryonic tissue is influenced. After the change from endogenous to exogenous energy sources at yolk absorption, the nature and abundance of food also become primary determinants of the rate of larval growth. At this stage the larva must receive sufficient food to meet its maintenance requirements which include the cost of searching and capturing prey; it must also take in the energetic equivalent of whatever growth in biomass it is able to achieve. Because the energetic costs of activity and maintenance are intimately related to temperature, it is important in determining the amount of energy available for growth. When the diet is sufficient to meet the larva's nutritional requirements, maximum growth will occur at a temperature where appetite is high and maintenance requirements are relatively low.

There have been numerous studies of the effect of temperature on the rate of development and growth of larval fish; many of these have been reviewed by Blaxter (1969). The period between fertilization and hatching has received the most attention. This is also true for striped bass (see Bayless, 1972). The time course of developmental events prior to hatching has been observed at one constant temperature in striped bass by Bayless (1972) and at a slowly rising temperature by Mansueti

(1958). Although striped bass have been reared extensively over the past 10 years, there have been few detailed studies of the rate of growth of larvae as a function of temperature. Humphries and Cumming (1973) presented a composite growth curve for wild and hatchery reared striped bass grown under rising, but unspecified, temperature conditions. Rhodes and Merriner (1973) reported the growth of larvae and juveniles under intensive culture conditions and slowly rising temperature.

MATERIALS AND METHODS

Source of Study Material

The eggs and larvae used in these experiments were obtained from striped bass collected on the spawning grounds in the Hudson River between Cornwall and Croton, New York. Samples of fertilized eggs were provided by Texas Instruments, Inc., which operated a striped bass hatchery at Verplank, New York. Ripe adults were captured using haul seines or gill nets. They were then taken to the hatchery where they were either allowed to progress toward ovulation naturally, or were induced to ovulate artificially using human chorionic gonadotropin hormone injections according to the methods of Bayless (1972). A total of nine lots of eggs were used, each derived from a separate mating. Data on the brood females used and time and date of stocking of each lot are summarized in Table 1. Lots 1-7 were stocked as eggs. Lots 8-9 were obtained as newly hatched larvae after incubation in 20-21°C hatchery water.

Water Source, Water Quality, and Temperature Control

Water drawn from a flooded gypsum quarry owned by the Consolidated Edison Company of New York was used to supply the Texas Instruments hatchery. The majority of the eggs used in these investigations were water hardened and incubated in water from this source. Analyses of both quarry water and samples from the Hudson were provided by Texas Instruments and are presented in Table 2. Newly fertilized striped bass eggs water hardened to a slightly smaller chorion diameter in quarry water than in Hudson River water. In other respects this water supply appeared to be an adequate incubation medium.

TABLE 1

Summary of egg and larvae sources for life stage duration studies.

Lot #	Date Fertilized 1975	T.I. Hatchery Roe #	Female Weight (kg)	Female Length (cm)	Time of Fertilization	Time of Stocking	Water Source Water Hardening	Water Source Initial Culture
1	5/20	5	8.4	N.A.*	1115	1130 eggs	Quarry	Quarry
2	5/21	6	10.7	N.A.	0100	0115 eggs	Quarry	Quarry
3	5/21	7	10.4	N.A.	0845	0900 eggs	Quarry	Quarry
4	5/21	N.A.	7.7	N.A.	1345	1415 eggs	Quarry	Quarry
5	5/22	11	9.7	88.7	2015	2030 eggs	Quarry	Quarry, Hudson
6	5/22	12	12.0	93.2	2215	2230 eggs	Quarry	Quarry with antibiotic
7	5/25	14	7.3	54.6	0015	0030 eggs	Hudson	Quarry with antibiotic
8	5/27	15	7.0	54.6	N.A.	1300 larvae	Quarry	Quarry
9	5/31	16	N.A.	N.A.	N.A.	0930 larvae	Quarry	Quarry with antibiotic

*N.A. - data not available.

Table 2

Results of Water-Quality Analysis on Verplanck Quarry and Hudson River Water
(from: Texas Instruments, Inc., 1974. Table C-1, p. C-1.)

Parameter	Quarry	River
Alkalinity		
Methyl Orange (mg/ℓ-$CaCO_3$)	136.60	44.46
Phenophthalein (mg/ℓ-$CaCO_3$)	0.00	0.00
Aluminum (mg/ℓ)	0.081	0.232
Arsenic (mg/ℓ)	<0.001	0.002
Barium (mg/ℓ)	0.004	0.038
Beryllium (mg/ℓ)	<0.001	<0.001
BOD (mg/ℓ)	0.8	1.2
Boron (mg/ℓ)	0.007	0.026
Cadmium (mg/ℓ)	<0.001	0.001
Calcium (mg/ℓ)	76.80	20.65
COD (mg/ℓ)	17.8	14.2
Chlorides (mg/ℓ)	21.25	134.80
Chromium (hexavalent) (mg/ℓ)	<0.001	0.005
Chromium (total) (mg/ℓ)	0.001	0.005
Color (APHA units)	10	15
Conductivity (μmho/cm)	560	320
Copper (mg/ℓ)	0.002	0.006
Cyanides (mg/ℓ)	<0.001	<0.001
Fluorides (mg/ℓ)	0.0	0.2
Free CO_2 (mg/ℓ)	4.8	5.5
Total Hardness (mg/ℓ-$CaCO_3$)	338.40	67.20
Iron (mg/ℓ)	0.136	0.316
Lead (mg/ℓ)	0.001	0.003
Lithium (mg/ℓ)	0.0043	0.0068
Magnesium (mg/ℓ)	34.60	3.22
Manganese (mg/ℓ)	0.064	0.048
Mercury (mg/ℓ)	0.0005	0.0000
Molybdenum (mg/ℓ)	0.030	0.030

Parameter	Quarry	River
Nickel (mg/ℓ)	0.001	0.002
Nitrogen, ammonia (mg/ℓ-N)	0.019	0.094
Nitrogen, nitrate (mg/ℓ-N)	0.07	0.76
Nitrogen, nitrite (mg/ℓ-N)	0.008	0.008
Nitrogen, total Kjeldahl (mg/ℓ-N)	0.12	0.40
Oil and grease (mg/ℓ)	0.1	0.5
pH (units)	8.00	7.42
Phenols (mg/ℓ)	<0.001	0.004
Phosphorus, condensed phosphate (mg/ℓ-P)	0.000	0.002
Phosphorus, organic phosphate (mg/ℓ-P)	0.004	0.016
Phosphorus, orthophosphate (mg/ℓ-P)	0.050	0.031
Phosphorus, total phosphate (mg/ℓ-P)	0.056	0.048
Potassium (mg/ℓ)	5.00	2.256
Selenium (mg/ℓ)	<0.001	<0.001
Silica, suspended (mg/ℓ-SiO_2)	0.38	0.46
Silica, total (mg/ℓ-SiO_2)	2.66	5.08
Silver (mg/ℓ)	<0.001	<0.001
Sodium (mg/ℓ)	13.82	20.72
Solids, total dissolved (mg/ℓ)	532	302
Solids, total suspended (mg/ℓ)	2.4	22.0
Solids, volatile (mg/ℓ)	76.0	56.6
Sulfates (mg/ℓ-SO_4)	282	51
Sulfides (mg/ℓ-$S^=$)	0.01	0.04
Titanium (mg/ℓ)	<0.001	<0.001
Turbidity (FTU)	3	39
Vanadium (mg/ℓ)	<0.001	<0.001
Zinc (mg/ℓ)	0.040	0.022

In one experiment both quarry water and Hudson River water were used. In the same experiment sub-lots of eggs incubated in both Hudson River water and quarry water were treated with an antibiotic to retard bacterial growth. The antibiotic dosage used was 50,000 I.U./liter Penicillin G plus 50 mg/liter Streptomycin sulfate.

Most prolarval and larval rearing experiments were performed using filtered Narragansett, Rhode Island, tap water. This water was drawn from a well and contained no chlorine. As development progressed the salinity in the rearing containers was increased by the admixture of 10 micron filtered sea water. The salinity was maintained below 8‰, which is well within the range encountered by young bass on their estuarine nursery grounds.

Constant temperature treatments of 12°, 15°, 18°, 21°, and 24°C were maintained throughout all experiments. Temperatures were maintained by keeping all rearing containers immersed in temperature controlled water baths. Haake (E-52) heater-thermoregulators operating against cooling coils were used to maintain the bath temperatures.

During egg incubation experiments temperatures were monitored every two hours. During larval rearing experiments, rearing container temperatures were monitored at least three times daily. A continuous record of each bath temperature was maintained using a Y.S.I. recording thermometer. Although the mean daily temperature closely approximated the design temperature, short-term temperature excursions of up to several degrees occurred during the time rearing containers were being inspected or cleaned. A record of water bath temperatures monitored for each design temperature throughout the study period is provided in Appendix A.

Dissolved oxygen, pH, ammonia, and salinity measurements were made regularly throughout these experiments. Dissolved oxygen was determined using a Y.S.I. D.O. probe, supplemented periodically with determinations using the azide-modification of the Winkler titration. The pH was measured using an Orion pH electrode. Ammonia was determined using a micro-modification of the indophenol technique of Solórzano (1969). Salinity measurements were made using an American Optical salinity refractometer. A record of water quality measurements is presented in Appendix A. With frequent water changes most of the water quality parameters changed insignificantly during the course of each experiment.

Experimental Procedures Using Eggs

Fertilized eggs were rinsed and stocked volumetrically into 4-liter glass beakers at a rate of 100 to 250 per liter. The beakers, which contained fresh hatchery water, were stocked and placed in constant temperature water baths within 15 minutes after fertilization. Each beaker was agitated with a stream of compressed air. This was sufficient to maintain the eggs in suspension and to maintain a dissolved oxygen level near the air saturation level. The water in each beaker was changed at least once a day with fresh hatchery water of the same temperature. Dead eggs were removed and counted. A sample of [illegible] live eggs was taken every two hours during the incubation period from each temperature treatment. Sampled live eggs were examined under the microscope and staged by visually comparing each with the photographs of a striped bass developmental series (Bayless, 1972) and with the staged drawings of Mansueti (1958). After examination, live samples were preserved in Stockard's solution for subsequent examination. The cumulative time since fertilization was recorded for each lot at each sampling.

Experimental Procedures Using Larvae

Lots 6 and 7 were the only groups of eggs which yielded a sufficient number of larvae to merit continued rearing through the prolarval and larval stages. Lots 8 and 9 were not incubated under controlled temperature conditions, but were hatched in 20-21°C quarry water in the Texas Instruments hatchery. They were obtained 2-3 hours after hatching had begun. Larvae in these lots were gradually transferred to the test temperatures where they remained through the rest of the experiments.

Larvae were stocked into 18 liter glass aquaria immersed in a temperature controlled water bath. A semi-static larval rearing system similar to that outlined by Houde (1973) was used in the experiments. Three-quarters of the volume of each rearing aquarium was exchanged each day. When the population in each container was reduced, water changes were made three time per week. Initial stocking densities ranged from 30 to 150 newly hatched larvae per liter. Dead larvae were removed and preserved as soon as they were observed. Uneaten food was removed daily with a pipette. Samples of live larvae were removed at regular intervals throughout the experiments. Both the frequency of sampling and the number of individuals in each sample were determined to a large extent by the number of larvae remaining in each temperature treatment population. In sampling each treatment an effort was made to bracket the size range present in each tank. Where the sample size was necessarily limited, attempts were made to sample the largest and smallest fish in each treatment as well as several "average sized" individuals. In addition to providing a better representation of the size of individuals in each treatment population this procedure prevented extreme size disparities which, in our experience, generally resulted in a high incidence

of cannibalism. If left unchecked, cannibalism can decimate a treatment population and shorten the observation period.

The rates of larval mortality in each treatment population are reported in Appendix B. The actual numbers of animals in each population at a given point in time, are recorded, as well as an estimate of the number of individuals that might have been present had none been removed in periodic samples. Where mortality rates between treatment populations are compared, the rate based on the estimated size of the population from which no samples had been removed was used. Estimated mortality rates, thus obtained, were unaffected by the cumulative number of individuals removed in samples, but contain the assumption that sampled individuals would have undergone no mortality had they remained in each population. Mortality estimates presented here should be interpreted in the light of these qualifications. Samples of larvae were preserved in 10% buffered formalin and measured to the nearest 0.1 millimeter using either an ocular micrometer or dial indicating caliper.

Feeding was initiated in each population when an examination of the samples of larvae revealed peristalsis and the presence of functional mouth parts. Newly hatched Artemia nauplii were provided as the only food source in all treatments until near the termination of observations. In certain later treatments frozen adult Artemia were fed to the remaining post-metamorphosis juveniles. Artemia nauplii were fed twice daily. In most cases nauplii remained from the previous feeding. Food was available at all times, although the food density varied between feedings.

Larval size at hatching was determined by either measuring larvae as close to hatching as possible, or by back-calculating to the time of hatching from a series of measurements made every few hours up to forty

hours after the time of 50% hatching. Growth in length during this period was essentially linear.

Larval dry weights were determined by drying to a constant weight in a vacuum desiccator at 80°C and weighing on a Cahn Gram electrobalance.

Other procedures used are discussed in the appropriate section.

Statistical Procedures

All statistical analyses were performed according to procedures prescribed by Snedecor and Cochrane (1967). Linear regression analysis was performed on untransformed data using the method of least squares. Calculations were performed using a programmable Monroe 1860 statistical calculator. As part of the linear regression package, a correlation coefficient (r) was provided as a measure of the degree to which the data in question could be approximated by a straight line. An (r) value of 1.0 denotes perfect fit. Linear regression equations are presented in the form:

$$y = bx + a$$

where: y = dependent variable; most often stage duration, mortality or length in this study,

a = y intercept,

b = slope of regression line,

x = independent variable; most often time or temperature in this study.

Where growth is approximated using an exponential equation, length was transformed to $\log_{10}$. The transformed variable was regressed against time using linear regression techniques yielding a regression equation of the form:

$$\text{Log}_{10} \text{ length} = bx + a.$$

Time to hatching as a function of temperature is expressed in the form:

$$T_h = ae^b,$$

where T_h = time to hatching in hours,
a = y-intercept of regression equation,
b = slope of regression equation,
e = base of natural logarithms.

Life Stage Definition

Three major developmental stages have been recognized within the period between fertilization and the attainment of essentially adult form. The egg or incubation stage begins at fertilization and ends at hatching when the embryo loses its protective chorion. The prolarval period or yolk sac stage extends from hatching until the young fish changes from an endogenous to an exogenous food source. The larval period begins when the prolarva has consumed all of its yolk and lasts until metamorphosis. At this time the fish has attained the full fin ray complement and characteristic silhouette of the adult fish.

Life Stage	Stage Demarcation Point
	fertilization
egg	
	hatching
prolarva	
	yolk absorption
postlarva	
	metamorphosis

Of the four major developmental landmarks, fertilization and hatching are most discrete. The exact time of yolk sac absorption and metamorphosis are more difficult to measure precisely.

Fertilization is assumed to have occurred at the time milt and eggs were mixed at the hatchery. Of all developmental landmarks used here, the timing of fertilization can be determined with greatest

precision. In practice, it is impossible to determine whether fertilization has occurred until the eggs are examined for cleavage several hours after spawning. Where large numbers of eggs are involved, the first sign of incomplete fertilization is the appearance of opaque, dead eggs 10 to 24 hours after spawning. The percentage of eggs that are fertilized varies between matings.

In following the time-course of developmental events between fertilization and hatching at different temperatures, we noted the developmental stages of eggs in samples taken every two hours, then compared these to the photographs of a developmental series provided by Bayless (1972). Bayless' hour-by-hour series permitted us to express the developmental stages we observed at each temperature in terms of equivalent hours of development at 19°C, the temperature at which his observations were made. In Figure 1, observed hours of development at five temperatures have been plotted against equivalent hours of development at 19°C. Development time in hours after fertilization was accurate to a few minutes and was considered to qualify as an independent variable. Least-squares regression lines applied to these observations at each temperature fitted the data well. They indicated not more than one '19°C-hour of development' error in staging eggs at each temperature. Correlation coefficients on the regression of equivalent 19°C-hours of development on observed hours after fertilization ranged from $r = 0.987$ to $r = 0.997$ ($N = 13$-15). Within ten hours after fertilization equivalent stages were difficult to identify. The failure of regression lines for development at 12° and 15°C to extrapolate to zero hours of equivalent and observed development suggest that this approach is not applicable during the early hours after fertilization.

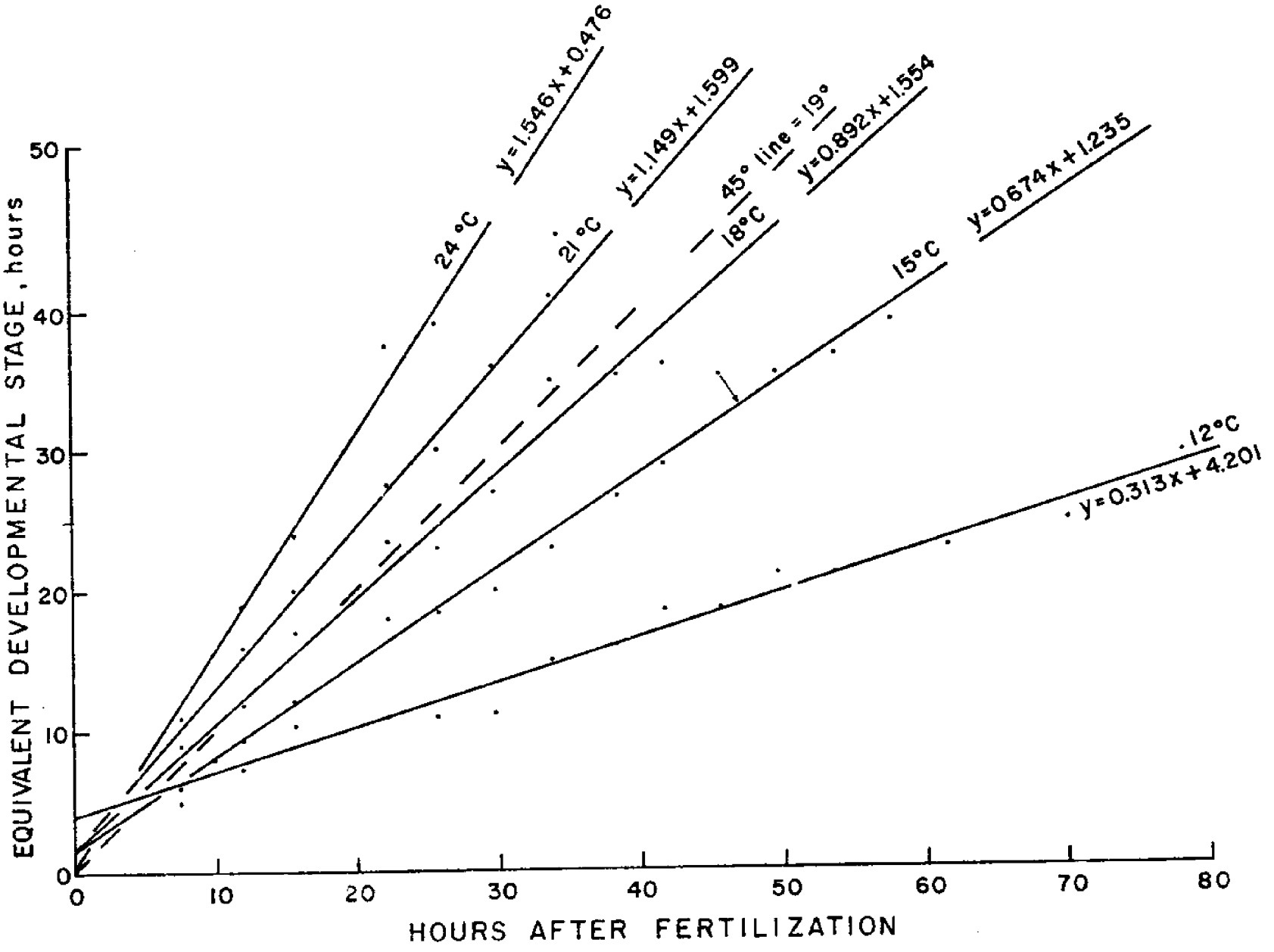

Figure 1

The regression of hours of embryonic development observed in this study at five experimental temperatures against those observed by Bayless (1972) at 19°C for the attainment of equivalent levels of structural development.

By connecting points representing the time of attainment of several readily identifiable developmental stages at each temperature (Figure 1), incubation temperature was related to the time since fertilization at which each stage was reached (Figure 4). Figure 4 was drawn by eye using data obtained from Figure 1.

Hatching occurs when the embryo emerges from its chorion. A group of eggs fertilized at the same time did not necessarily hatch at the same time; the hatching process may last several hours. The estimated time at which 50% of a group of eggs had hatched was used to mark the end of the egg stage in this study. It was impossible to maintain an accurate cumulative count of emerging larvae within each culture container once hatching had begun. Although hatching is a relatively discrete event, the assignment of a time of hatching was necessarily somewhat arbitrary.

The end of the prolarval or yolk sac stage is less easily determined. The functional definition of the end of the yolk sac stage (i.e., the change to active feeding from passive yolk absorption) is difficult to determine from a specimen in hand. Feeding typically begins before all yolk has been absorbed and well before the oil globule disappears. For those reasons a structural definition of the end of the yolk sac stage was determined. In addition, the use of anatomical characters, where possible, rather than behavioral or nutritional criteria to separate life stages, was reasoned to provide the best basis for comparing laboratory stage duration estimates with those derived from field studies using preserved larvae obtained in plankton hauls. A number of larvae which appeared to have consumed nearly all their yolk were examined using Mansueti's (1958) figure #21 as a model (Figure 2). The mean total

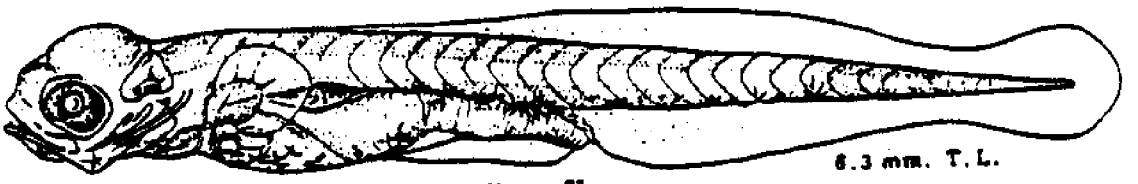

Figure 21

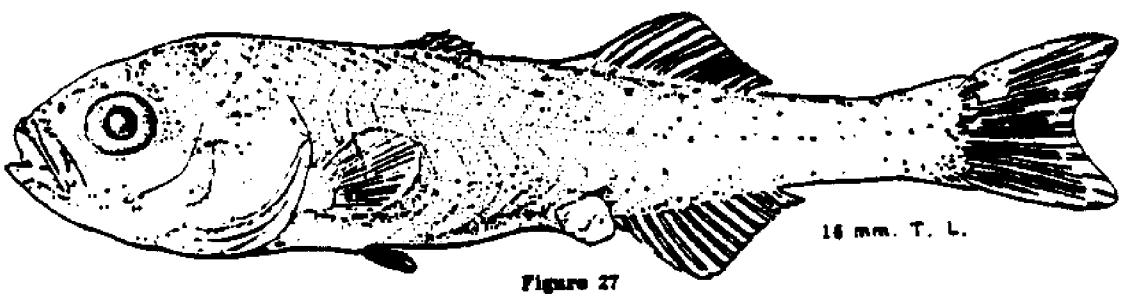

Figure 27

Figure 2. Drawings from Mansueti (1958) illustrating larva at yolk sac absorption (Fig. 21) and larva near metamorphosis (Fig. 27).

length of a sample of 32 larvae judged to have just absorbed all their yolk was 5.84 mm ± one standard deviation of 0.54 mm.

To help confirm the validity of this approach total lengths and yolk lengths of a series of prolarvae approaching yolk absorption were measured. Figure 3A shows plotted yolk length as percent of total length against total length. As complete absorption was approached the regression line approached 0% at a length of 6.2 mm. This was close to an estimate of 5.8 mm based on direct examination. Based on these considerations a length range of from 5.30 mm to 6.39 mm (5.84 ± one standard deviation) was adopted as being typical of the size at which most of the larvae had absorbed all of their yolk and graduated from prolarval to postlarval status. In Figure 3B are plotted similar measurements from Mansueti (1958) for prolarvae of either Patuxent or Roanoke River stock. These appear to be somewhat larger at yolk absorption than the Hudson River fish used in this study.

Where there is a smooth transition from yolk nutrition to live food, growth in length should increase without interruption. However, there may be a period of adjustment during which early larvae perfect their abilities to capture and consume the food organisms which are offered them. This adjustment to exogenous food is particularly evident in laboratory and hatchery populations where the food that is offered is of a type unlike that to which they may have been adapted in their wild existence. Once all yolk is consumed all maintenance requirements must be met through active feeding or else larval tissues already laid down will be consumed, resulting in suspended or reduced growth or even some shrinkage in total body length. For shrinkage to occur it is clear that all yolk must already have been consumed. As a result, the

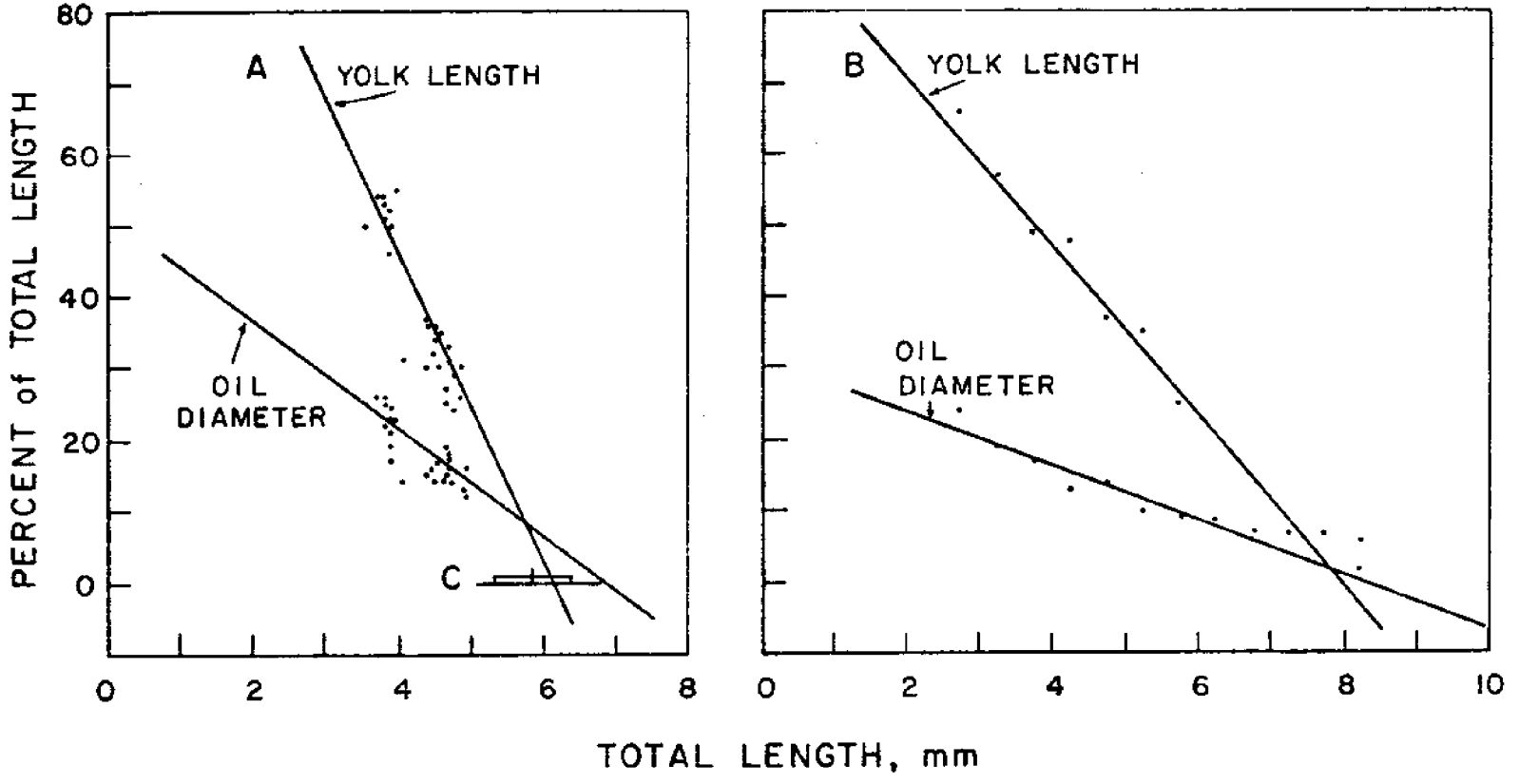

Figure 3. The determination of total length at yolk sac absorption from the regression of yolk length as a percent of total length (y) against total length (x). A. Observations on Hudson River prolarvae for which y = -21.885 x +133.759 (r = -0.900). B. Data from Mansueti (1958) for Chesapeake or Roanoke stocks for which y = -11.909 x +94.916 (r = -0.968). C. Range and mean ± one standard deviation of prolarvae measured at the point of complete yolk absorption.

occurrence of reduced or negative growth in laboratory populations at the point where yolk absorption might be expected to occur was considered evidence that all yolk has been consumed and that the yolk sac stage was complete. To mark the end of the yolk sac stage, then, two alternate criteria were used: 1) the attainment of a total length of 5.84 mm ± one standard deviation (i.e., 5.30 to 6.39 mm) or; 2) the occurrence of a length maximum followed by a period of reduced or negative growth beginning at the point on the growth curve at which yolk absorption might be expected to occur.

Like yolk absorption, the point at which metamorphosis occurs is difficult to define. Fully metamorphosed striped bass resemble Mansueti's (1958) figure #28. The lateral silhouette is essentially that of the adult. The first dorsal is not fully developed and pigmented, but all bony meristic characteristics have attained their adult complement. While the fully metamorphosed fish is easy to recognize, the point of transition to this state is less distinct. As a working standard for a striped bass at metamorphosis a fish which resembled Mansueti's figure #27 (Figure 2) was chosen. While the juvenile in this drawing has not quite reached full metamorphosis, it is easy to recognize in the preserved state. In cleared and stained specimens the full adult number of fin rays is evident. The average total length of a sample of 35 figure #27 juveniles was 16.32 mm ± one standard deviation of 1.33 mm. In this study the time to the attainment of a total length of from 14.90 mm to 17.60 mm (16.32 ± one standard deviation) from the time of yolk absorption was used as a measure of the duration of the larval stage.

Efforts were made to define the prolarval and larval stages in terms of the range in lengths attained by individuals in laboratory

populations maintained under specified temperature conditions. The duration of each stage was determined from empirical growth curves constructed for each treatment population. Because the length at the point of transition between stages was defined by a length interval rather than a fixed length, the duration of each life stage in each treatment population is expressed as a range in time units (Table 4, 7) corresponding to the shortest and longest expected duration for the stage in question.

RESULTS

Developmental Events Prior to Hatching

Increased incubation temperature decreased the time between fertilization and the achievement of four developmental stages prior to hatching (Figure 4). From 15° through 24°C the decrease in development time to each stage was approximately linear with temperature. The attainment of stages early in development was accelerated by higher incubation temperatures to a greater degree than events closer to hatching. This is evident from the clearly steeper slope for the attainment of one-half yolk envelopment by blastoderm (Figure 4a) than for free tail bud stage (Figure 4d). The over-all development time-temperature relationship for each stage was curvilinear with the greatest inflection between 12° and 15°C. Twelve degrees C is a marginal temperature for incubation. Below 12°C incubation time appears to become infinite.

The Incubation Period (Fertilization to Hatching)

Eight observations were made on the effect of temperature on the time from fertilization to hatching. The data have been plotted with that of other workers in Figure 5. This information is presented in tabular form in Table 3. Observations made during the course of this study fit well with earlier published observations. The incubation period vs. temperature relationship is curvilinear and fitted by an exponential curve with the equation

$$\text{Time to hatching (hrs.)} = 258.5e^{-0.0934\ \text{temp.}(^{\circ}C)}$$

with correlation coefficient (r) = 0.93, (N = 42).

The degree of curvilinearity is determined predominantly by terminal observations. Between 15° and 24°C, the range over which incubation

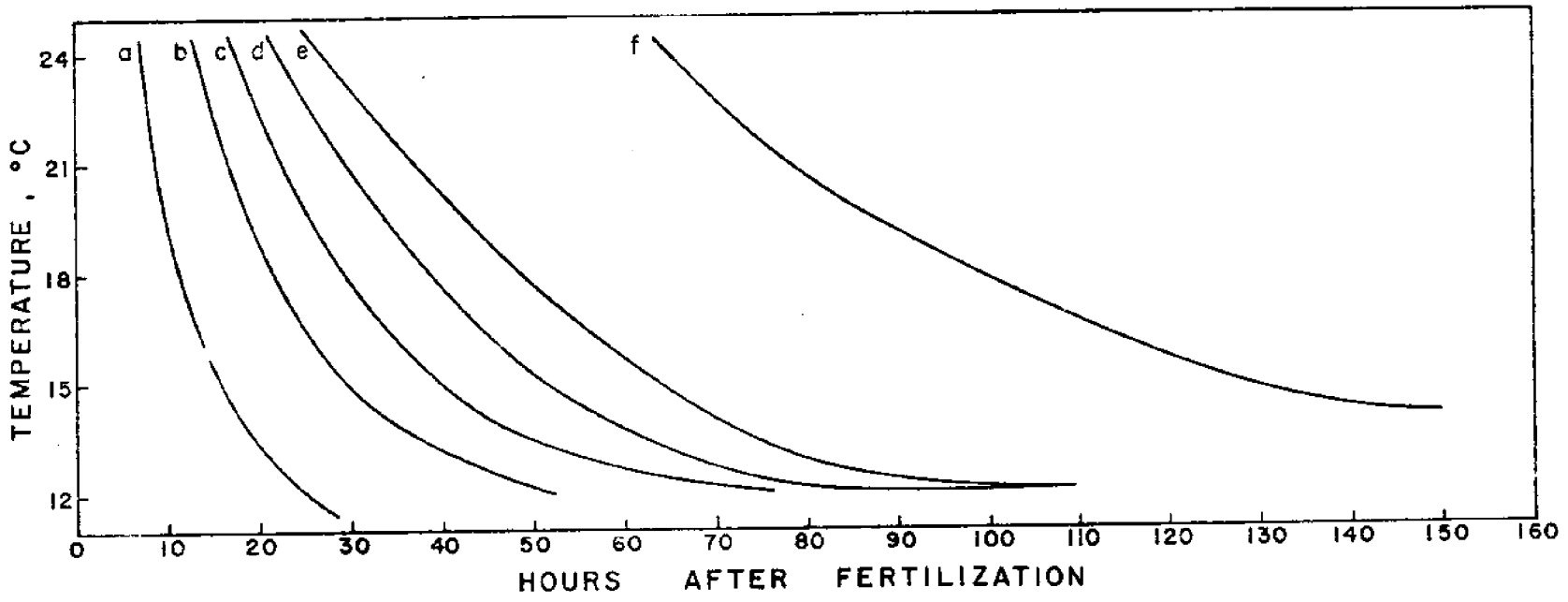

Figure 4A. The effect of incubation temperature on the time from fertilization to selected developmental stages before and after hatching.

a - half of yolk enveloped by blastoderm
b - embryo extending over half of yolk curvature
c - early tail development
d - free tail bud
e - hatching
f - development of eye pigmentation in prolarva

See figure 4B.

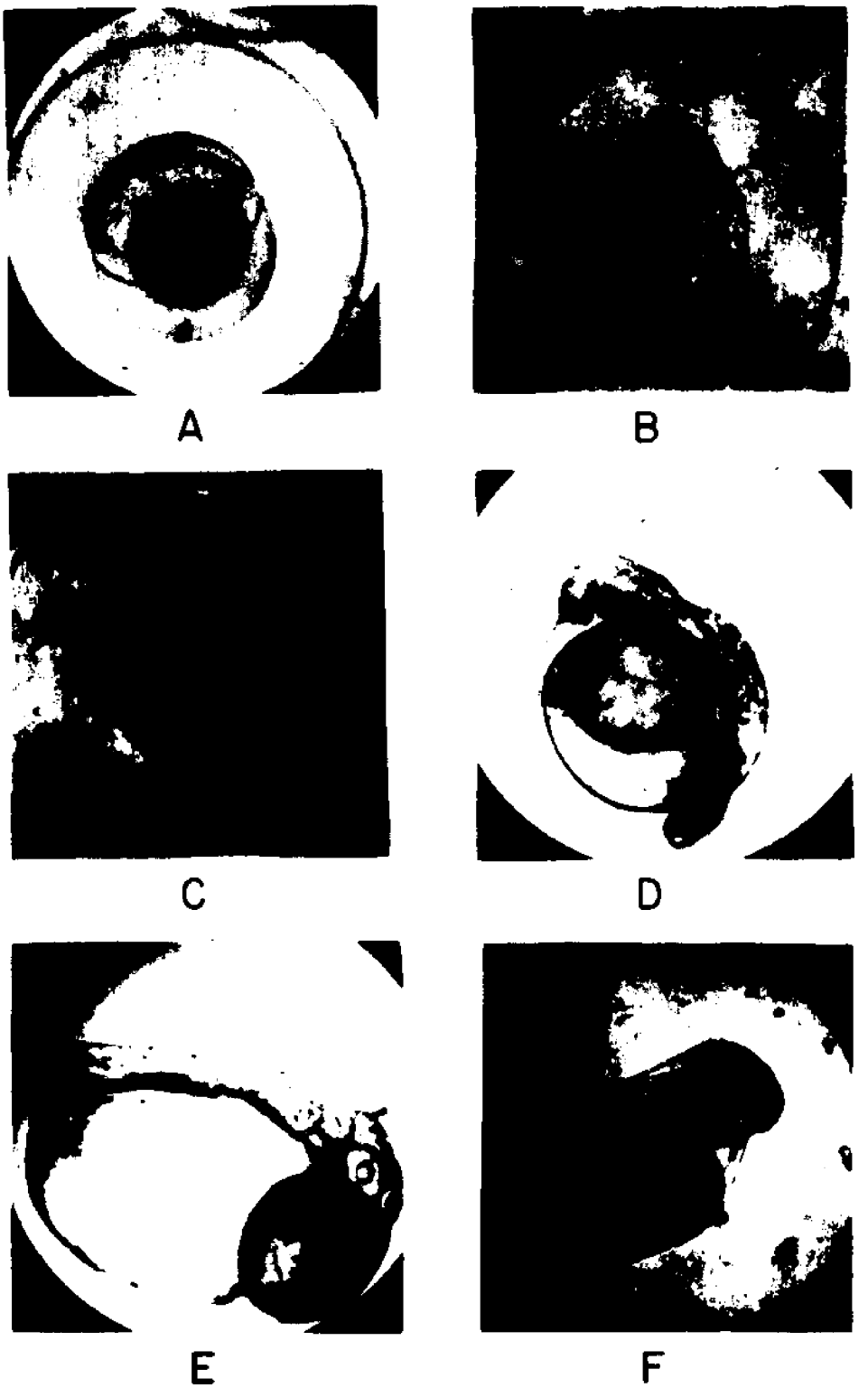

Figure 4B. Illustration of developmental stages described in Figure 4A. Original photographs from Bayless (1972).

TABLE 3

Hatching time of striped bass eggs in relation to water temperatures.

Incubation Time (hours)	Water Temperature (°C)	Location	Author
25	26.67	N.C.	Shannon and Smith (1967)
25.8	24.00	N.Y.	Present study
28	23.89	N.C.	Shannon and Smith (1967)
28.5	24.00	N.Y.	Present study
30	23.33	N.C.	Shannon and Smith (1967)
30	23.33	S.C.	Bayless (1972)
30	21.7-22.2	N.C.	Bigelow and Schroeder (1953)
30	21.7-22.2	-	Merriman (1941)
33	21.11	S.C.	Stevens (1965)
33	21.1	N.C.	Regan et al. (1968)
34	21.11	N.C.	Shannon and Smith (1967)
35	22.22	S.C.	Bayless (1972)
36	21.67	N.C.	Worth (1884)
37	21.00	N.Y.	Present study
36-48	17.22	N.C.	Mansueti (1958)
38	19.4	N.C.	Regan et al. (1968)
38	21.11	S.C.	Bayless (1972)
40	20.00	S.C.	Bayless (1972)
43	18.3	N.C.	Regan et al. (1968)
44	18.33	S.C.	Stevens (1965)
44	18.89	S.C.	Bayless (1972)
48	19.4	N.C.	Bigelow and Schroeder (1953)
48	18.33	S.C.	Bayless (1972)
48	17.2	N.C.	Regan et al. (1968)
48	17.89	-	Pearson (1938)
48	18.89-19.44	N.C.	Worth (1882)
50	15.6	N.C.	Regan et al. (1968)
50	17.78	S.C.	Bayless (1972)
51.8	18.00	N.Y.	Present study
54	14.4	N.C.	Regan et al. (1968)

Table 3 (cont'd.)

Incubation Time (hours)	Water Temperature (°C)	Location	Author
56	16.67	S.C.	Bayless (1972)
58	15.56	N.C.	Shannon and Smith (1967)
62	15.00	N.Y.	Present study
62	15.56	S C.	Bayless (1972)
66.3	18.00	N Y.	Present study
70	15.56	S.C.	Stevens (1965)
70-74	14.4-15.6	N.C.	Bigelow and Schroeder (1953)
74.3	15.00	N.Y.	Present study
74	14.4-15.6	-	Merriman (1941)
74	14.44	Md.,Va.	Brice (1898)
91.8	15.00	N.Y.	Present study
109	12.00	N.Y.	Present study

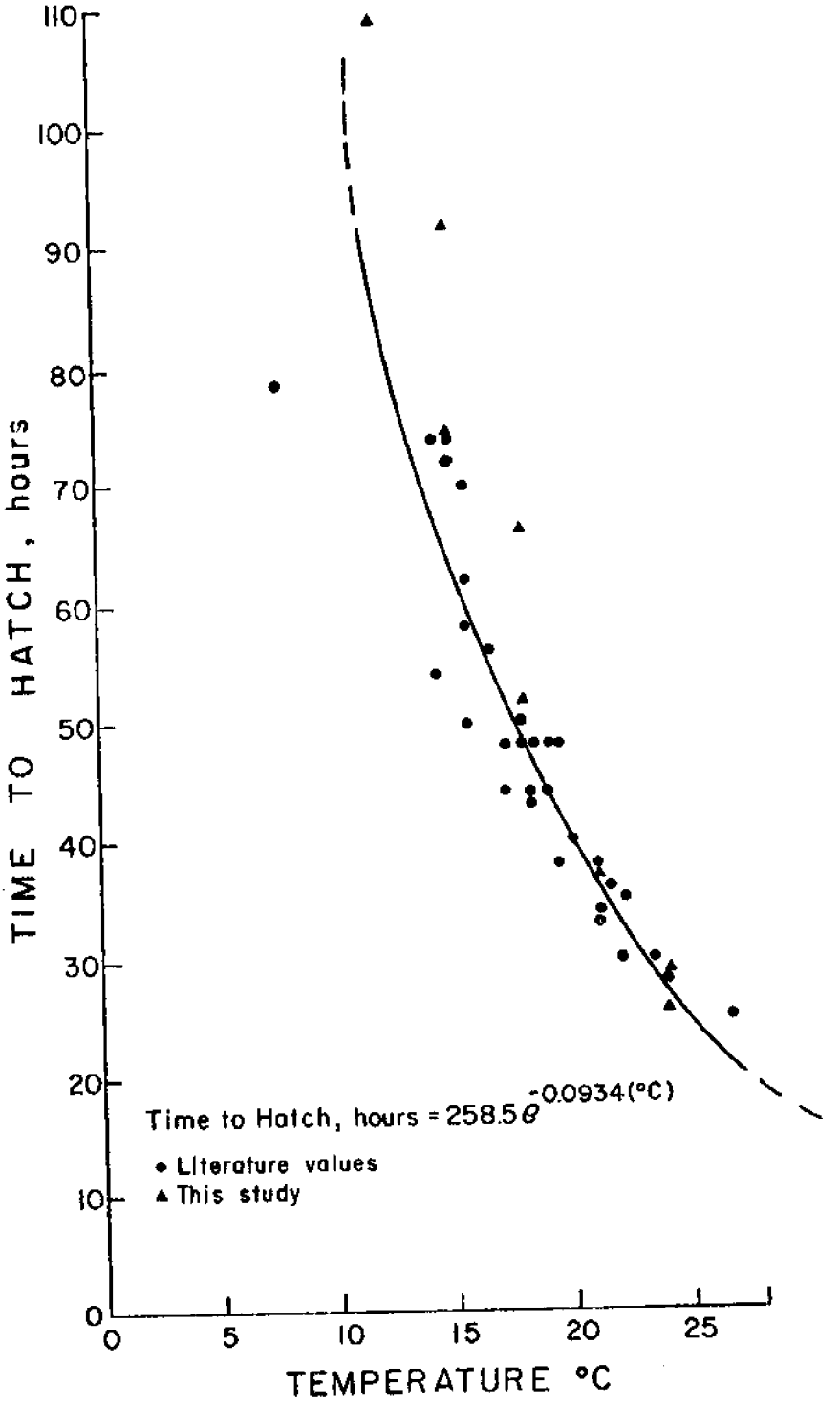

Figure 5. The effect of temperature on the incubation period of striped bass eggs based on observations listed in Table 3.

most often occurs, incubation time can be predicted as a linear function of temperature by the regression equation:

Time to hatching (hrs.) = -4.616 (Temp.°C) + 134.310,

with correlation coefficient (r) = 0.878, (N = 36).

Incubation time is reduced approximately 4.62 hours for each increase of 1°C in incubation temperature between 15° and 24°C. The dotted portions of Figure 5 mark incipiently lethal temperatures and define the limits of utility of this relationship.

Mortality during the incubation period ranged from 30 to 100 percent in our experiments. Egg mortalities appeared to vary in extent between lots. Highest survival occurred in 15-18°C temperature treatments. Extremely low survival among lots 1-3 at all temperatures led to varying the water source and to the use of antibiotic treatments in lot 5. The results of this experiment are presented below.

Percent Survival

	Hudson River Water		Quarry Water	
	with antibiotic	no antibiotic	with antibiotic	no antibiotic
15°C	70.6 n=930	2.1 n=529	0 n=563	0.6 n=508
18°C	62.5 n=1041	7.3 n=975	3.2 n=836	3.3 n=839

The use of Hudson River water in combination with antibiotic treatments clearly improved egg survival to hatching in this lot. The use of quarry water was continued in lots 6 and 7, but all experimental containers were treated with antibiotics. Survival in these lots was improved, with 50% or higher survival at 15° and 18°C in both lots and 76% survival in lot 7 at 21°C. Eggs incubated at 12°C seldom survived to hatching. In all the lots used, only four live larvae hatched at 12°C. Survival at 21°C and 24°C varied from lot to lot but was lower than at 15°C and 18°C.

The Yolk Sac Stage

Growth during the yolk sac stage was characterized by a period of rapid, essentially linear, growth during the first two to three days after hatching. This period of rapid increase in length occurred among larvae reared at all temperatures. There followed a reduction in the rate of increase in length, which in most experiments culminated in a growth plateau from three to eleven days after hatching. Observations of larvae in each experimental treatment clearly linked this marked reduction in the rate of larval growth with the consumption of the last of the larval yolk reserves. The pattern of growth observed, a rapid increase in length followed by a cessation of growth at yolk absorption, was characteristic of growth at all temperatures. Rearing temperature affected the rate at which the plateau was attained and there were indications that it also affected the length at which the length plateau occurred. Records of larval growth in each treatment are presented in Appendix B.

The use of a particular length range as a datum to mark the attainment of yolk absorption proved unsuccessful. In nearly all treatments a length maximum was reached beyond which some shrinkage or suspended growth occurred. The mean length of larvae in samples taken at or near this first length maximum, when it occurred, was generally lower than the mean length that had been established earlier to be characteristic of larvae at the point of yolk absorption, and was frequently closer to this mean length less one standard deviation.

Among early prolarvae, growth in length could only occur as a result of the consumption of stored yolk. Any reduced growth or shrinkage in length revealed in samples of larvae removed from each treatment population must have occurred after all of the yolk reserves had been

consumed. For this reason the maximum length achieved before any period of shrinkage was used to mark the point of complete yolk absorption. The duration of the yolk sac stage was defined by the time between hatching and the attainment of a length maximum which preceeded periods of reduced or negative growth within the first two weeks of larval life. The time in days between hatching and yolk absorption, thus defined, for each experimental lot and treatment temperature are summarized in Table 4. Although there was considerable variation between test lots, there was an increase in the duration of the yolk sac stage with decreasing temperature. The mean observed time between hatching and yolk absorption was 3.8, 5.1, 7.75, 8.3 and 9.0 days at 24°, 21°, 18°, 15°, and 12°C, respectively (Figure 7). The mean length at yolk absorption, marked by the attainment of a first length maximum, was highest (5.7 mm) at 18°C. At lower and higher temperature treatments larvae which had absorbed all of their yolk were shorter. Here again, variation between lots was great.

Mortality During the Yolk Sac Stage

Mortality was high in all lots during the yolk sac stage. Mortality records for each lot and temperature treatment are presented in Appendix B. The time-cumulative mortality relationship typically had the sigmoid shape characteristic of a dose-response curve. The maximum daily mortality occurred three to six days after hatching at 24° and 21°C, and eight to twenty days after hatching at 18°, 15°, and 12°C. The sigmoid portion of the time-mortality relationship typically lasted four to twelve days at 24°C, five to sixteen days at 12°C, sixteen to twenty-one days at 18°C, and twenty to forty days after hatching at 15°C. From 60 to 90% of each larval population died during this period. No clear relation between rearing temperature and the overall extent of

TABLE 4

Duration of the yolk sac stage for prolarvae held at five temperatures.

Temperature	Lot	Stage Duration Based on the Attainment of Length of 5.3 mm (5.85-1 std. dev.) (Days)	Stage Duration Based on the Attainment of Maximum Mean Length Before Cessation of Growth (Days)	Maximum Mean Length Attained (mm)	Stage Duration Based on the Attainment of Mean Length of 5.85 mm (Days)
24°C	6	1.75	3.5	5.65	NA*
	8	4.0	4.0	5.30	NA
	9	4.0	4.0	5.30	NA
	Mean	3.25	3.8	5.386	
21°C	7	3.0	2.3	5.047	NA
	8	2.4	6.0	5.90	NA
	9	5.0	7.0	5.48	NA
	Mean	3.47	5.1	5.475	
18°C	6	2.0	9.0	5.88	NA
	7	3.0	6.0	5.58	NA
	8	3.0	9.0	6.012	6.0
	9	6.2	7.0	5.395	NA
	Mean	3.55	7.75	5.709	
15°C	7	5.0	9.0	5.57	NA
	8	4.8	11.0	5.59	NA
	9	NA	5.0	5.20	NA
	Mean	4.9	8.3	5.45	
12°C	8	NA	11.0	5.52	NA
	9	NA	7.0	5.28	NA
	Mean		9.0	5.40	

* NA = not applicable

losses was evident. Table 5 summarizes observations on the time course of mortality during the yolk sac stage in all temperature treatments and experimental lots. By the time yolk absorption has been completed in each group somewhat less than half of the population alive at hatching had died in most cases.

Between lots at each temperature treatment, there were wide variations in the percent mortality that had occurred by the end of the yolk sac stage. The day after hatching in which the greatest single mortality occurred closely coincided with the completion of yolk absorption at 24°, 21° and 18°C. At the two lower temperatures used, yolk absorption was completed well before the period of maximum mortality took place. The percent of the total mortality that occurred per day was greatest at higher temperatures where total stage duration was short. At lower temperatures the daily percentage loss decreased. Both stage duration and the period of maximum daily mortality were protracted at lower temperatures.

The Larval Stage (Yolk Sac Absorption Through Metamorphosis)

In the majority of the lots observed, the beginning of the larval stage was marked by a period of shrinkage in length or of suspended growth. In some populations the mean length of larvae decreased or fluctuated from sample to sample for periods of up to three weeks. In other lots the mean length of larvae revealed in regular samples remained essentially unchanged for a week or more. The duration of the period of negative or suspended growth was shortest at higher temperatures and proportionally longer in the lower temperature treatments.

In all populations except those at 12°C, the growth plateau ultimately came to an end and growth in length increased rapidly at a rate

TABLE 5

Mortality during the yolk sac stage at five temperatures.

Temperature	Lot	Days to Yolk Absorption	Day After Hatching When Greatest Mortality Occurred	Percent of Original Population Dead by Yolk Absorption (%)	Percent Mortality Per Day During Yolk Sac Stage (%)
24°C	6	3.5	5.0	6.0	1.7
	8	4.0	4.0	84.0	21.0
	9	4.0	3.0	59.0	14.75
	Mean	3.8	4.0	49.66	12.48
21°C	7	2.3	4.0	11.0	4.7
	8	6.0	5.0	37.0	6.16
	9	7.0	4.0	65.0	9.28
	Mean	5.1	4.3	37.66	6.71
18°C	6	9.0	-	43.0	4.7
	7	6.0	5.0	30.0	5.0
	8	9.0	9.0	66.0	7.3
	9	7.0	6.0	40.0	5.7
	Mean	7.75	7.0	44.75	5.6
15°C	7	9.0	12.0	35.0	3.88
	8	11.0	9.0	52.0	4.73
	9	5.0	21.0	1.0	0.20
	Mean	8.3	14.0	29.33	2.9
12°C	8	11.0	9.0	66.0	6.0
	9	7.0	27.0	10.0	1.4
	Mean	9.0	18.0	38.0	3.7

closely associated with the rearing temperature. Lots held at 12°C survived up to a month after hatching but never recovered from the period of suspended growth that followed yolk absorption, and were never observed to feed. From the growth plateau through metamorphosis the rate of growth in length followed an exponential pattern. Although at 24°C there is considerable between-lot variability (see Table 6), the mean (between-lot) exponential growth equation slope at each temperature appears to increase at higher rearing temperatures (Figure 6):

$$\text{slope } (\times 10^3) = 2.4 \text{ (temp.°C)} - 27.966$$
$$4 = 0.728 \text{ (n = 4)}.$$

The time between hatching and the end of the larval stage at metamorphosis is summarized in Table 7. The use of a length standard to define the end of the larval stage worked well. The time to metamorphosis increased with decreasing temperature; however, a variable portion of that period was made up of the growth plateau that occurred in most populations. The fact that the duration of the period of suspended growth was itself, in most instances, apparently temperature related helped maintain the relationship between the time between yolk absorption and metamorphosis and rearing temperature. The duration of the larval stage alone for each lot and temperature treatment is presented in Table 8. Here the duration of the yolk sac stage has been subtracted from the observed time between hatching and metamorphosis. Mean larval stage duration at each temperature is summarized in Figure 7.

Mortality During the Larval Stage

The rate of mortality that took place through the course of these rearing experiments was high during the yolk sac and early larval stages. However, after the sigmoid portion of the mortality curves had taken

TABLE 6

Total length versus days after hatching. Regression equations for larvae between yolk-sac absorption and metamorphosis where:
y = total length (mm) (sample mean)
x = days after hatching
r = correlation coefficient.

Temperature and Lot		Yolk Sac Absorption Through Metamorphosis	
24°C	Lot 6	$\log_{10} y = 0.017x + 0.662$	r = 0.938
	8	$\log_{10} y = 0.018x + 0.643$	r = 0.971
	9	$\log_{10} y = 0.048x + 0.089$	r = 0.983
21°C	Lot 7	$\log_{10} y = 0.024x + 0.491$	r = 0.928
	8	$\log_{10} y = 0.024x + 0.496$	r = 0.960
	9	$\log_{10} y = 0.028x + 0.352$	r = 0.998
18°C	Lot 7	$\log_{10} y = 0.017x + 0.504$	r = 0.979
	8	$\log_{10} y = 0.012x + 0.672$	r = 0.961
	9	$\log_{10} y = 0.017x + 0.472$	r = 0.984
15°C	Lot 7	$\log_{10} y = 0.007x + 0.679$	r = 0.977
	8	$\log_{10} y = 0.007x + 0.652$	r = 0.989
	9	$\log_{10} y = 0.007x + 0.565$	r = 0.994

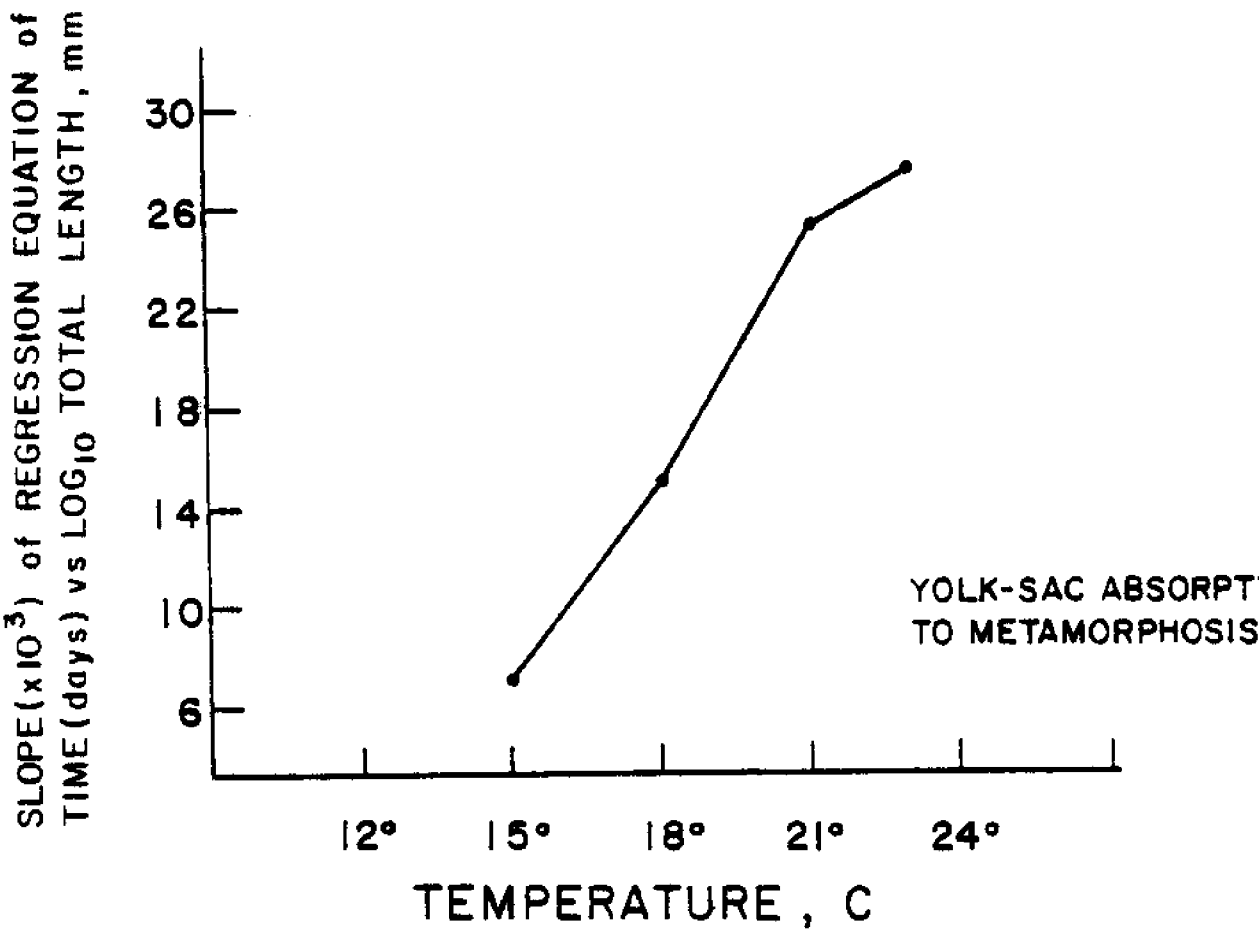

Figure 6. The effect of temperature on the mean slope, b ($x10^3$) of the regression equations of total length against days since hatching for growth between yolk sac absorption and metamorphosis. The regression equations were in the form $\log_{10}$ length = b(days) + a (see Table 6).

TABLE 7

The range in time (days) from hatching to the attainment of adult fin-ray complement based on a mean total length of 16.32 mm at metamorphosis ± one standard deviation (SD) of 1.33 mm, at four rearing temperatures.

Temperature	Lot	-1 SD (16.32-1.33) 14.99 mm	Days to Mean Total Length at Metamorphosis 16.32 mm	+1 SD (16.32+1.33) 17.65 mm
24°C	6	26.0	28.0	29.0
	8	27.0	28.0	29.0
	9	23.0	23.5	24.0
	Mean	25.3	26.5	27.3
21°C	7	26.0	28.0	30.5
	8	28.0	28.5	31.0
	9	29.0	30.5	31.5
	Mean	27.6	29.0	31.0
18°C	7	36.0	40.0	44.0
	8	38.0	40.5	43.0
	9	38.0	41.0	44.0
	Mean	37.3	40.5	43.6
15°C	7	66.0	73.0*	82.0*
	8	66.0	70.0*	74.0*
	9	81.0	85.0*	90.0*
	Mean	71.0	76.0*	82.0*

* Estimates from fitted growth curve - no larvae attained this size.

TABLE 8

The effect of temperature on the duration of the larval stage (yolk absorption through metamorphosis).

Temperature	Lot	Hatching to Metamorphosis (Days) A	Duration of Yolk Sac Stage (Days) B		Duration of Larval Stage (Days) A-B
24°C	6	28.0	3.5		24.5
	8	28.0	4.0		24.0
	9	23.5	4.0		19.5
				Mean	22.66
21°C	7	28.0	2.3		25.7
	8	28.5	6.0		22.5
	9	30.5	7.0		23.5
				Mean	23.9
18°C	7	40.0	6.0		34.0
	8	40.0	9.0		31.0
	9	41.0	7.0		34.0
				Mean	33.0
15°C	7	73.0*	9.0		64.0*
	8	70.0*	11.0		59.0*
	9	85.0*	5.0		80.0*
				Mean	67.66

* Estimated from fitted growth curve - no larvae attained this size.

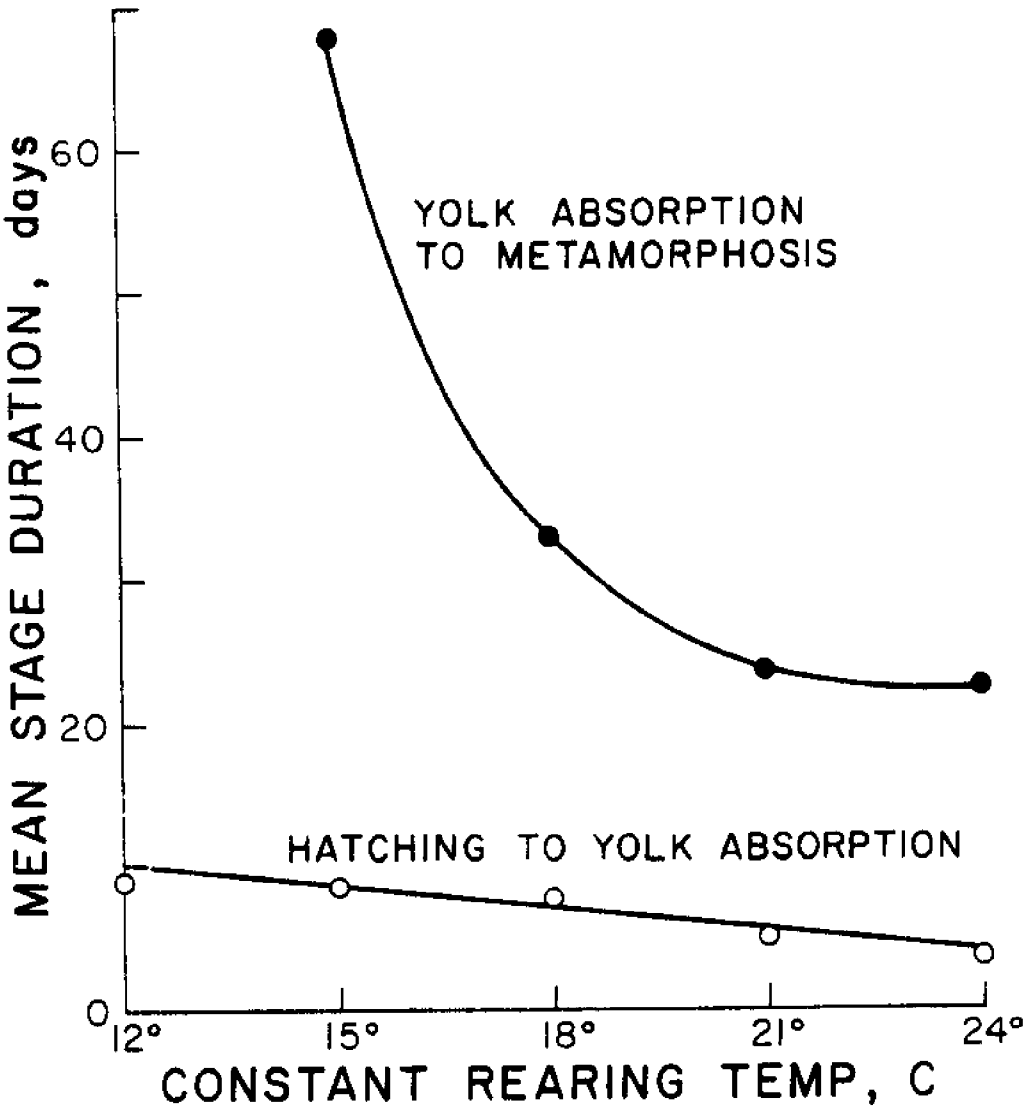

Figure 7. The effect of rearing temperature on the duration of the yolk sac and larval stages of striped bass. Each point represents the mean of at least three stage duration observations at each temperature treatment.

place relatively little additional mortality occurred (Appendix B). By the time metamorphosis had taken place an average of from 75 to 85% of the individuals originally present in each treatment population had died (Table 9). During this period the removal of individuals for growth measurements became the major source of mortality. Sampling mortality was not included in mortality estimates through metamorphosis. Overall and daily mortality rates through metamorphosis were higher in groups reared at 24°C. Estimated losses through metamorphosis and estimated percentage losses per day were lower at 21° and 18°C than at 24°C, and both estimates decreased slightly with decreasing temperature. No larvae survived through metamorphosis at 15°C. Removal of larvae in regular length determination samples depleted all of these populations by the time metamorphosis was near.

Most of the deaths that occurred within the larval stage occurred immediately following yolk absorption. The exceptions occurred predominantly at 15°C.

TABLE 9

Mortality during the larval stage at four temperatures.

Temperature	Lot	Larval Stage Duration (Days)	Percent of Population Alive at Hatching that Had Died by Yolk Absorption (%)	Estimated Percent of Original Population That Had Died by Metamorphosis (%)	Estimated Percent Mortality Per Day During Larval Stage (%)
24°C	6	24.5	6	77	2.89
	8	24.0	84	92	0.33
	9	19.5	59	85	1.33
	Mean			84.6	1.5
21°C	7	25.7	11	75	2.49
	8	22.5	37	67	1.34
	9	23.5	65	89	1.02
	Mean			77	1.6
18°C	7	24.0	30	68	1.117
	8	31.0	66	86	0.64
	9	34.0	40	76	1.06
	Mean			76.6	0.75
15°C	7	64.0*	35	100	
	8	59.0*	52	100	
	9	80.0*	1	100	

* Estimated from fitted growth curve - no larvae attained this size.

DISCUSSION

Development Through Hatching

The effect of temperature on the incubation time of striped bass eggs has been reported by a number of workers (see references in Table 3). In this study these published observations have been supplemented, particularly at lower incubation temperatures. Our data fall among points determined by other authors.

The exponential equation used to describe all of the available temperature-incubation time data for striped bass (Figure 5) is similar in form to the same relationship for other species (Blaxter, 1969; Lasker, 1964; Alderdice and Forrester, 1968). Most of the scatter of points around this regression line may be explained by the use of different hatching criteria by various authors. For example, the time of 50% hatching was used in this study while Bayless (1972) used the time of first observed hatching.

The time course of events prior to hatching is related to temperature in much the same way as is the length of the incubation period as a whole. Figure 4 is very similar to the same relationship for the garfish, Belone (Fonds et al., 1974). A marked increase in the rate of development occurs between 12° and 15°C. Morgan and Rasin (1973) noted a similar rate increase between 13.5° and 16°C in striped bass eggs from upper Chesapeake Bay, but noted no significant effect of temperature on the developmental rate between 16° and 27°C. The results of this study indicate that the rate of development increases continuously with temperature between 15° and 24°C at all stages. From Figures 4 and 5 it appears that below 12°C incubation time becomes infinite. Morgan and Rasin (1973) noted no successful hatching at 10.5° and 11°C. Eggs incubated at 12°C

in our experiments experienced a steady mortality throughout the incubation period, which in most cases depleted the treatment population before hatching had occurred. Hatching at 12°C was complicated by the occurrence of premature chorion loss and the appearance of living but immobile and clearly moribund prolarvae at the time hatching would have been expected to occur. While striped bass eggs are taken in the Hudson when river temperatures are below 10°C (Carlson and McCann, 1969), it is doubtful that successful development occurs at temperatures of 12°C or less.

Hatching occurred successfully in our 24°C temperature treatment. Morgan and Rasin (1973) considered 23°C the upper end of the survival optimum for striped bass eggs in their study. They observed 100% mortality at 27°C. That 24°C is near the upper limit for successful development in striped bass is supported by the observations of Albrecht (1964) and Shannon (1970). The occurrence of temperature optima for the development of stages early in life are important in the consideration of stage duration, because rearing under optimum conditions permits a greater portion of the available nutritional resources to be used for growth. An early size advantage may be perpetuated into later stages, which is important in this study because the attainment of a particular size has been used to mark the boundry between life stages, the duration of which are under consideration.

Earlier studies on striped bass (Albrecht, 1964; Morgan and Rasin, 1973) defined a rather broad temperature range for maximum development rate and survival through hatching (16°-23°C). Bayless (1972) suggests that best survival through hatching occurs at 62°-65°F (16.7-18.3°C). Our limited mortality data suggest that best survival occurs at 15°

and 18°C. Theoretically, at an optimum temperature the conversion from yolk to embryonic tissue should be most efficient. Larval length at hatching has been used as a measure of the efficiency of yolk utilization through hatching (Alderdice and Forrester, 1968). The relationship between incubation temperature and length at hatching is presented in Figure 8c. Larval length at hatching was greatest after incubation at 15° and 18°C and least at 24°C. Length measurements presented in Figure 8c were taken from live larvae at hatching rather than from fixed specimens, hence lengths referred to here may be somewhat greater than those of prolarvae of a similar stage of development mentioned earlier in this report.

The dry weight of the excised embryo, less its yolk and oil, was lowest at 24°C and approximately the same at all temperatures below 21°C (Figure 8a), while the dry weight of whole larvae, including all of their stored reserves, increased regularly from a low after incubation at 15°C to a high at 24°C (Figure 8b). These data indicate a general retardation of larval development at the higher temperatures within the range used. Although the time from fertilization to hatching decreased with increasing temperature, the rate with which stored yolk reserves were converted into embryo tissue did not. A temperature optimum for egg development at or below 18°C is suggested. This coincides with the temperature range at which peak spawning occurs among striped bass populations in many rivers which lies between 15.6° and 19.4°C (Talbot, 1966).

While these experiments permitted observation of the rate of development at all of the temperatures used, mortality from fertilization through hatching was generally high. No single lot survived well at all

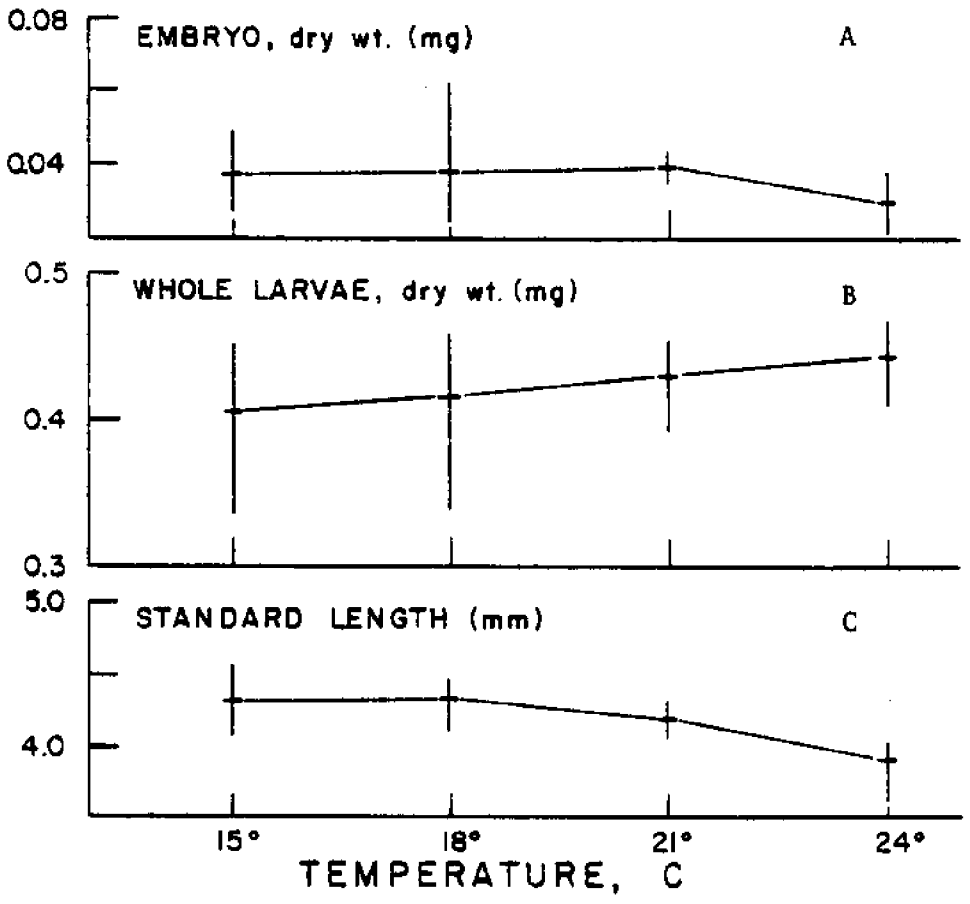

Figure 8. Measurements made in New York 1977 newly hatched striped bass prolarvae after incubation at four temperatures. Each measurement of ten individuals.

temperatures. Within each lot, one or more temperature treatments experienced heavy egg mortalities which correlated in no reproducible way with the treatment temperature. Survival at 15° and 18°C was generally higher than at 12° or 24°C. Among treatments not affected by catastrophic losses, survival ranged from 50 to 67%.

Egg mortality in these experiments can be attributed to several factors. Eggs were stocked into their rearing containers within 15 minutes after fertilization. Variable proportions of the mortality observed may have been due to non-fertilization. Hence, these losses may have had no relation to the temperature treatment. The semi-static incubation methods used are vulnerable to 'chain-reaction' deterioration in water quality. Heavy egg mortality early in an experiment can affect the quality of the incubation water to such an extent that the whole treatment population is affected before scheduled water changes can be made. Losses of this type are more likely at higher temperatures, where bacterial proliferation is more rapid.

Survival in culture vessels was much improved by the use of a broad spectrum antibiotic mixture to reduce the microbial population. Similar success was observed using this antibiotic on Maryland striped bass eggs held in river water. Albrecht (1964) used the same antibiotic in his studies with striped bass eggs. Nash and Kuo (1975) suggest that much of the mortality observed among cultured fish eggs at temperatures between 18° and 25°C is not, in fact, a direct result of temperature per se, but instead a result of rapid bacterial growth that culture at this temperature permits. There is the possibility that what Nash and Kuo propose may be true in past work on striped bass, particularly where a natural water supply was used. Chemical or physical water sterilization

methods are gaining wider acceptance in experimental studies using early life stages, e.g., Shelbourne (1964), Houde (1973), Nash and Kuo (1975).

A single experiment comparing quarry water and Hudson River water was run using eggs from lot 5. This experiment revealed that both antibiotic treated and untreated sub-lots reared in Hudson River water showed better survival through hatching than similarly treated lots in quarry water. We have no theories at present why survival in quarry water was reduced in this experiment. There is no evidence that incubation in quarry water in any way affected the rate of development observed in these studies.

Development During the Yolk Sac Stage

Increase in larval length during the yolk sac stage generally took place in two phases: 1) a rapid increase in length for the first few days after hatching, and 2) a period of depressed growth as the last of the yolk reserves were consumed. The pattern of growth observed in these studies is not unique to striped bass. The initial period of rapid growth following hatching is equivalent to section A of the growth curves of four species of marine fish described by Farris (1959). An initial period of rapid growth immediately following hatching was also described by Kuznetzov (1972) for a diverse group of fresh water species. As in other species, the period of essentially linear growth following hatching in striped bass ends well before full yolk absorption.

In other species the end of the period of linear growth following hatching is concurrent with the beginning of free swimming by the developing larva. Once free swimming has begun, growth in embryo length and weight declines and the use of remaining yolk is accelerated (Toetz, 1966; Laurence, 1969).

The onset of free swimming just followed mouth formation in these studies. Doroshev (1970) noted an increase in larval activity at about the same time as mouth formation in striped bass two to five days after hatching at 17°-18°C. These observations correlate well with the timing of the beginning of the growth plateau in our experiments at this temperature. Before free swimming, all of the yolk energy available is used for maintenance and growth. After swimming is begun the remaining yolk energy is divided between maintenance and activity at the expense of growth in length or weight. Lasker and Theilacker (1962) showed that activity can increase the oxygen consumption, hence energetic demands of sardine larvae, up to 3.5 times over that required by inactive larvae. It has been a common practice among striped bass culturists to provide heavy agitation in larval rearing containers. This turbulence probably induces larval activity sooner than it would normally occur. In later prolarval development it probably increases the level of forced activity, thus increasing the rate at which yolk is consumed.

A portion of the rapid increase in length that occurs following hatching may be explained in osmotic rather than nutritional terms. The water content of whole prolarvae (including yolk and oil) increases between hatching and yolk absorption (Figure 9). It is probable that the rapid increase in larval length following hatching is in part a result of the hydration of embryo tissues.

The standard length of larvae at the point of yolk absorption was nearly the same after development at all temperatures between 15° and 24°C* (Figure 10c). Whole larva dry weight is similarly little affected

*Length measurements on this experimental series were made on living rather than preserved material. The lower mean length at yolk absorption used earlier in this study may be explained by shrinkage during fixation.

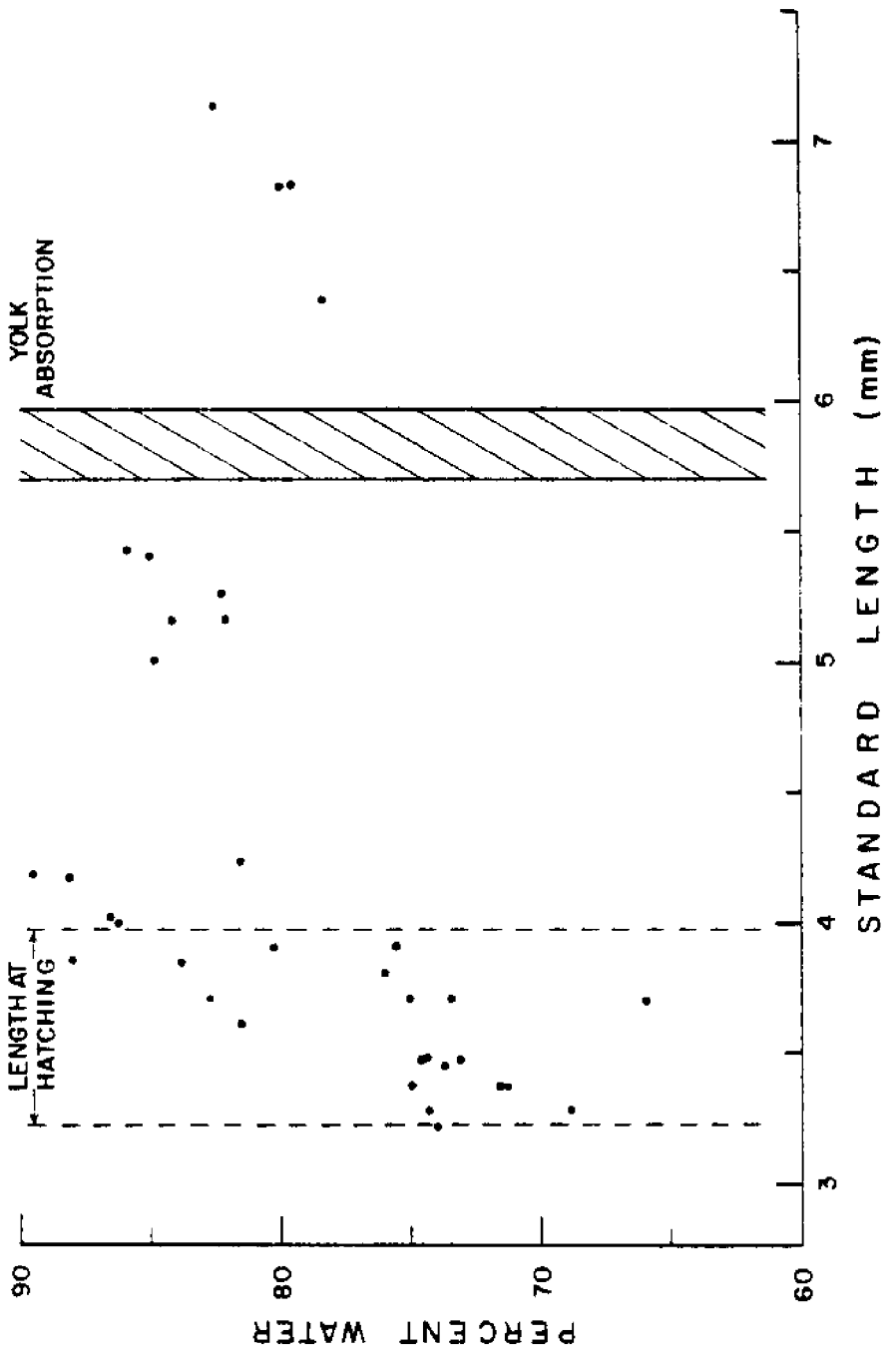

Figure 9. Observation on the water content of striped bass prolarvae.

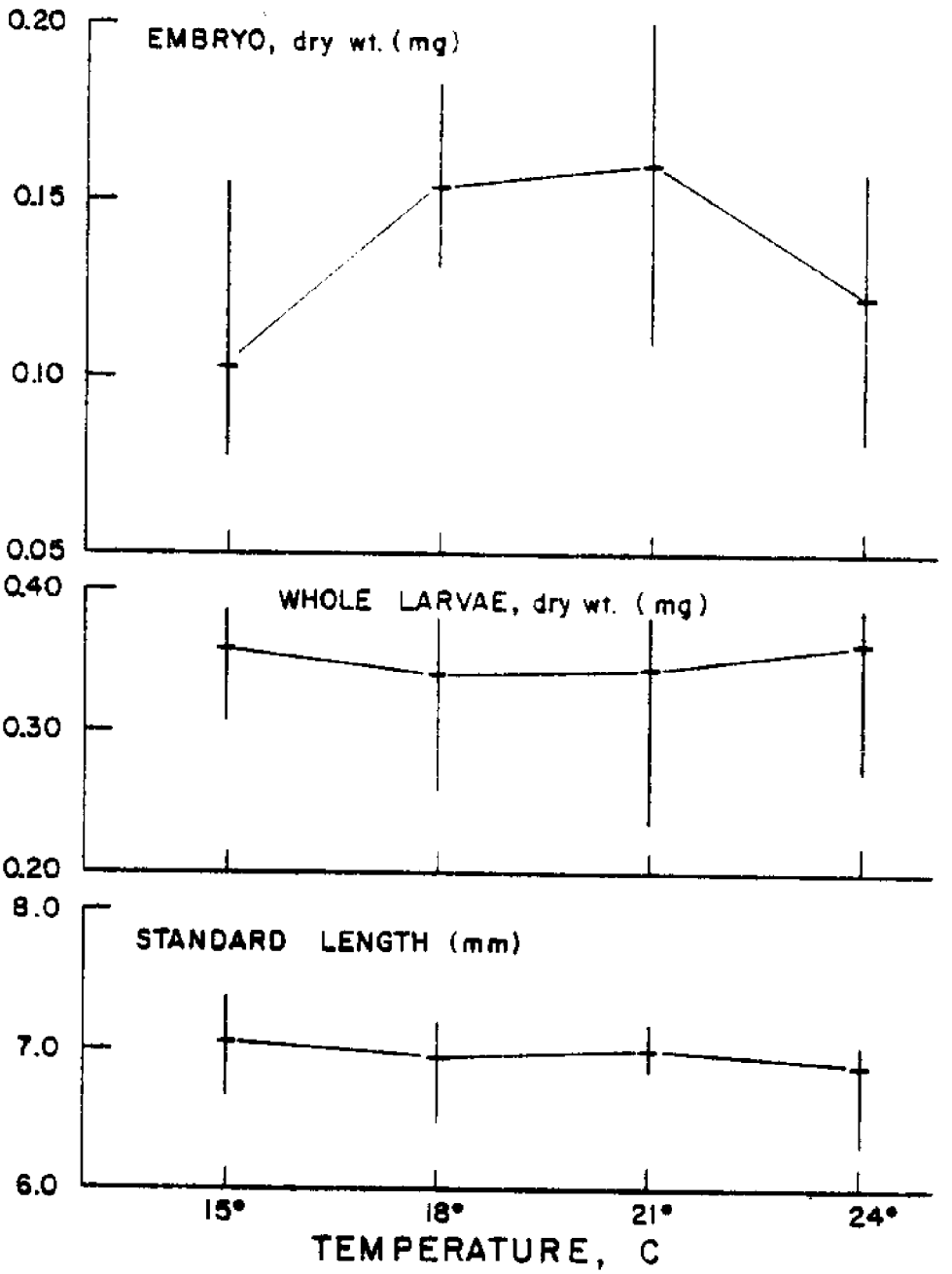

Figure 10. Measurements made on New York 1977 striped bass prolarvae at yolk absorption after incubation and maintenance at four temperatures. Each measurement of ten individuals.

by holding temperature within this range (Figure 10b). At yolk absorption, the dry weight of the embryo alone with its oil globule removed, was higher after rearing at 18° and 21°C than after being held at 15° or 24°C. Consequently, a higher proportion of total larval dry weight may be accounted for by an increase in growth of larval (embryo) tissue at 18° and 21°C than at higher or lower temperatures. These observations support the hypothesis that a physiological optimum for growth between hatching and yolk absorption exists within this temperature range. This means that although the mean duration of the yolk sac stage decreased regularly with increasing temperature (Table 4, Figure 7), a greater mass of larval tissue was laid down after rearing at 18° and 21°C. Larval length at a hatching, after rearing over the entire range in temperatures, does not reveal the existence of such a peak. If faced with a scarcity of food, it is likely that larvae having a greater amount of body tissue to draw upon, would have a distinct survival advantage over those which were less robust at yolk absorption.

Development Between Yolk Sac Absorption and Metamorphosis

Growth during the larval stage as it was observed in these studies could also be broken down in two distinct phases. The first, a period of arrested growth following yolk absorption, was followed after a period of up to several weeks by the second, which was characterized by rapid exponential growth in length through metamorphosis.

A break or inflexion point at yolk absorption has been reported frequently in laboratory studies of larval fish growth. Farris (1959) noted a period of reduced growth following yolk absorption in four species of marine fish. Kuznetzov (1972) noted a similar reduction in larval growth at, or slightly before, yolk absorption in several species

of freshwater fish. He associated the change in growth rate with the period of transition from endogenous to exogenous nutrition. Other authors have presented growth data in which an inflection at yolk absorption was evident (e.g., Kramer and Zweifel (1970) and Sette (1943)). Zweifel and Lasker (1976) proposed that two-cycle growth curves more appropriately described the growth of fish larvae near yolk absorption, and suggested that a change in growth rate at this point was a general phenomenon common to a number of fish species.

However, more than a growth inflection was encountered in most of the treatment lots in this study. In some groups the length of larvae remained unchanged for a number of days following yolk absorption. In other lots the mean length of larvae decreased from the size at yolk absorption and remained at this depressed level for up to two weeks.

Shrinkage in size of the sort encountered here occurs only when larvae have been starved. Farris (1959), Lasker (1964), May (1971) and Zweifel and Lasker (1976) describe a similar reduction in total length in the larvae of other fish species which had been starved following yolk absorption. Among larvae which receive no food at all this reduction in length ends in death after a period of time, which varies with the fish species and the holding temperature.

That delayed initial feeding may produce a characteristic shrinkage in length following yolk absorption was demonstrated in an experiment performed one year after the original temperature growth series were run, using striped bass larvae from South Carolina. Groups of larvae maintained at 18°C were starved from hatching. Food was provided for the first time to individual starved groups over a period of two weeks. The results of this experiment are presented in Figure 11.

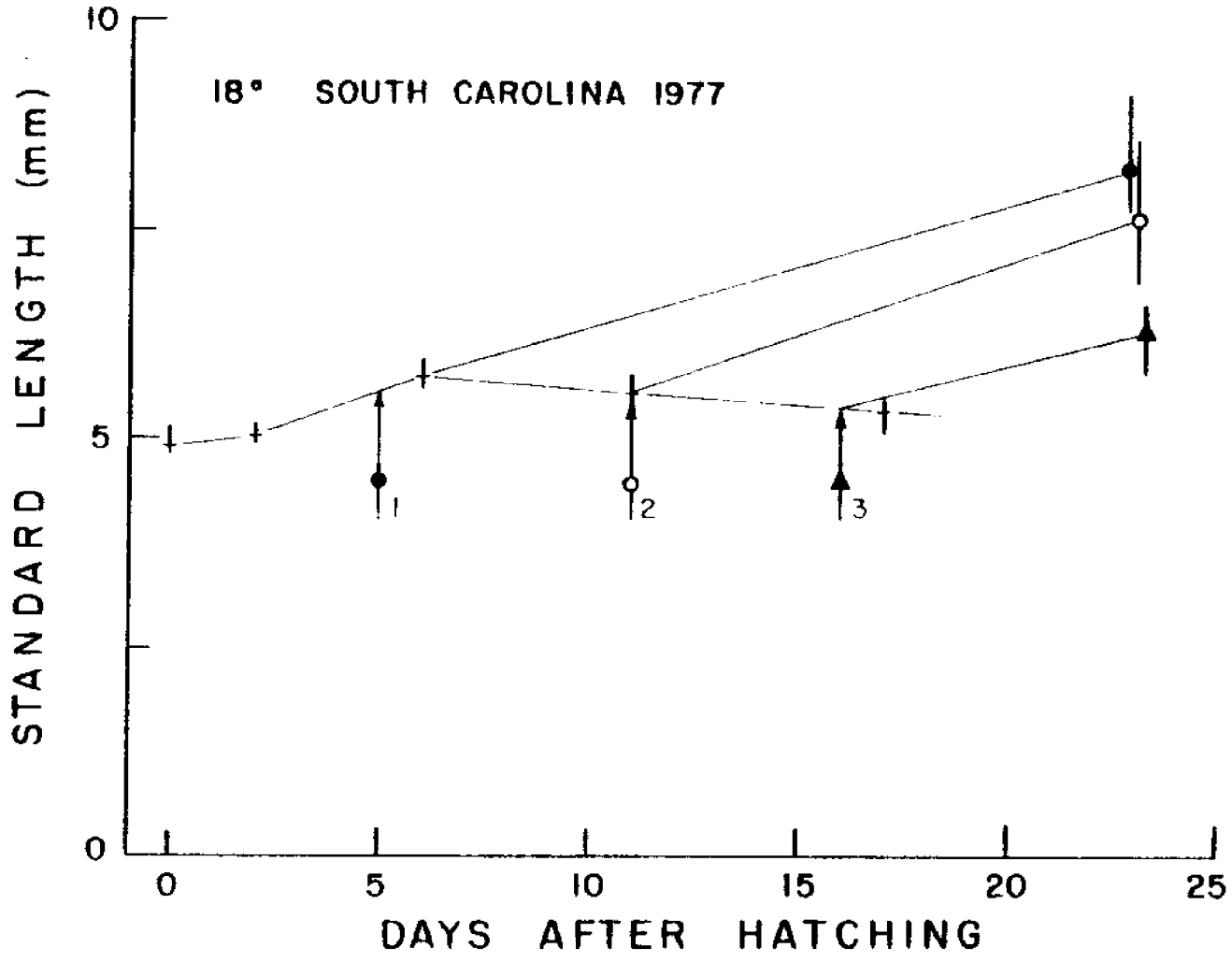

Figure 11. The effect of delayed initial feeding on the growth of South Carolina striped bass larvae maintained at 18°C, in relation to unfed control group. Horizontal bars denote sample means. Vertical bars indicate sample range. Symbols mark the time and length at which feeding was begun for each group (1-3). Standard sample size N=10.

The length of starved larvae reached a maximum at yolk absorption near or before day six after hatching, after which a gradual shrinkage in length took place. For groups fed for the first time at day six there was no detectable period of negative growth. In groups fed later than this, a marked period of negative growth took place before positive growth recommenced after food was provided.

It seems clear that the negative growth periods noted in the original temperature growth series were the result of inadvertant food deprivation during the course of the experiment. Although the feeding regime used assured that Artemia nauplii were always present within each culture container, they were apparently not available in sufficient concentration to support optimal growth.

The second phase of larval growth could be readily described using an exponential growth equation (Table 6) and followed a pattern that was characteristic of that encountered in a number of other fish species (e.g., Ryland (1966), Kramer and Zweifel (1970)). The slope of the exponential growth equations for groups reared at different temperatures increased as the rearing temperature increased (Table 6, Figure 6). Kramer and Zweifel (1970) noted a similar temperature response in the Pacific anchovy, and Laurence (1975) encountered a similar relationship between growth rate and rearing temperature in larval winter flounder. Cushing (1974) notes that a rapid increase in size has survival value in nature. As a larval fish grows larger, the number of potential prey organisms increases while potential predators become fewer in number and larger. Other conditions being equal, temperature conditions which permit the larva to make efficient use of the available food and grow at a rapid rate would offer the developing bass a greater opportunity to

survive through metamorphosis. Most rapid growth during the larval stage occurred at temperatures of 21° and 24°C in these studies. Food abundance was an important factor in determining the growth rates of larvae in these experiments and this factor was not controlled. Nonetheless, larval development at the higher temperatures used yielded the shortest stage durations and therefore the greatest rates of larval growth.

Size-hierarchy effect (Blaxter, 1969; Brown, 1957) became a prominent feature of the distribution of larval lengths in all treatment populations. Size-hierarchies or ranges in length among larvae of the same age are a common phenomenon in captive fish populations. It is not known whether or not they occur to the same extent among natural populations as they do in the laboratory or hatchery. Our sampling procedure tended to reduce the size range in each population. We sampled the largest and smallest fish as well as what appeared to be average sized individuals. The size hierarchies we observed occurred in spite of our sampling technique. The range in length within each sample appeared to increase in each treatment population as the time of metamorphosis was approached (see growth figures, Appendix B). The occurrence of size-hierarchies tends to reduce the predictive power of a growth curve in defining the time of metamorphosis. We based our estimates on the time of metamorphosis on our observations of the time in days after hatching it took the larvae in our experimental populations to reach a mean length of 16.32 mm. The range in lengths that occurred among individuals in the populations before this mean length was attained would determine the actual time course of the arrival of metamorphosis in the population as a whole. Our sampling procedure ideally amounted to periodic cropping

of the population which had no size related bias. The extent of size-hierarchies is certainly a function of the size of the population. The treatment populations near the end of our experiments were quite small; as a result the range in sizes observed probably underestimates the range that would have occurred in a larger population.

The rate of mortality during the larval stage was less than that observed up to yolk sac absorption (Table 9).

Mortality curves for all of the experimental treatments are found in Appendix B. A common characteristic of nearly all treatments is a sigmoid pattern in the reduction in numbers. Less than half of all mortalities that occurred during the whole experimental period took place before yolk sac absorption was complete. Mortality immediately following hatching was low, typically amounting to no more than five percent of the treatment population. A linear decline in numbers followed beginning three to four days after hatching at 24°C and progressively later at lower temperatures. The maximum mortality for one day followed a similar pattern, occurring at three to five days at 24°C, four to six days at 21°C, six to nine days at 18°C and nine to twenty-one days at 15°C. The period of heavy mortality ended when the treatment populations at 24°C had been reduced to an average of 16% of their original level, and when the treatment populations at 21°, 18° and 15°C had been reduced to an average of 24% of the number present at stocking.

The cause of this pattern of mortality is not clear. A number of factors which could have led to mortalities of this sort were investigated. None that might be active in as many different lots and temperature treatments as were observed in these experiments were found. Our experience confirms the observations of Otwell and Merriner (1975) and

Davies (1973) that striped bass larvae are relatively hardy and can accommodate to a wide range in temperature and water qualtiy conditions. Crowding was considered a possible predisposing condition to mortality of this sort. There was a three-fold difference between treatments at all temperatures in the number of larvae per liter of culture water at the time mortality rate had stabilized. Some of the highest stocking densities persisted at 21° and 24°C. The effects of crowding and of epidemic disease remain as possible explanations for the mortalities observed.

The pattern of mortality greatly resembles that observed by other workers among groups of larvae which were deprived of food or maintained on reduced rations (May, 1971; O'Connell and Raymond, 1970). The larval populations were presented with Artemia nauplii two days after hatching at 24°C, three days after hatching at 21°C, and five to six days after hatching at 18° and 15°C. The time food was first presented was chosen on the basis of the apparent degree of structural development of larvae in samples from each population. Feeding typically begins before all yolk is absorbed. In other species larvae which have exhausted their yolk reserves and have begun to resorb their body tissues may lose their ability to capture and use food when it becomes available. This stage of 'irreversible starvation' has been labeled the 'point of no return' by Blaxter and Hempel (1963). The period of time between yolk absorption and irreversible starvation may be very short. Lasker et al. (1970), observed that for the northern anchovy irreversible starvation followed shortly by complete mortality occurred when food was withheld more than one day after yolk absorption. Bayless (1972) observed what appeared to be irreversible starvation in striped

bass just under ten days after hatching at 18.9° to 20°C. Among Bayless' fish which had undergone irreversible starvation, death followed four to five days after the ability to feed had been lost. To determine whether or not a reduced feeding level could have accounted for the mortality pattern observed in these experiments, another experiment was performed in which populations of early larvae were stocked in containers at each of the four test temperatures and purposely starved. Before the beginning of this experiment larvae were maintained without food at 15°C. The observation period began on the eighth day after hatching. Mortality curves for this series are presented in Figure 12. The time to death from starvation increased as the holding temperature decreased. In no case was total mortality observed prior to three weeks after hatching and no spectacular losses were observed in less than 14 days after hatching. Although the starvation experiment outlined above was performed a year after the majority of the experiments reported here were run, it is clear that losses of the magnitude and at the time of those observed in the earlier series were probably not attributable to a shortage of food.

A nutritional explanation of the pattern of mortality observed would entail the assumption that all larval populations received no food, or that the food presented was rejected or not in sufficient abundance to meet the demands of the entire population in each tank. Although we were unable to monitor the size of the ration presented each tank, food was always available in varying amounts. At least 20% of the fish in most populations ultimately accepted and were able to grow on the food presented, suggesting that the diet was nutritionally adequate. The food concentration required for optimal growth and survival

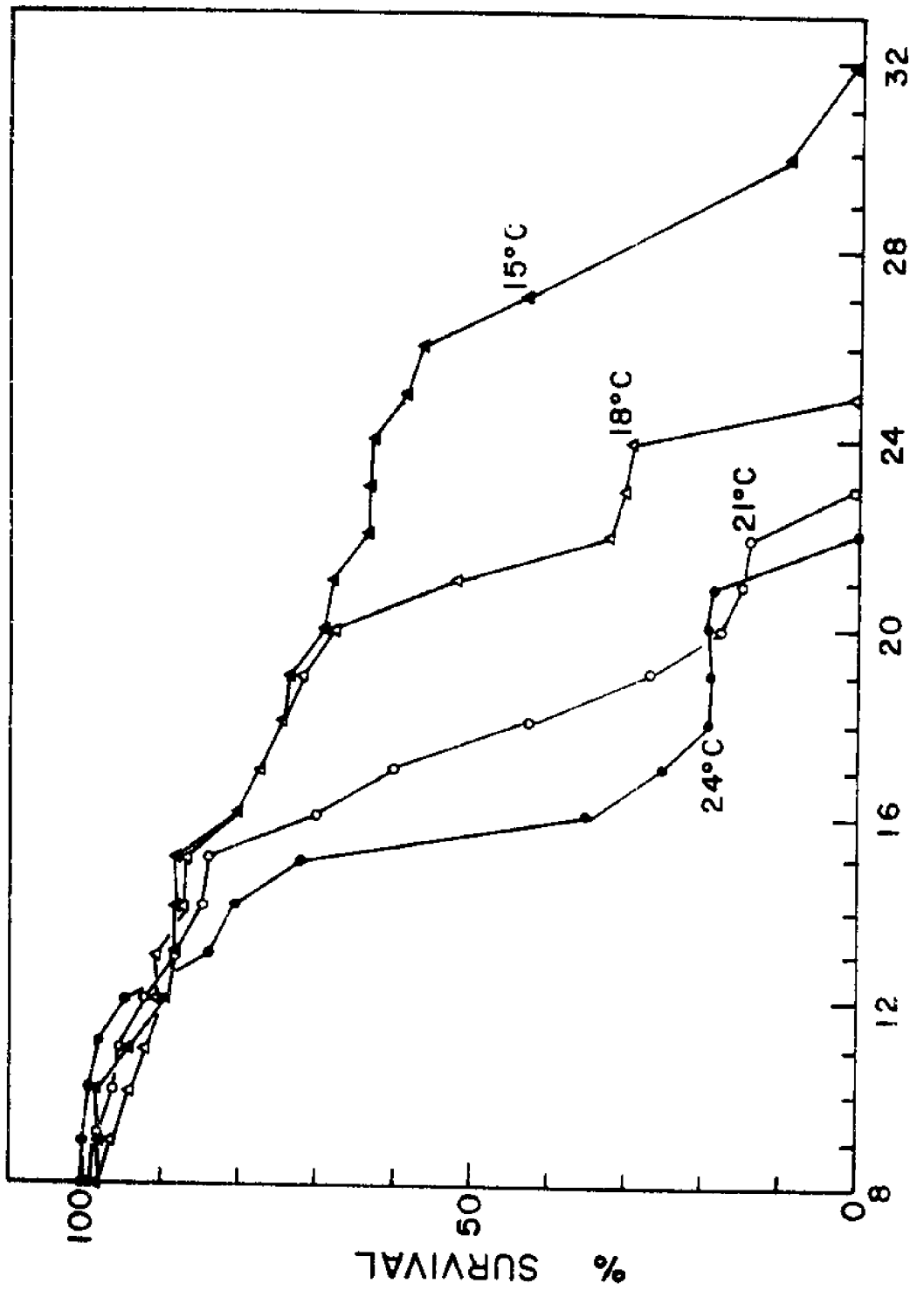

Figure 12. The effect of holding temperature on the rate of mortality among starved striped bass larvae. Initial population 100 larvae per treatment.

among striped bass larvae is unknown. However, Daniel (1976) has shown that survival and growth of larval striped bass fed on Artemia nauplii increased at higher food concentrations. The pattern of mortality in our experiments remains unsatisfactorily explained. Some factor other than starvation appears to have been responsible for the bulk of early losses.

Applicability of Stage Duration Estimates

Life stage duration estimates used in life cycle simulation models are designed to bracket the range in stage duration that may be expected under natural conditions. In models of Lawler et al. (1974), and the United States Nuclear Regulatory Commission (U.S.N.R.C.) (1975) fixed stage lengths are proposed. A comparison of the life stage duration estimates determined under fixed temperature conditions with those which have been used in the literature is presented in Table 10.

Our data indicate that the duration of life stages is strongly temperature dependent and probably affected by the nutritional state of the larvae as well. Nevertheless, the fixed duration estimates used in the models mentioned above fall within the range defined as a part of this study, and are, as a result, probably fairly good estimates of stage duration under average conditions. The validity of the stage duration estimates used on both models depends on which temperature more nearly approximates the temperature conditions which a striped bass egg or larva encounters during and after the spring spawning in the Hudson. Based on a ten year average (1959-1969) the temperature of the Hudson River at Indian Point rises at a rate of 1°C every five days between May 1 and July 1 (U.S.N.R.C., 1975). The interval between mid-May and mid-June (Rathjen and Miller, 1957) is the time in which spawning

TABLE 10.

A comparison of striped bass life stage duration estimates determined in this study under a range of fixed temperature conditions with fixed-length stage durations used in the preparation of striped bass life history models reported in the literature.

Stage	Temperature °C	Life Stage Duration		
		This Study (mean)	Lawler et al.+ (1974)	U.S.N.R.C.+ (1975)
egg	12	109 hours	36-48 hours	48 hours
	15	62 hours		
	18	51.8 hours		
	21	37 hours		
	24	28.5 hours		
yolk sac larva	12	9.0 days	6-10 days	6 days
	15	8.3 days		
	18	7.75 days		
	21	5.1 days		
	24	3.8 days		
post yolk sac larva	15	67.66* days	30 days	22 days
	18	33.00 days		
	21	23.90 days		
	24	22.66 days		

* estimated

\+ temperature not specified

occurs in the Hudson. During this period the average water temperature at Indian Point rises from approximately 15° to 21°C. Our studies were carried out under fixed temperature regimes, hence can only approximate the timing of development over a period of rising temperatures. Our work does not reveal to what degree the thermal history of a larva might affect its later growth. Our experiments do indicate that the period between yolk absorption and metamorphosis is more responsive than earlier stages.

The pattern of growth defined in this study is compared with previous studies in Figure 13. In this figure, growth at 15° and 24°C fixed temperatures bracket the growth observed by Mansueti (1958) and Rhodes and Merriner (1973). In Mansueti's experiments temperature was uncontrolled and ranged between 15° and 18°C. The temperature in Rhodes and Merriner's study rose irregularly from 17° to 27°C. The growth of fish in the latter study closely coincided with the growth of our fish at 18°C. Both Rhodes and Merriner and Mansueti state that their fish were "stunted" in comparison to wild populations. Compared to the growth rate attributed to "wild" striped bass (temperature unspecified) (Humphries and Cumming, 1973) both the present study and those of Mansueti and Rhodes and Merriner underestimate the growth rate of fish in nature. All three were laboratory investigations. In the present study, stage duration and growth were closely related. Our estimates of stage duration are too long to the extent that our observed growth rates underestimate those of wild fish.

In designing the experiments reported here, total length was chosen as a measure of larval growth over other criteria such as larval dry weight in the hope that these laboratory observations could be used in

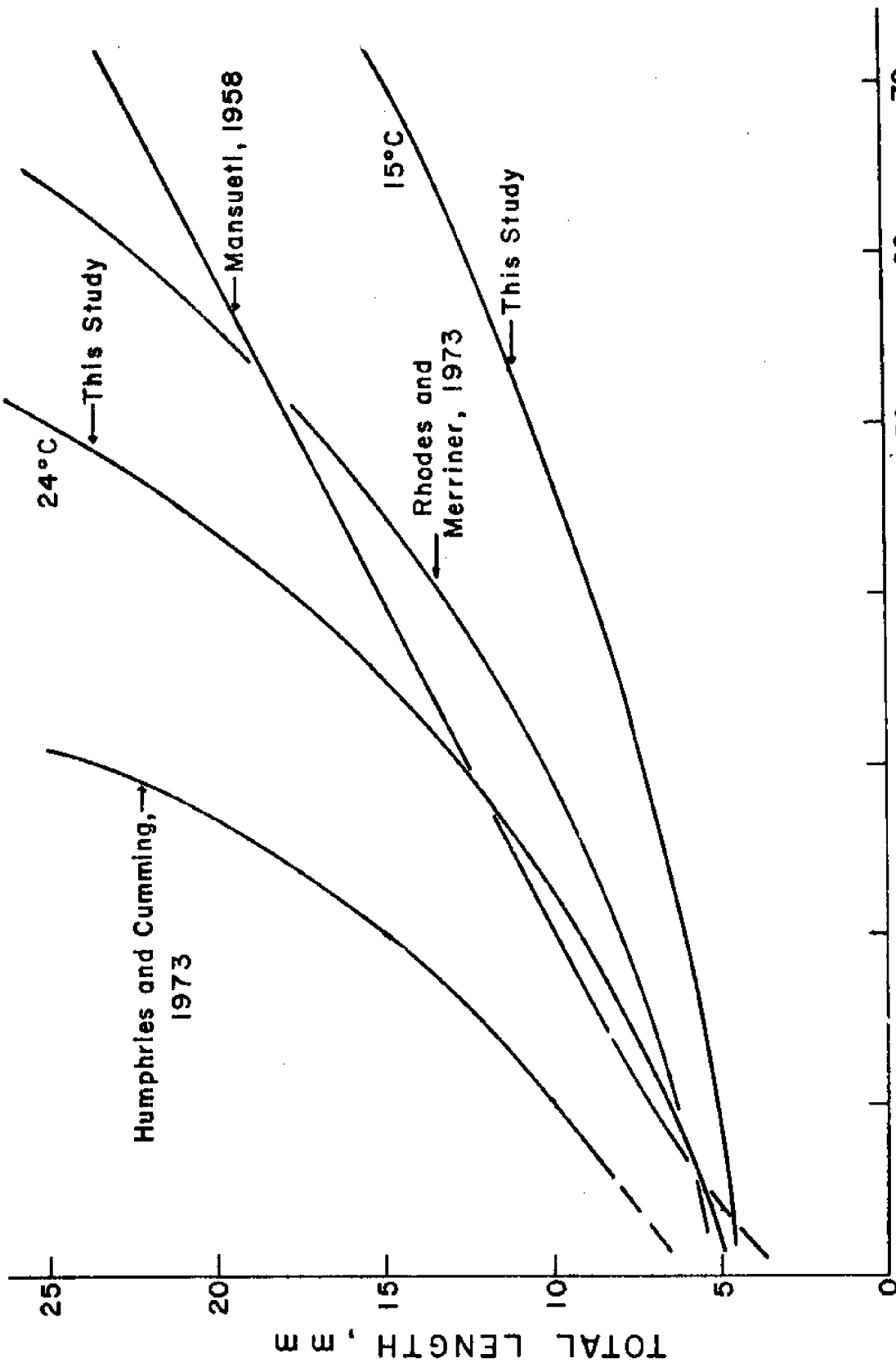

Figure 13. A comparison of growth rates observed under fixed temperature regimes with those obtained in earlier studies under conditions of increasing temperature.

conjunction with field studies to estimate the age distribution of striped bass larvae taken in icthyoplankton collections. The widespread occurrence of size-hierarchy effects and periods of suspended or negative growth that were observed here indicate that the relationship between larval length and chronological age may be somewhat tenuous. Attempts to age larvae taken in the field on the basis of their length distribution alone might well lead to serious interpretational errors. Incubation temperature affects the length of the earliest prolarvae. While the lengths of larvae at yolk absorption do not appear to be affected by temperature, the time between hatching and yolk absorption is decidedly temperature-dependent. After yolk absorption, temperature and nutritional conditions interact to affect the length of larvae of a given chronological age. Without some knowledge of the thermal and nutritional history of a given specimen it is not possible to estimate its chronological age with any confidence. Although temperature conditions in the field may be estimated with reasonable accuracy, the availability of suitable food to the developing larvae is more difficult to determine due to unknown food preferences of the larvae and to the 'patchiness' of microcrustacean distributions in natural waters. Larval length and structural development appeared to be closely related, so that even structural staging criteria might prove to be weak indicators of larval age.

In these experiments, stage duration between the chosen developmental landmarks decreased with increasing temperature within the temperature range investigated. On this basis, it might be reasoned that an overall increase in river temperature over the seasonal ambient level might decrease the period of larval vulnerability to power plant

entrainment and perhaps decrease the overall losses attributable to this source. Considering only the direct effects of temperature on striped bass survival and growth, such a strategy might have merit. However, some of the experiments reported here indicated that although stage duration decreased with increasing temperature, within each stage there appeared to be narrow temperature ranges within which the developmental processes proceeded most efficiently. Larval length at hatching was greatest after incubation at or just below 18°C. The efficiency of yolk utilization was greatest during the yolk sac stage between 18 and 21°C. The growth rate of post yolk sac larvae was greatest at 21 and 24°C. These observations suggest the presence of an ascending temperature optimum for development through each successive developmental stage. Physiological optima may be defined in many ways, and the ones used in these studies were crude. Efforts should be made to identify the conditions for optimum development in larval and juvenile striped bass. At present, it seems clear that a reduction in stage duration which might be achieved through an increase in the overall temperature in the larval environment, might not be achieved without some sacrifice in the growth efficiency of the life stages involved.

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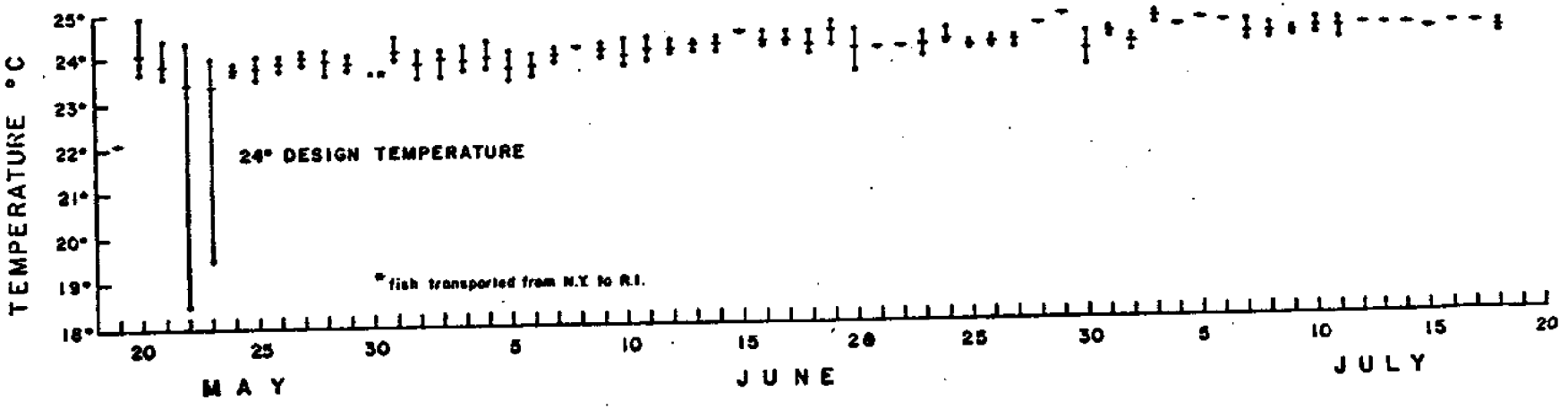
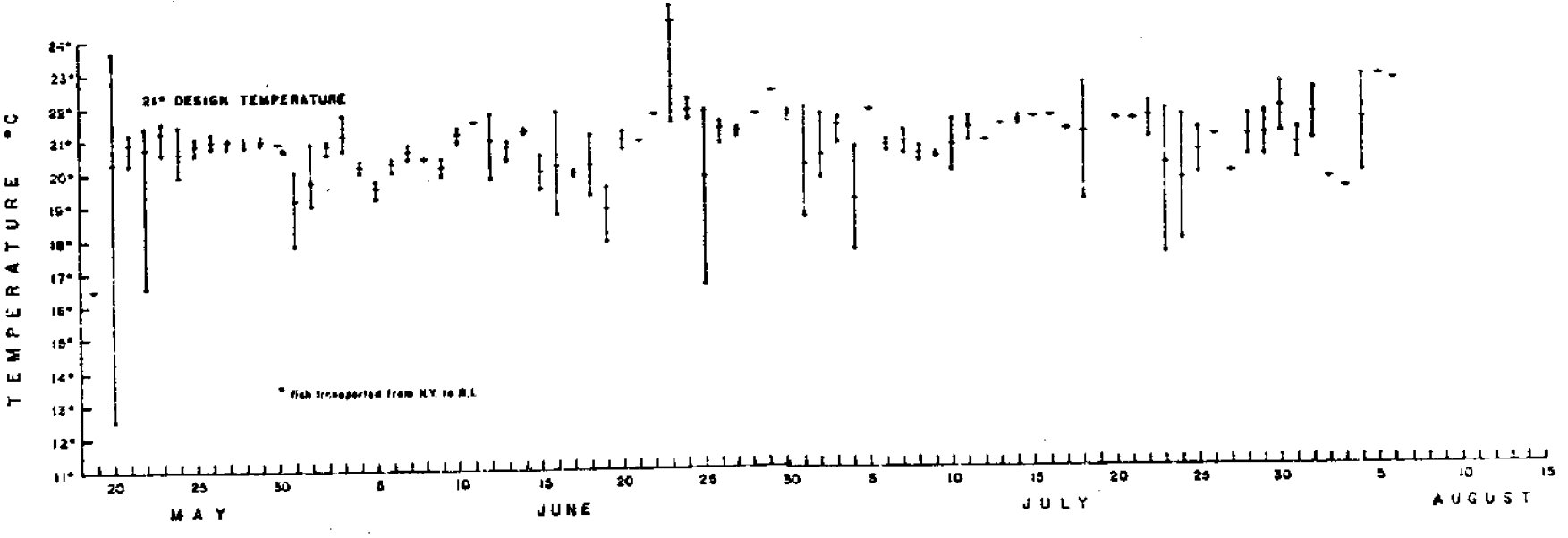
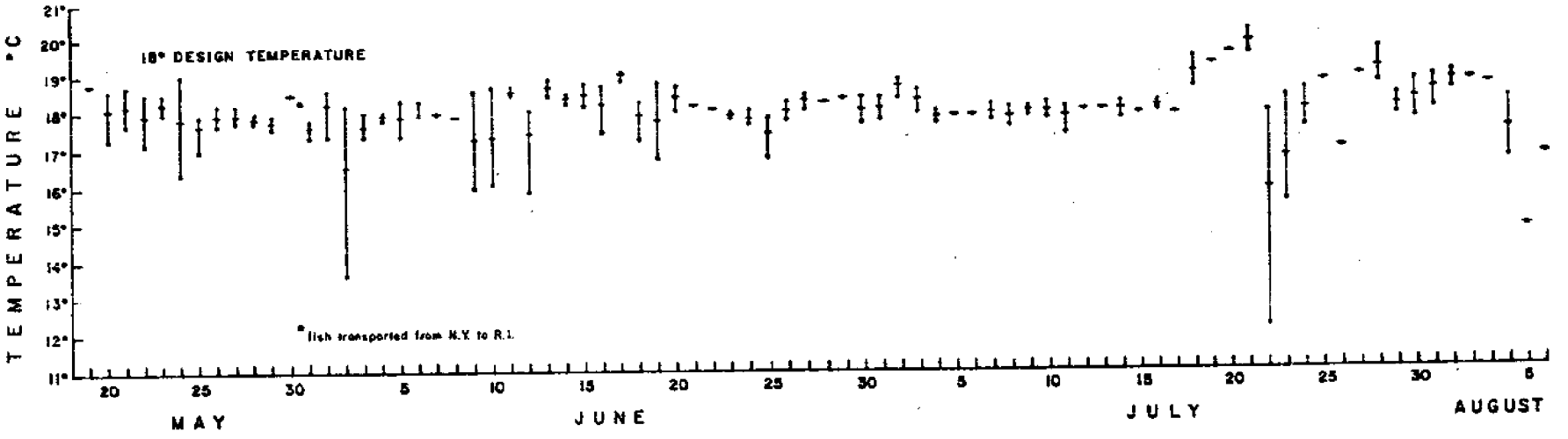
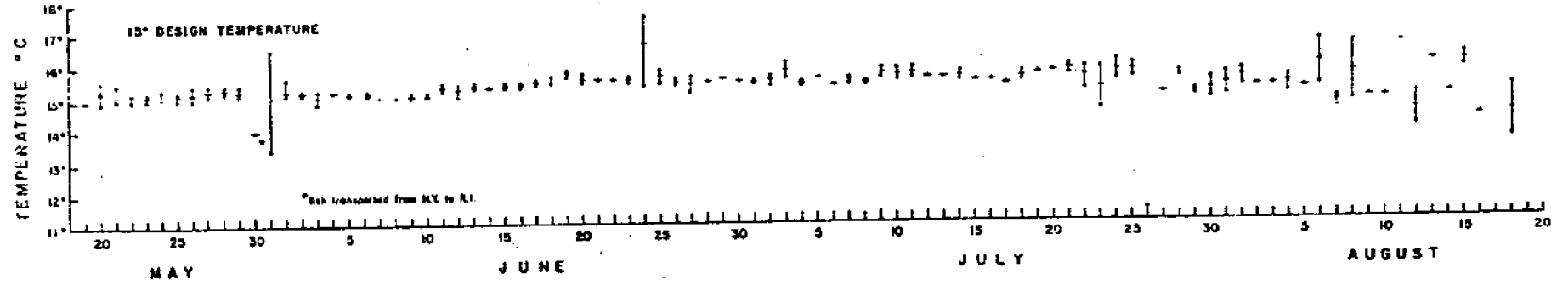
APPENDIX A





Record of observed temperatures in 24° and 21°C design temperature treatments.





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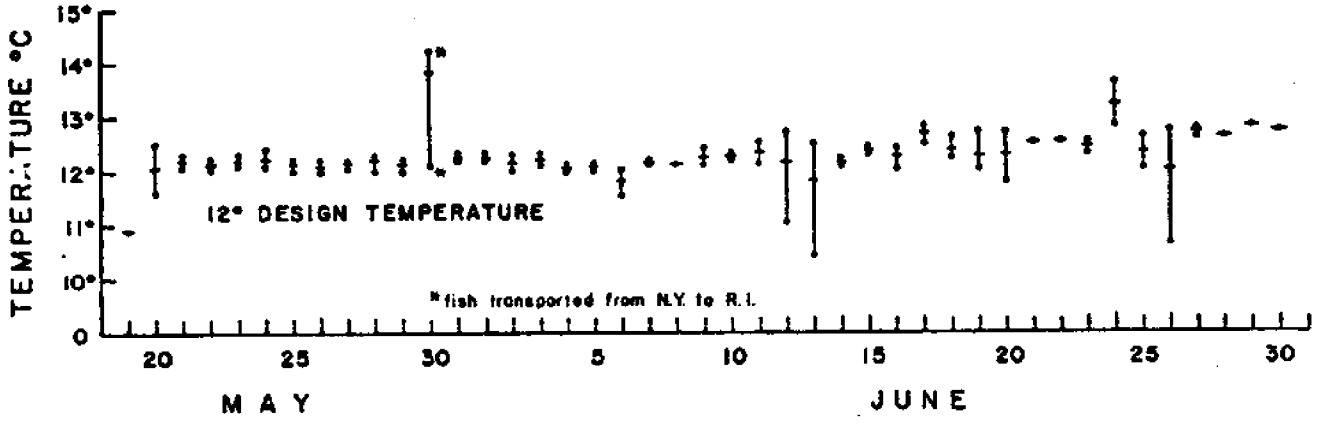


Record of observed temperatures in 12°C design temperature treatment.

AMMONIA CONCENTRATIONS (PPM) BEFORE WATER CHANGES

Date and Tank		12°	15°	18°	21°	24°C
20 May	#1	0.16	0.13	0.18	0.18	0.16
21 May	#1	0.33	0.23	0.33	0.69	--
	2	--	--	0.16	0.17	0.32
	3	--	--	--	--	0.14
23 May	#6	0.21	0.13	0.13	0.25	0.21
25 May	#7	0.13	0.17	0.13	0.19	0.63
28 May	#6	--	0.48	0.14	--	0.25
	7	0.13	0.21	0.35	0.30	0.28
	5	--	0.35	0.19	--	
5 June	#6	--	--	--	--	0.79
	7	--	0.30	--	1.56	--
	8	0.15	0.47	0.63	--	1.25
	9	--	--	0.18	0.43	0.31
16 June	#5	--	1.75	1.94	--	--
	6	--	--	--	--	2.31
	7	--	0.90	1.38	2.13	--
	8	0.80	1.11	1.16	1.44	>2.44
	9	0.56	0.89	0.89	1.56	2.13
17 June	#5	--	1.19	1.06	--	--
	6	--	--	--	--	1.25
	7	--	0.63	0.86	0.91	
	8	0.61	0.78	0.76	0.71	1.50
	9	0.63	0.61	0.60	0.94	1.25
19 June	#6	--	--	--	--	1.16
	7	--	0.90	1.16	0.83	--
	8	0.78	1.06	1.25	0.73	1.33
	9	0.88	0.75	1.11	0.99	1.25
26 June	#5	--	--	0.85	--	--
	6	--	--	--	--	1.28
	7	--	0.60	0.94	0.78	--
	8	0.74	0.73	0.75	0.81	0.68
	9	0.89	0.68	1.10	1.26	1.25

AMMONIA CONCENTRATIONS (PPM) BEFORE WATER CHANGES

Date and Tank		12°	15°	18°	21°	24°C
1 July	#5	--	--	1.12	--	--
	6	--	--	--	--	1.25
	7	--	0.71	0.86	0.66	--
	8	--	0.92	0.96	0.88	0.84
	9	--	0.96	1.70	1.10	1.08
17 July	(processing error)					
28 July	#5	--	--	1.10	--	--
	8	--	1.25	0.15	--	--
	9	--	0.89	0.30	--	--

DISSOLVED OXYGEN CONCENTRATIONS
(PERCENT SATURATION)

Date and Tank		12°	15°	18°	21°	24°C
22 May	#1	98	98	97	--	--
	2	100	99	97	91	--
	3	--	--	--	94	--
23 May	#4	--	95	92/95	--	96
	6	--	--	--	94	--
25 May	#6	--	98	99	--	--
	5	--	--	94/96* 80/81**	--	--
28 May	#5	--	98	98	--	--
	6	--	98	99	--	95
	7	87	98	99	91	96
	8	88	99	100	93	93
4 June	#7	--	98	95	98	--
	8	100	97	95	99	93
	9	96	96	96	--	95
23 June	#9	94	94	91	89	95

* Quarry/Hudson water with Penicillin (50 mg/l) and Streptomycin (50,000 I.U./l.)

** Quarry/Hudson water without Penicillin & Streptomycin

pH VALUES

Date and Tank		12°	15°	18°	21°	24°C
21 May	#1	8.2	8.1	7.8	7.85	--
	2				8.2	7.8
	3					8.15
23 May	#1			8.3		
	2			7.95		
	3			8.2		
	4			8.0/8.2		
25 May	#5*		7.9,-	8.0,7.8		
	**		7.8,7.6	7.7,7.5		
28 May	#6					8.2
	7		8.2	8.25	8.0	8.3
	5		7.8			
	4			8.1		
14 June	#8	8.15				
	9			8.0	8.0	8.0
	5		7.8			
16 June	All	8.0-8.3	8.1-8.2	8.0-8.4	8.3-8.4	8.1-8.2
24 June	#9	8.05	7.95	7.85	7.9	7.95
7 July	#8	--	8.0	7.95	7.9	8.0

* Quarry, Hudson water with Penicillin (50 mg/1) & Streptomycin (50,000 I.U./1.)

** Quarry, Hudson water without Penicillin & Streptomycin)

SALINITY (o/oo) RANGES BEFORE WATER CHANGES*

Date	12°	15°	18°	21°	24°C
3 June	0	2	2-3	2-3	0-3
6 June	0	2-4	3-5	3-5	4.5-5
10 June	0-1	2-4	3-4	3-4	4-6
16 June	2-4	4-7	5-8	6	6-8
20 June	5-8	6-9	7-10	9	10-12
23 June	3-5	6-8	5-9	8-10	12-13
24 June	4	5	7	6	8
25 June	5	5-6	6-9	7-8	8-10
26 June	3-4	4	4-6	4-6	4-6
27 June	2-3	3-4	4-5	4-6	4-6
30 June	--	4	4-7	4-5	5-6
1 July	--	4	4-6	4	4-6
2 July	--	5-6	6-8	6-7	6-8
3 July	--	5-6	6-9	5-6	8-10
7 July	--	5-6	6-8	6-7	8
8 July	--	4-5	4-6	5	7-9
9 July	--	6-7	6-9	6	8-10
10 July	--	4-5	4-6	4-5	5
11 July	--	7-8	6-8	8	10
14 July	--	6-8	6-8	7	12-14
15 July	--	5-6	5-7	4-5	7-9
17 July	--	4-6	4-6	4	7

SALINITY (o/oo) RANGES BEFORE WATER CHANGES*

Date	12°	15°	18°	21°	24°C
18 July	--	5-6	4-6	5-6	7
21 July	--	10-12	9-10	--	--
23 July	--	8-9	7-9	--	--
25 July	--	8-9	8-10	--	--
28 July	--	8-10	9-11	--	--
29 July	--	8-10	8-10	--	--
30 July	--	8-9	10	--	--
31 July	--	6-10	6-8	--	--
1 August	--	7-10	9-11	--	--
4 August	--	9-12	9-10	--	--
6 August	--	10-12	--	--	--
10 August	--	10	--	--	--
12 August	--	10	--	--	--
14 August	--	12	--	--	--

* Given as ranges for all tanks at each temperature.

APPENDIX B

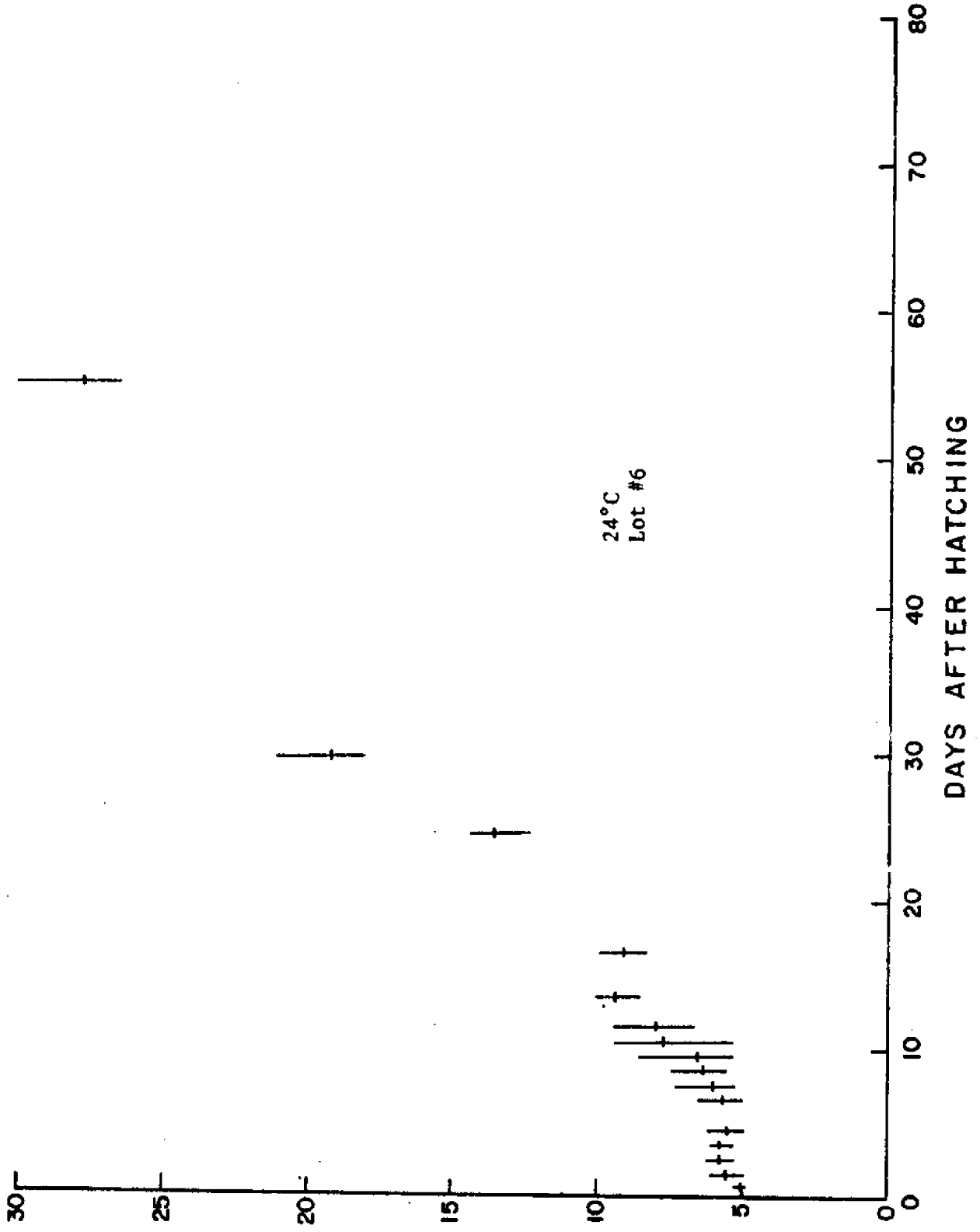
Appendix B

Larval Growth Figures

Legend

vertical bar represents range in length in each sample

cross bar is sample mean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Lot #6
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60
70
80
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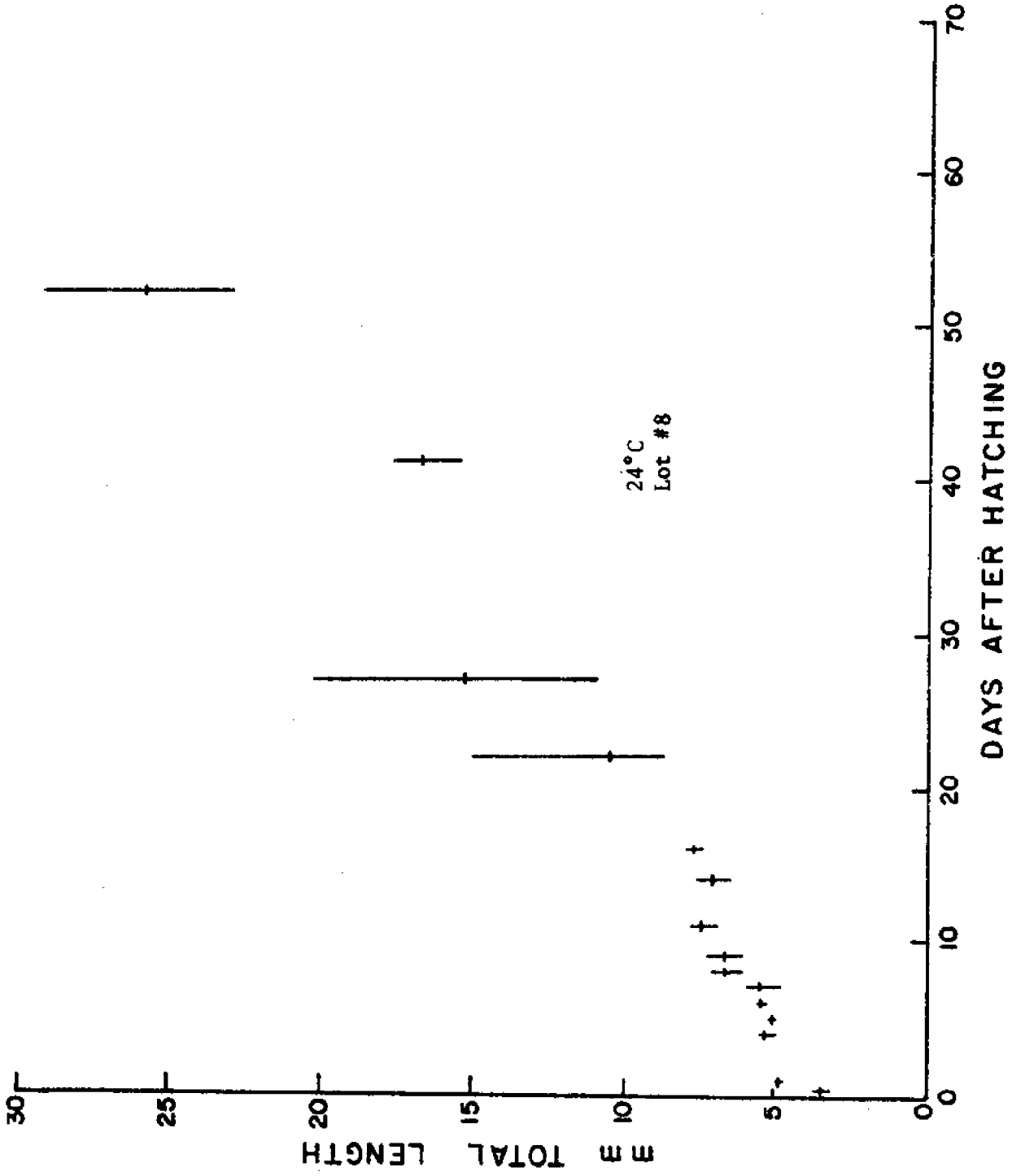
10
15
20
25
30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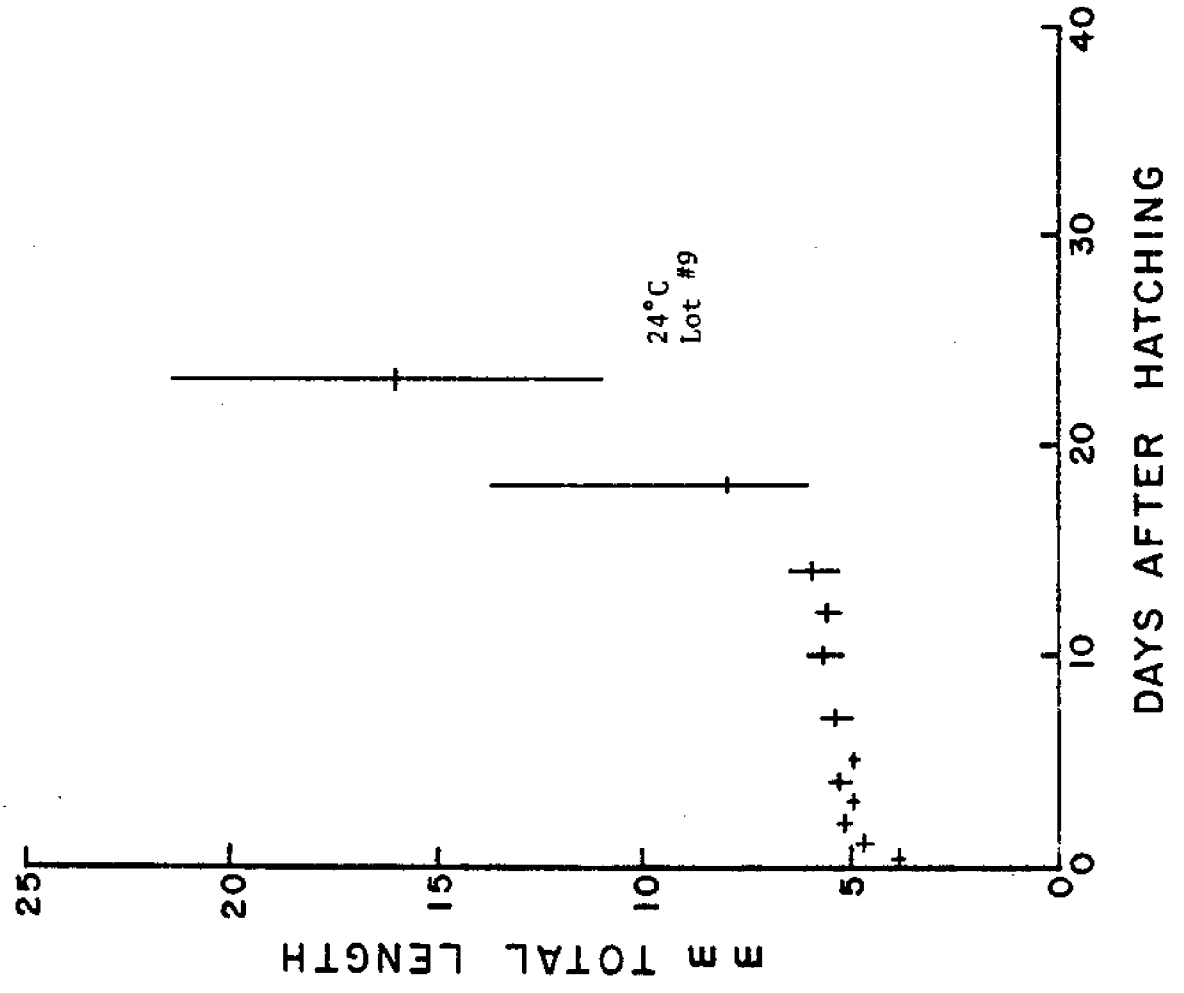
25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15
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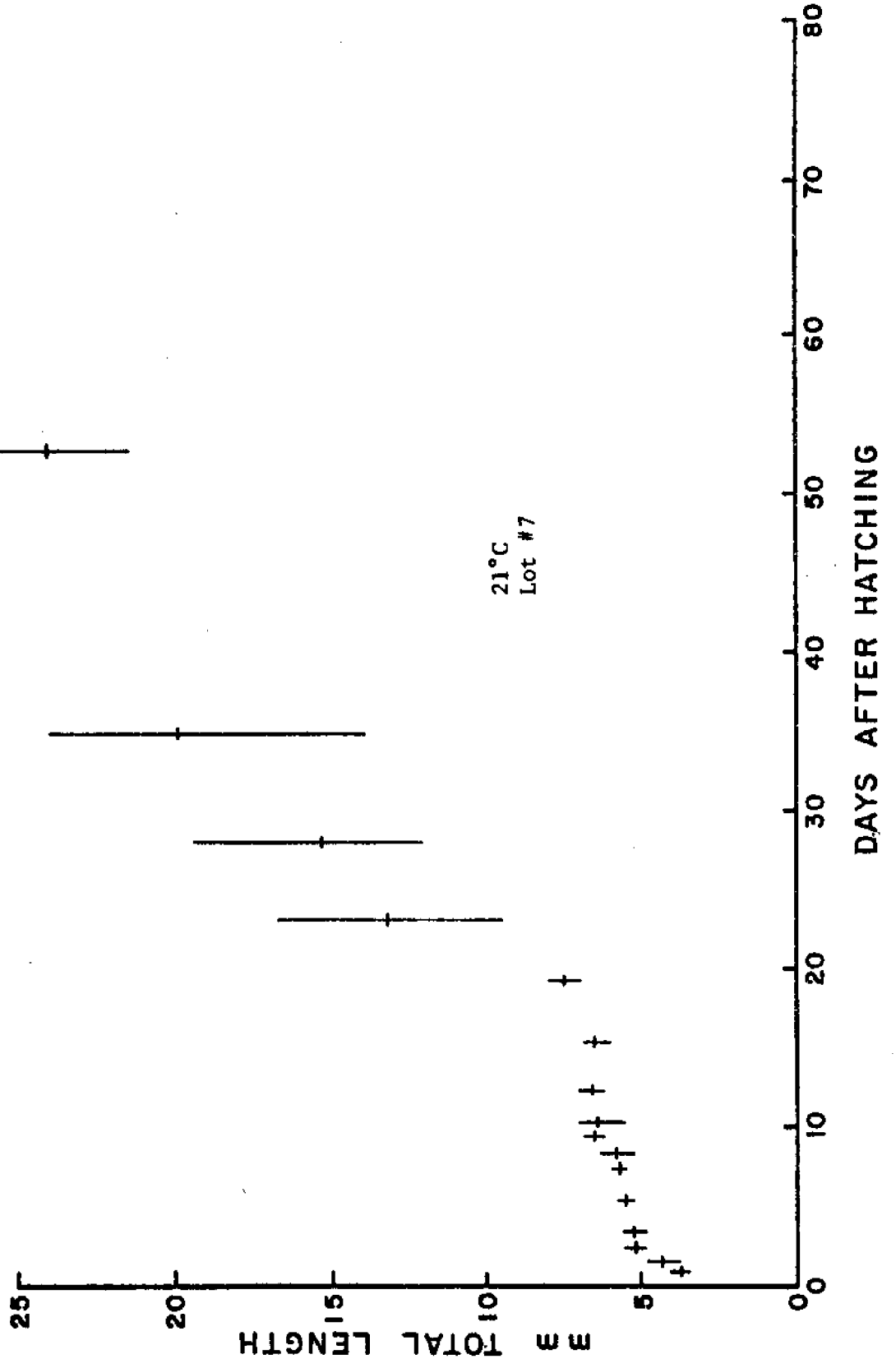
0
10
20
30
40


21°C
Lot #7
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15
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25
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10
20
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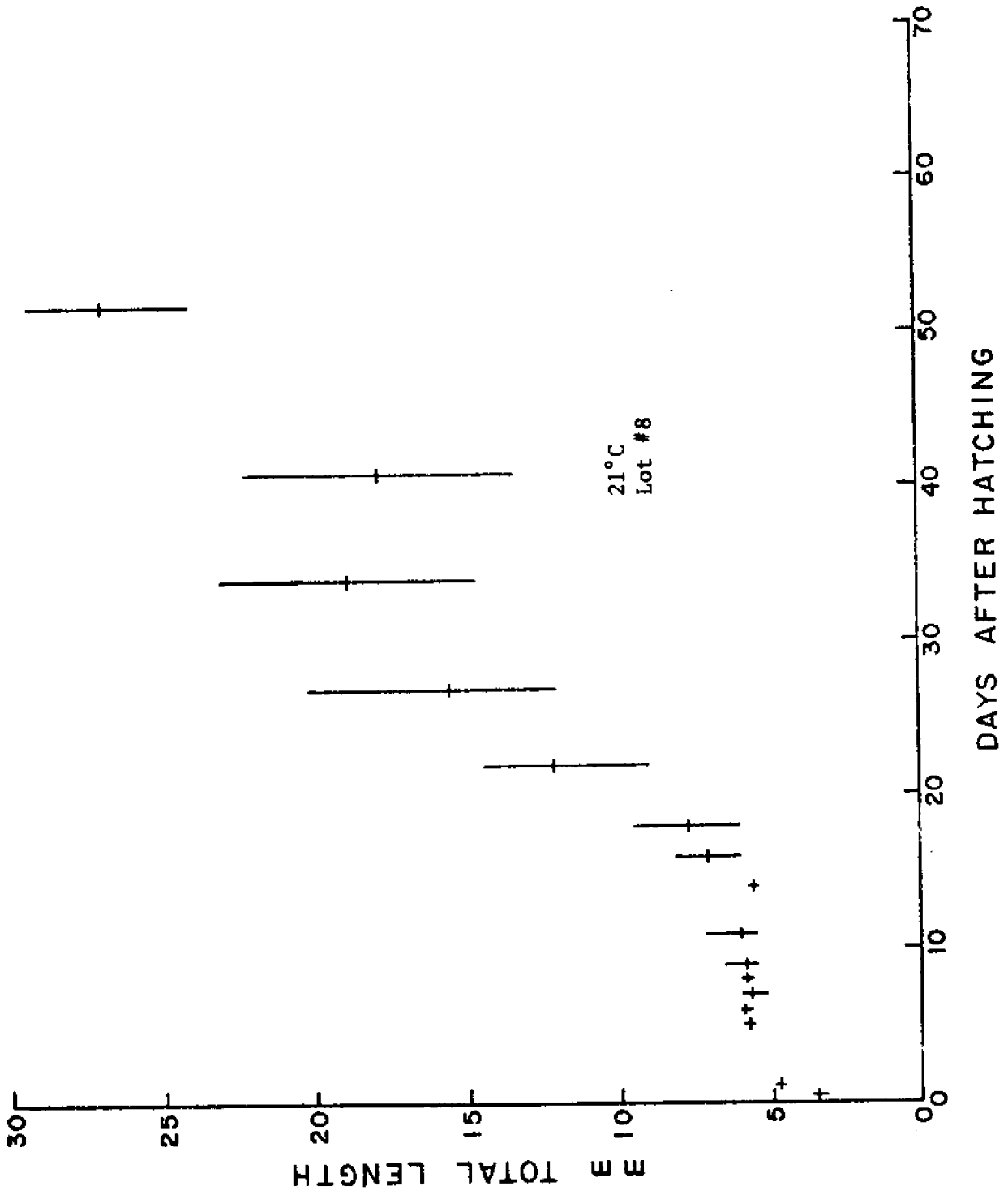
40
50
60
70
80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30
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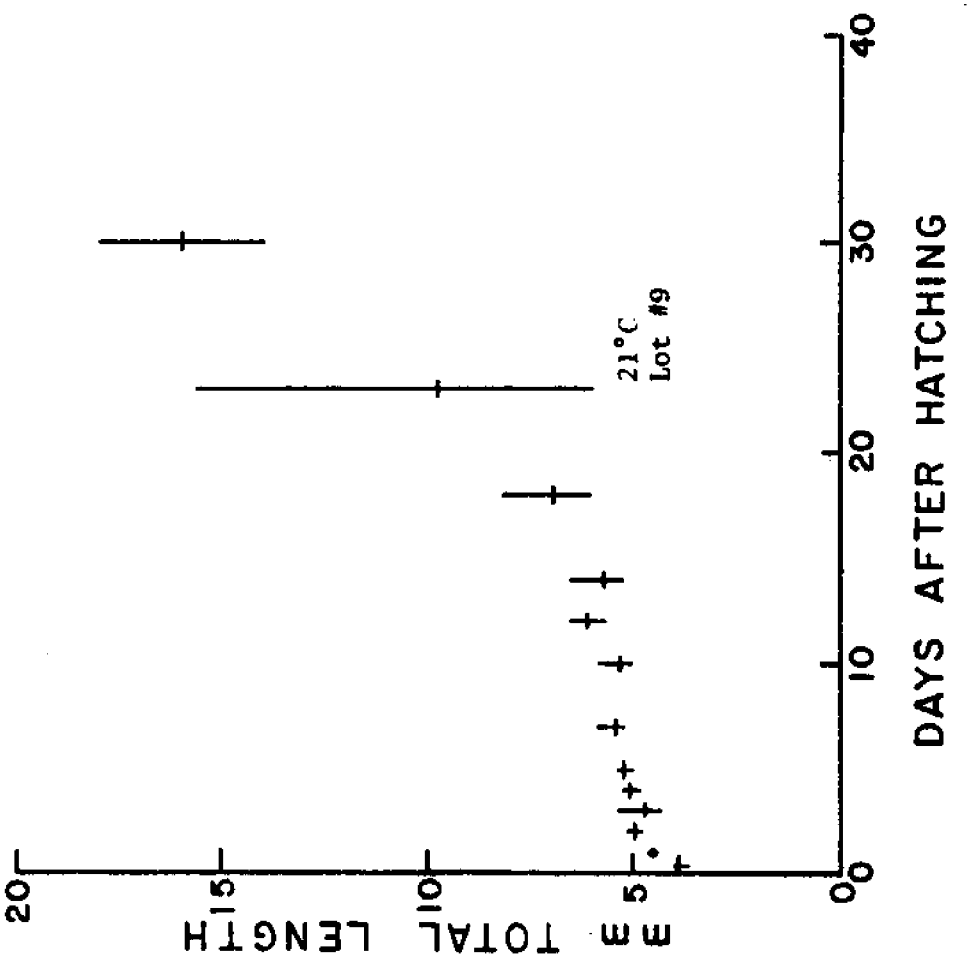
30
40
50
60
70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5
0
mm TOTAL LENGTH
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10
20
30
40
DAYS AFTER HATCHING
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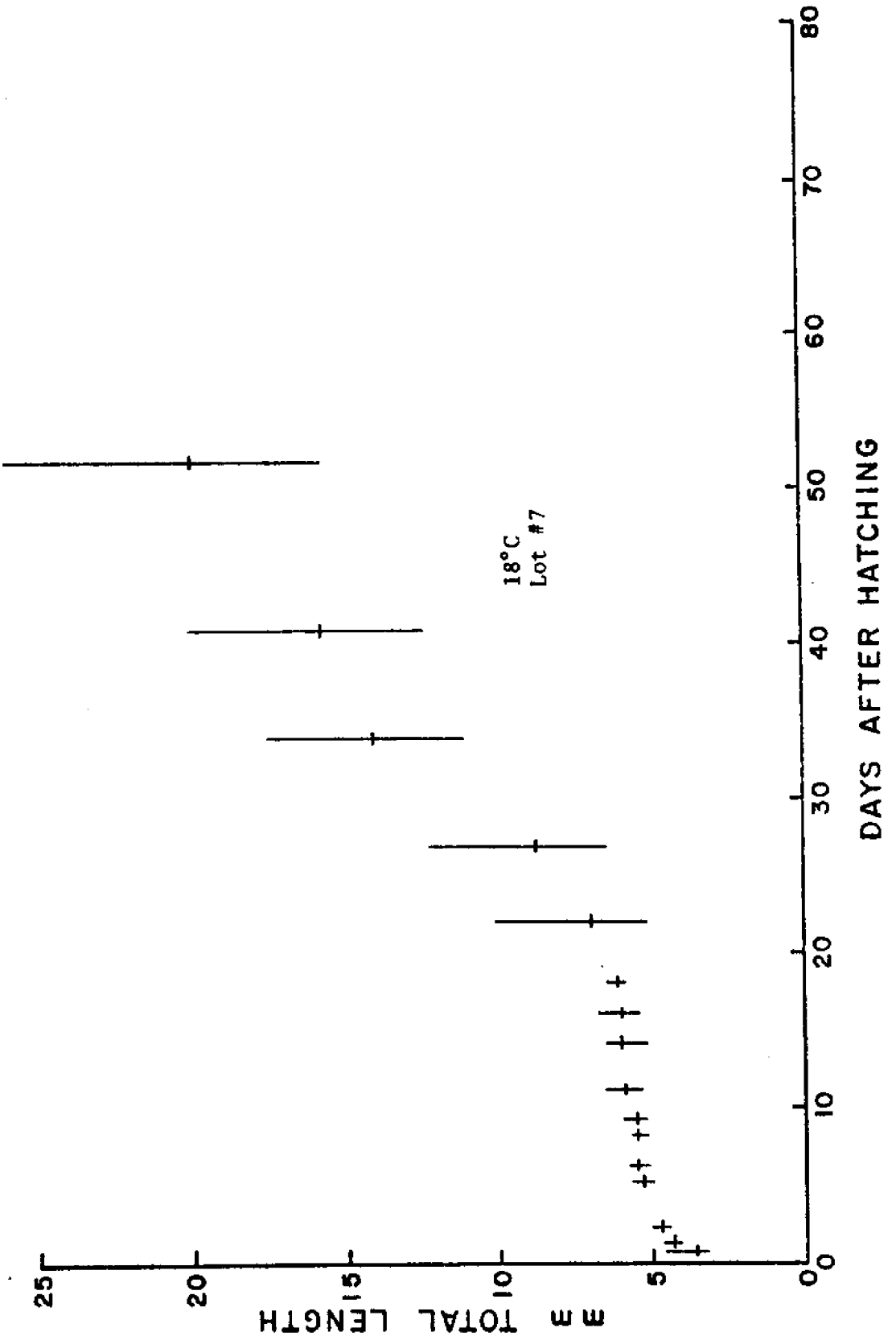
Lot #9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50
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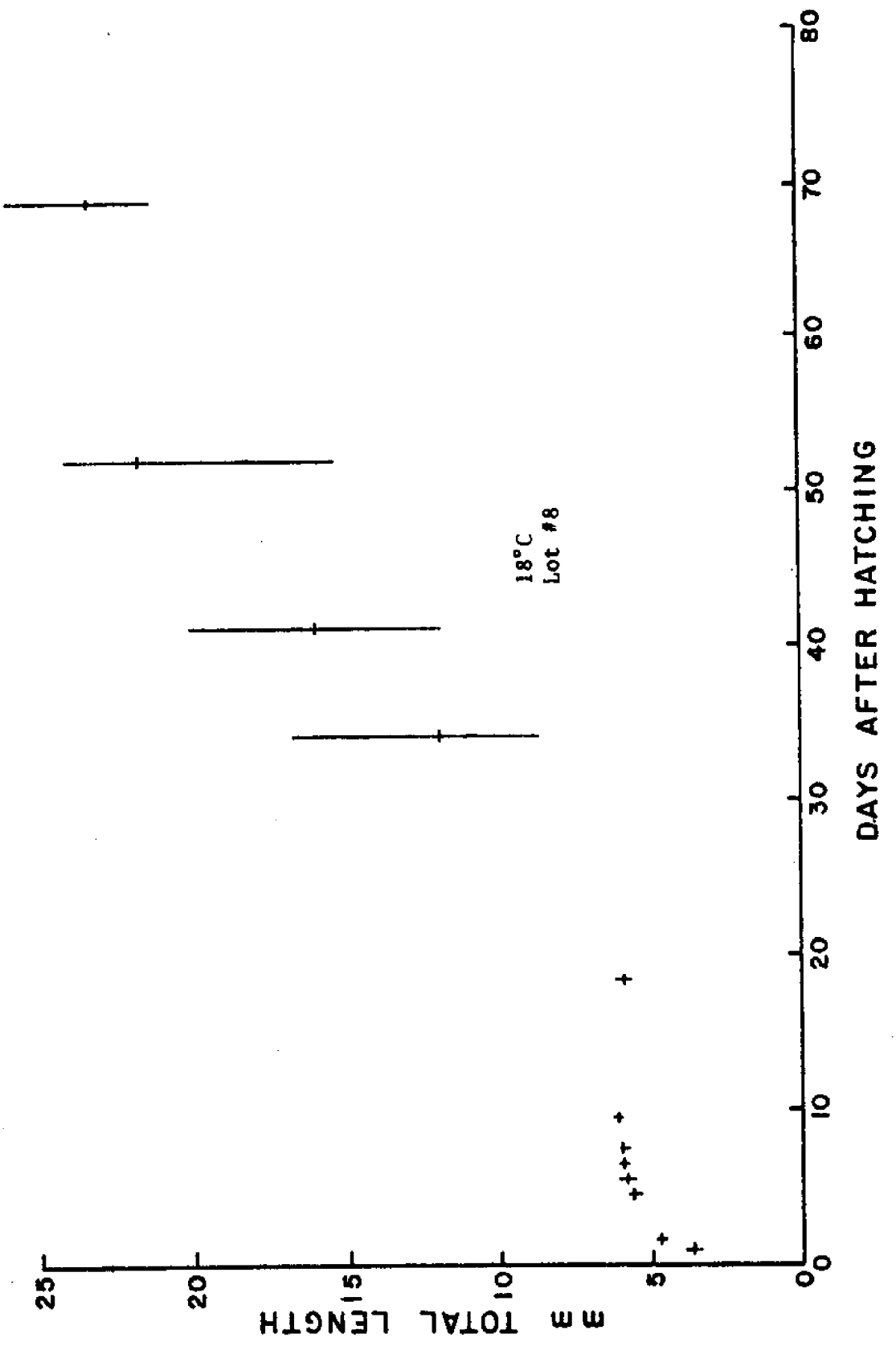
70
80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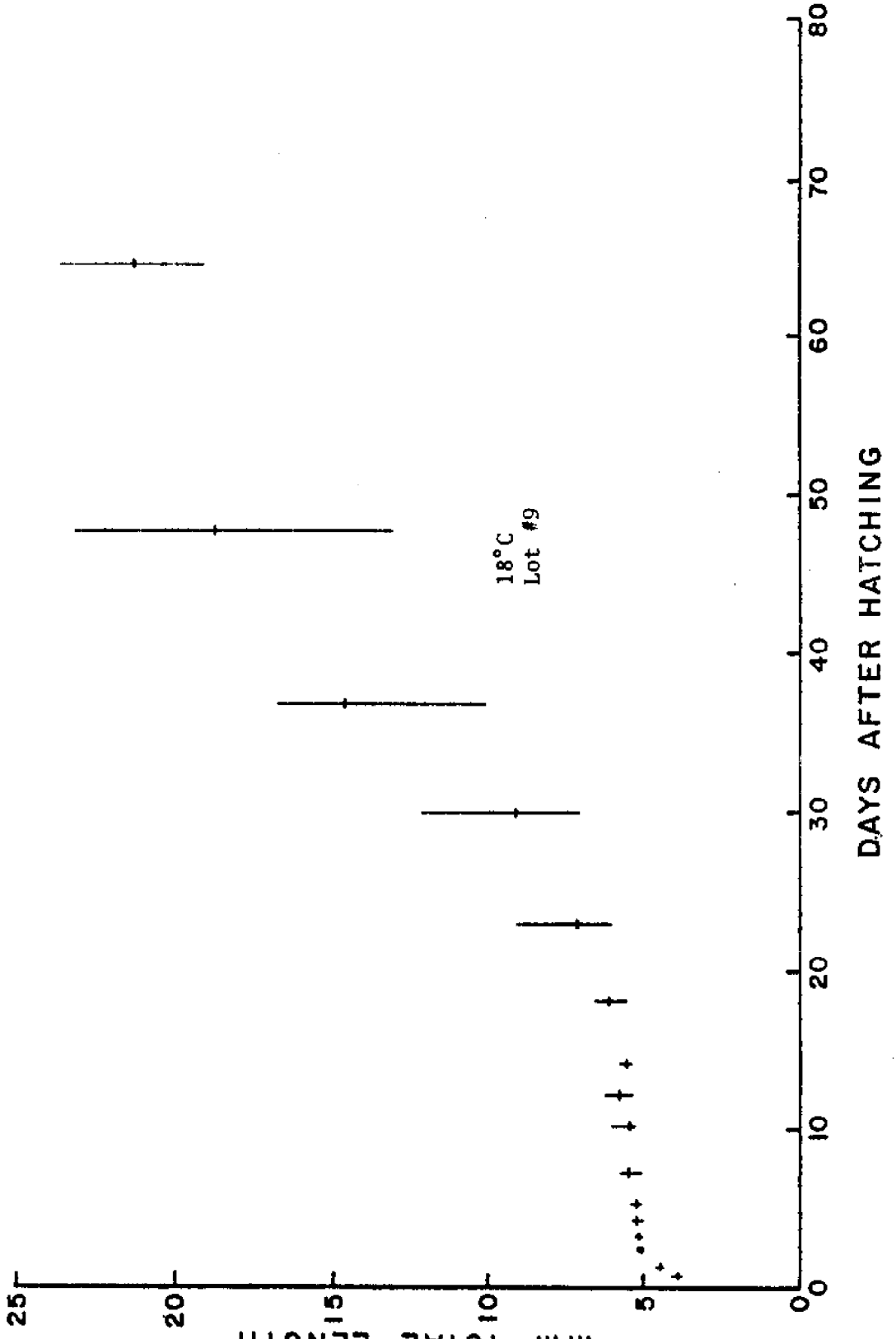
60
70
80
DAYS AFTER HATCHING
18°C
Lot #8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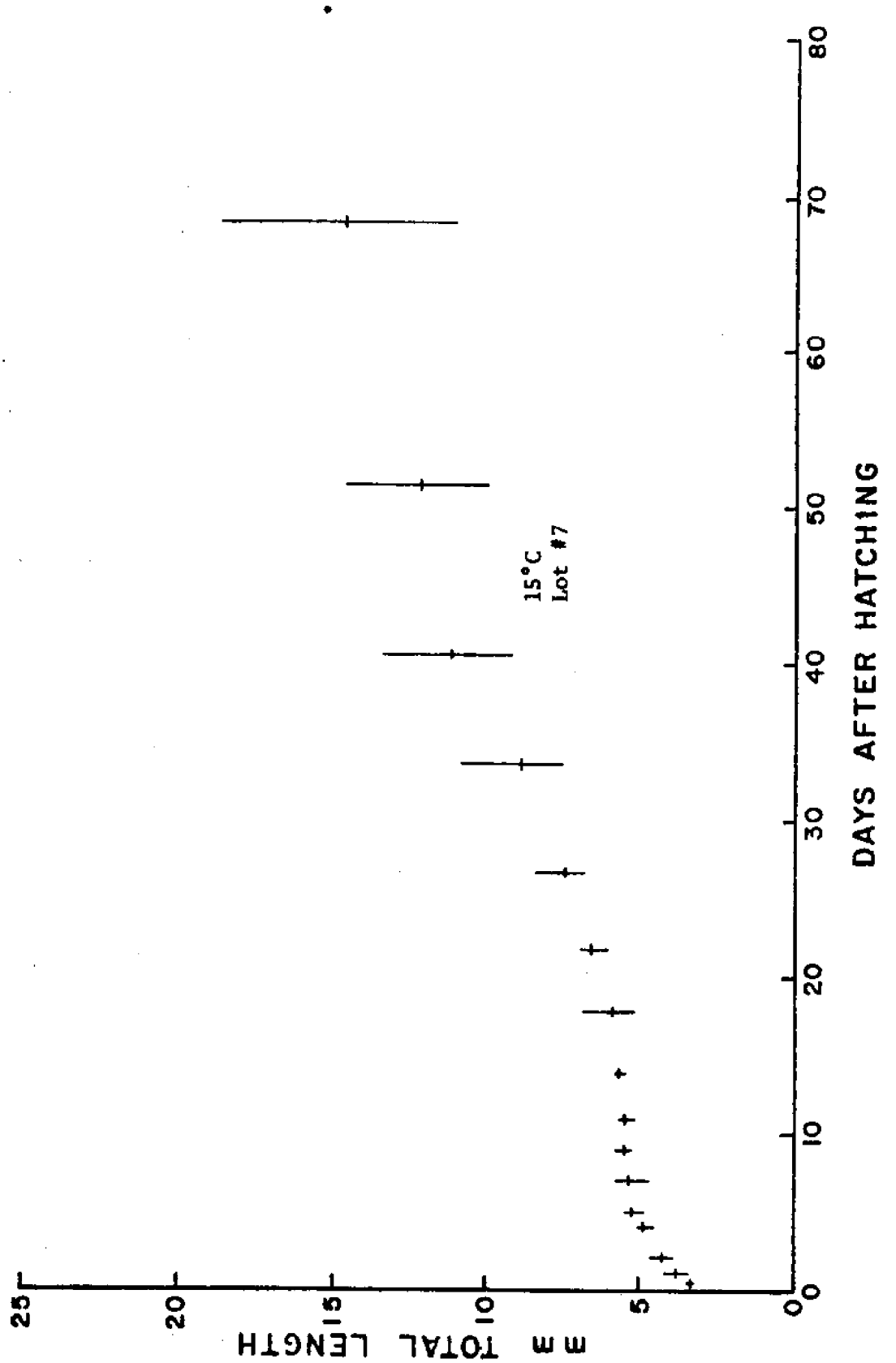
25
10
20
30
40
50
60
70
80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0
0
10
20
30
40
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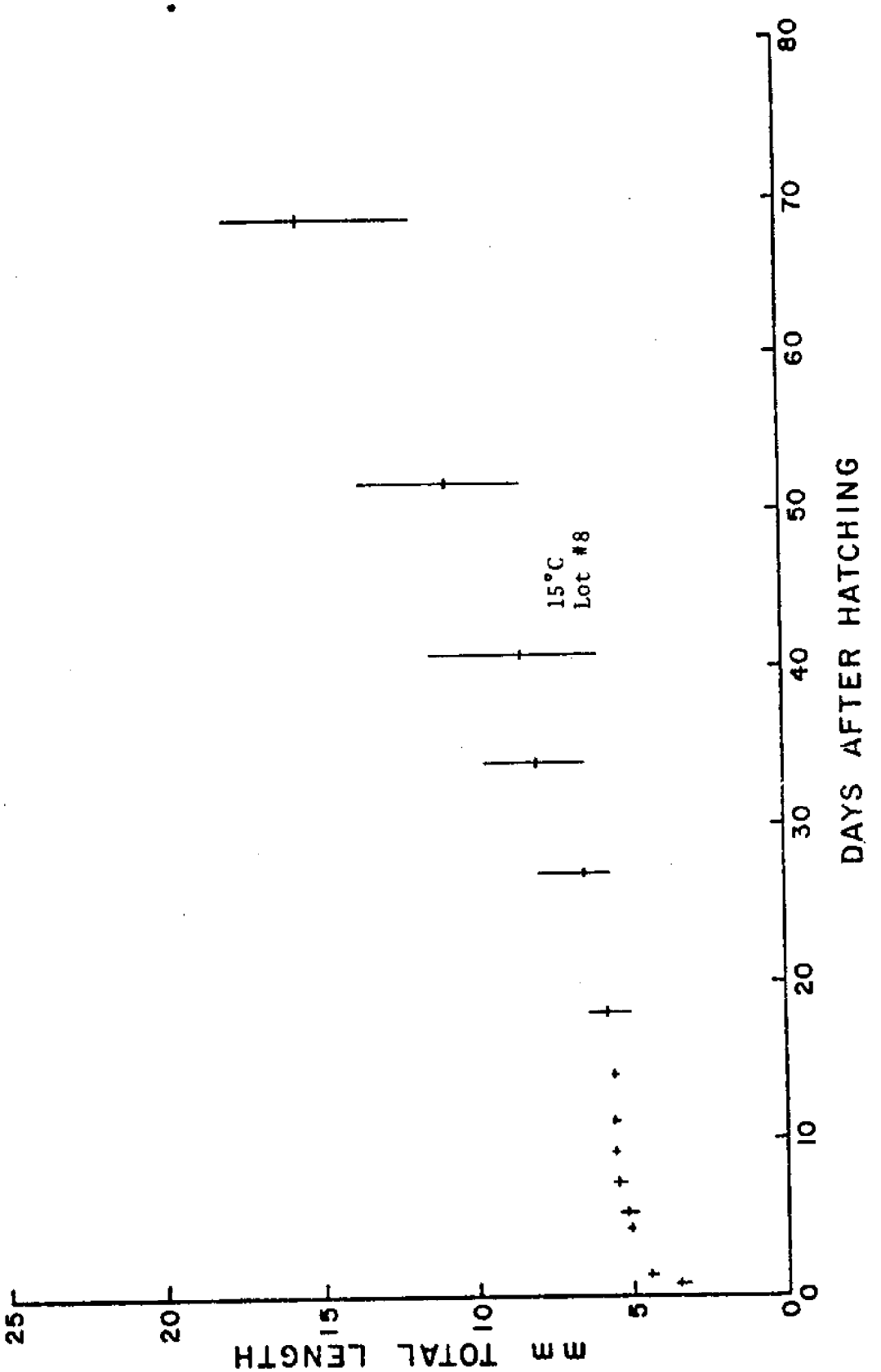
60
70
80
DAYS AFTER HATCHING
15°C
Lot #7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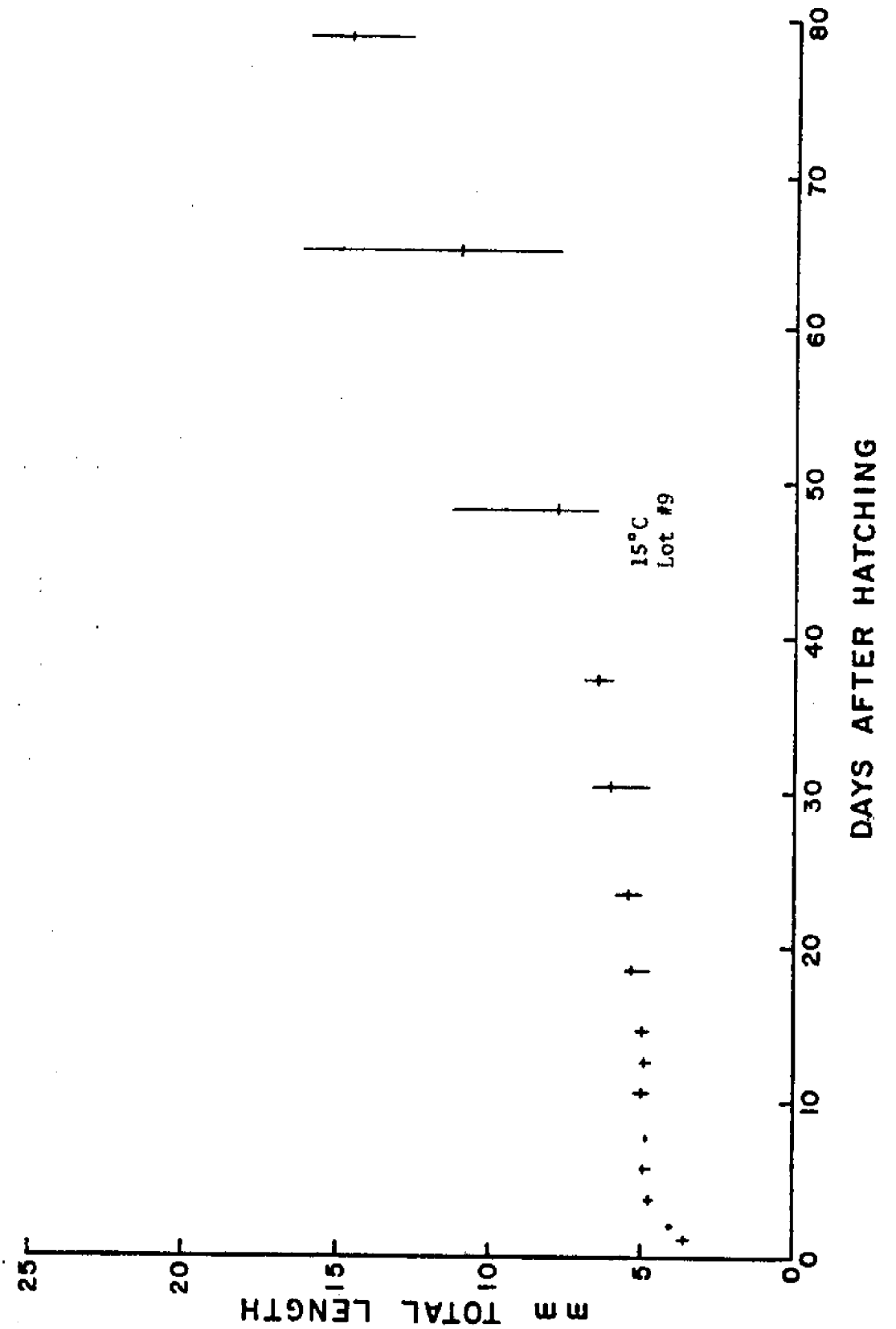
20
30
40
50
60
70
80
DAYS AFTER HATCHING
15°C
Lot #8


mm TOTAL LENGTH
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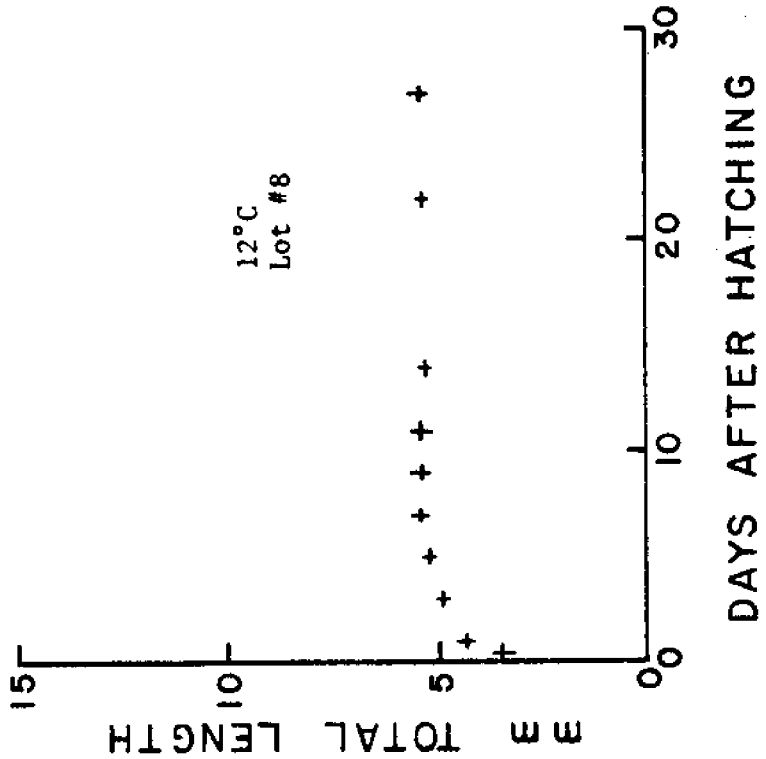
20
15
10
5
0
0
10
20
30
40
50
60
70
80
DAYS AFTER HATCHING
15°C
Lot #9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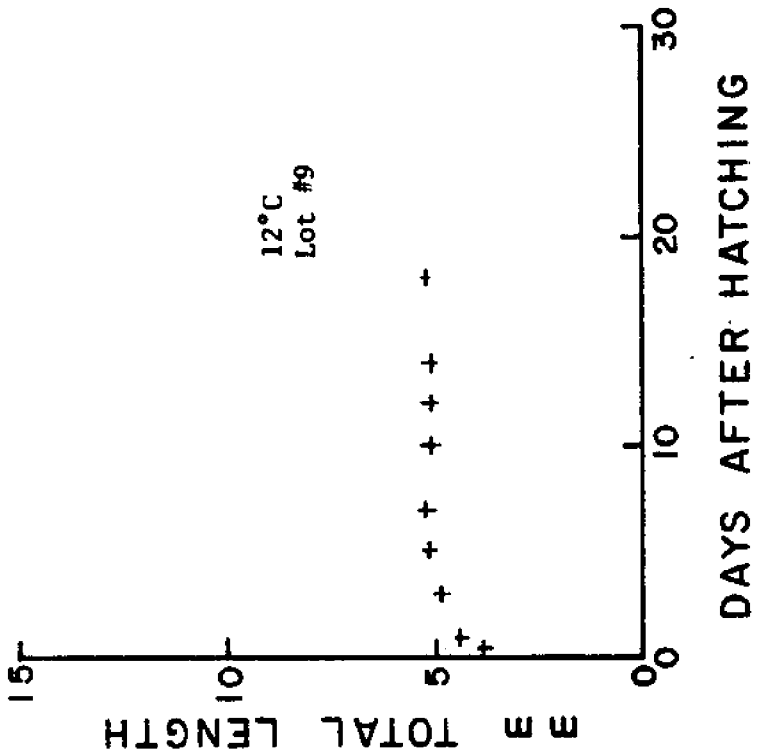
Lot #8
mm TOTAL LENGTH
15
10
5
0
0
10
20
30
DAYS AFTER HATCHING

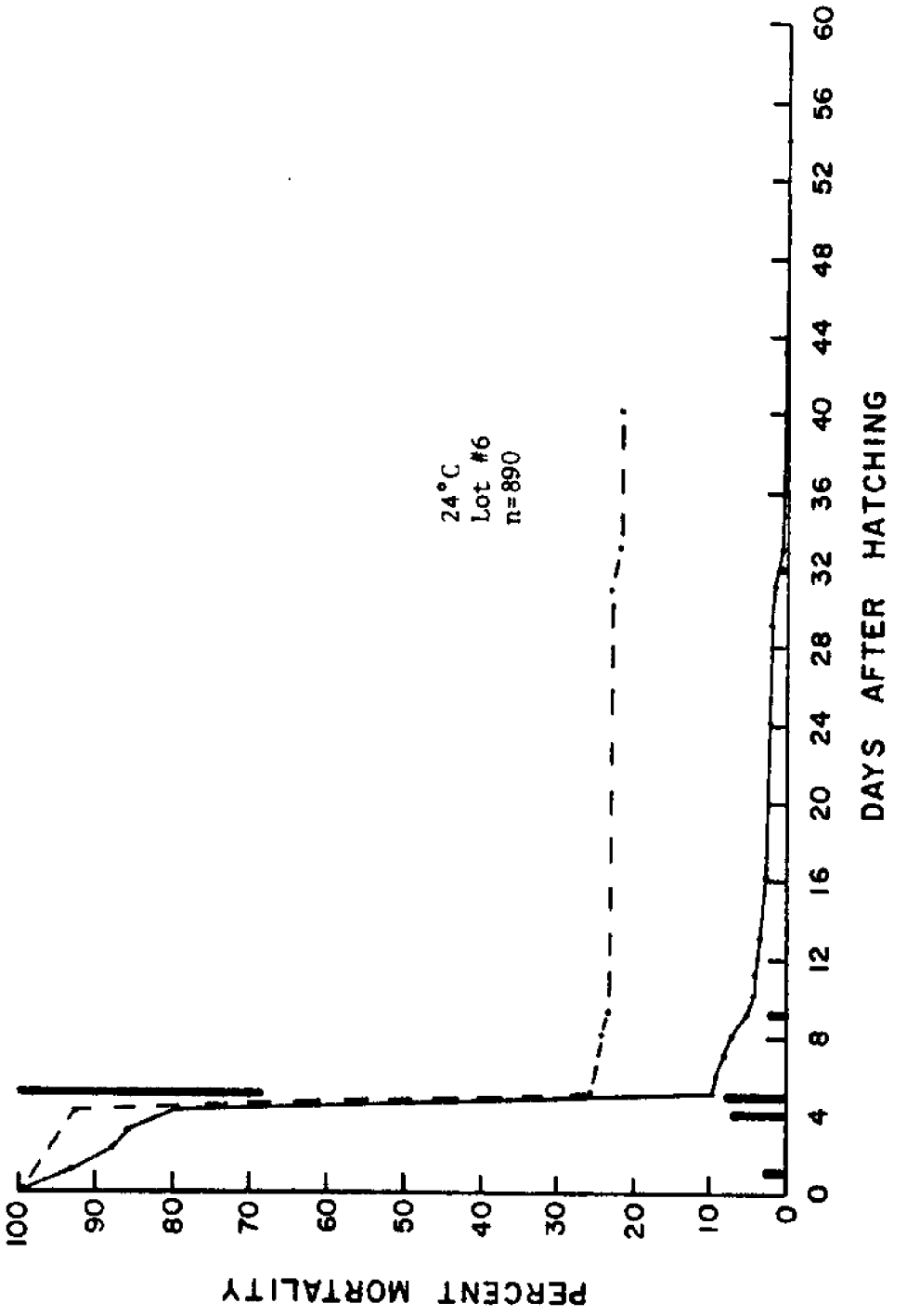

12°C
Lot #9
0
5
10
15
mm TOTAL LENGTH
0
10
20
30
DAYS AFTER HATCHING

Appendix B

Larval Mortality Figures

Legend

-----	non-sampling mortality
———	total mortality (sampling and non-sampling)
spike	mortality by day expressed as a percentage of the maximum observed mortality in one day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PERCENT MORTALITY
DAYS AFTER HATCHING
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30
40
50
60
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12
16
20
24
28
32
36
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44
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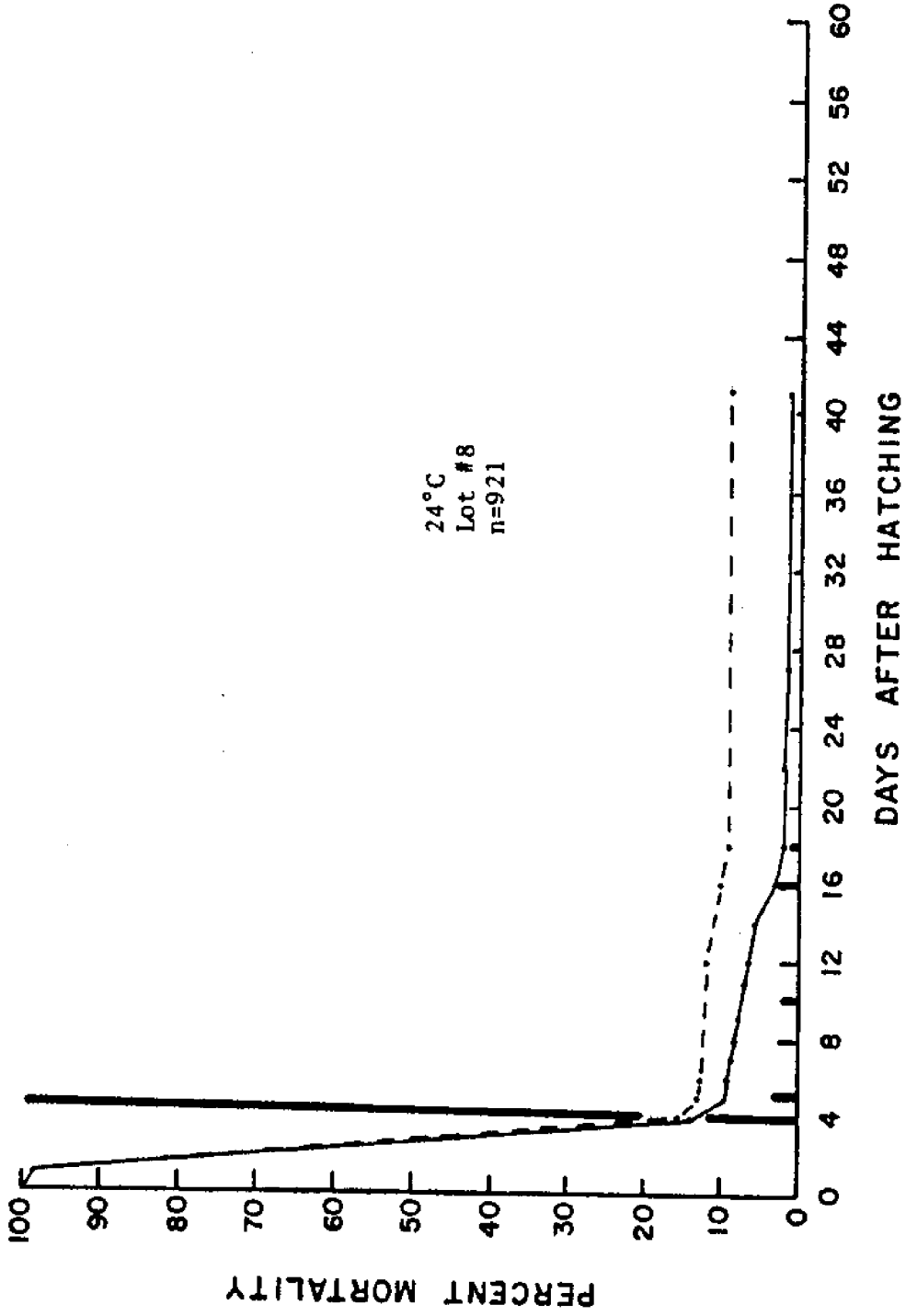
52
56
60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PERCENT MORTALITY
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70
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40
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20
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24
28
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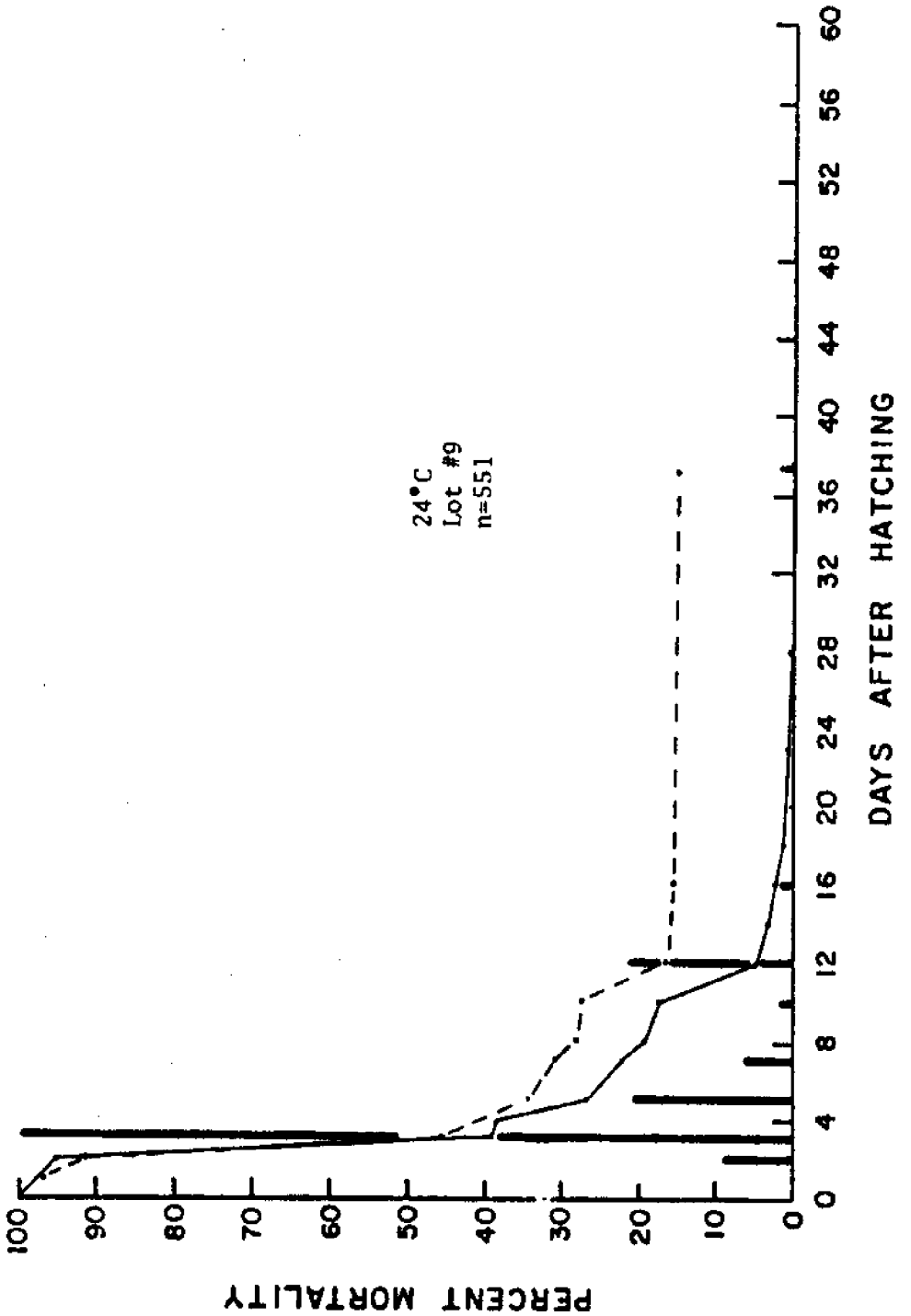
36
40
44
48
52
56
60
DAYS AFTER HATCHING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PERCENT MORTALITY
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70
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40
30
20
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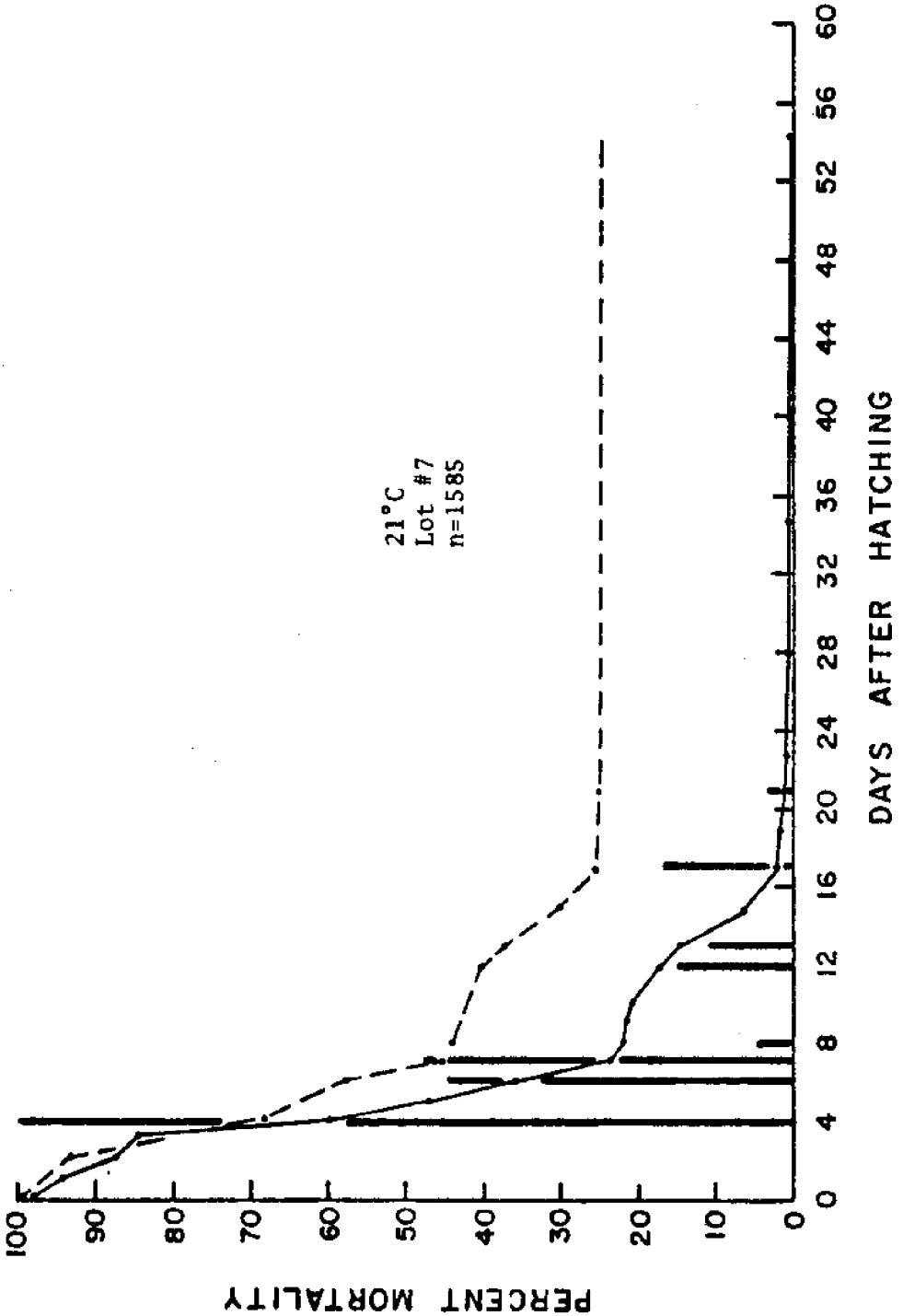
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
DAYS AFTER HATCHING


21°C
Lot #7
n=1585
PERCENT MORTALITY
100
90
80
70
60
50
40
30
20
10
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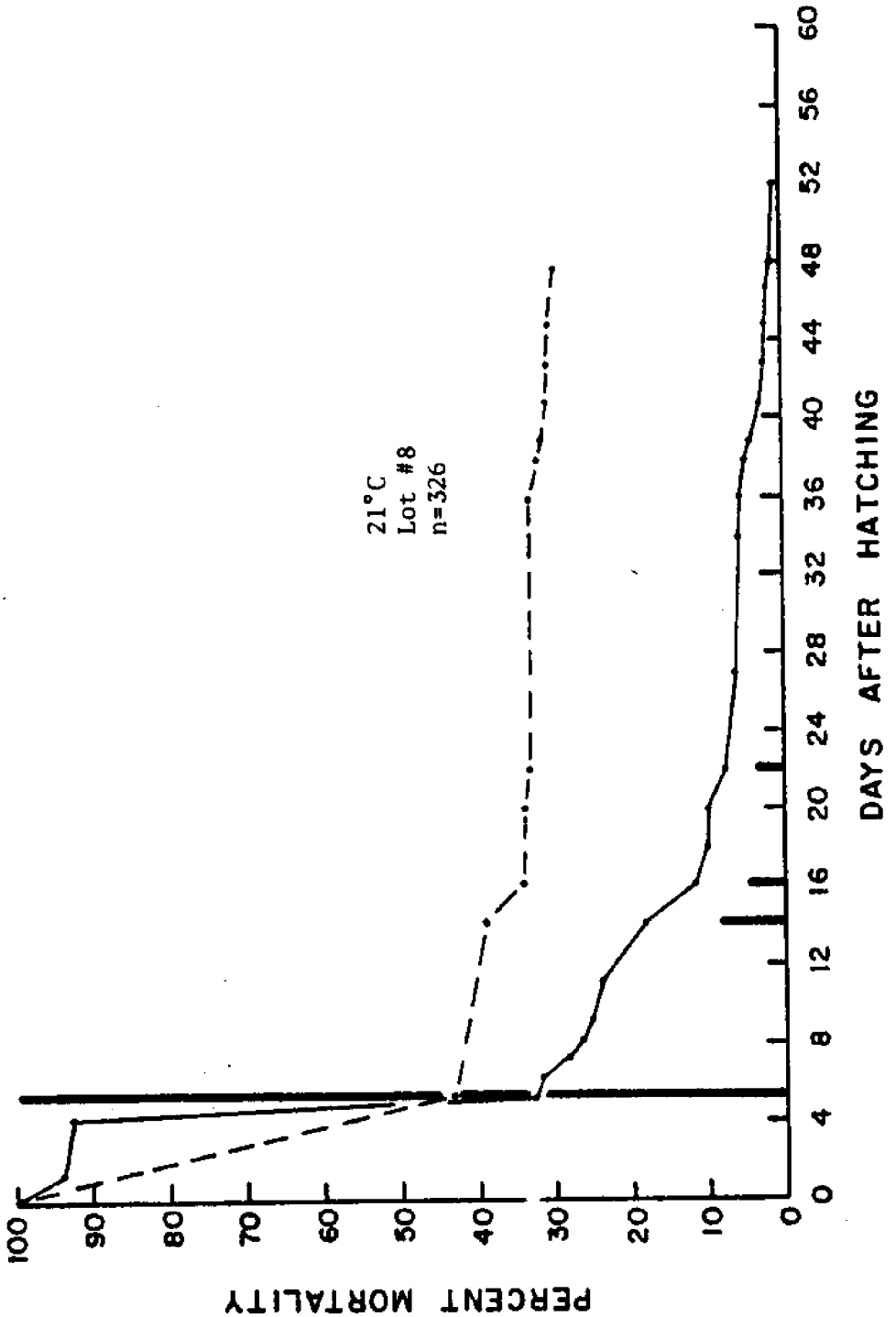
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
DAYS AFTER HATCHING


21°C
Lot #8
n=326
PERCENT MORTALITY
100
90
80
70
60
50
40
30
20
10
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0
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8
12
16
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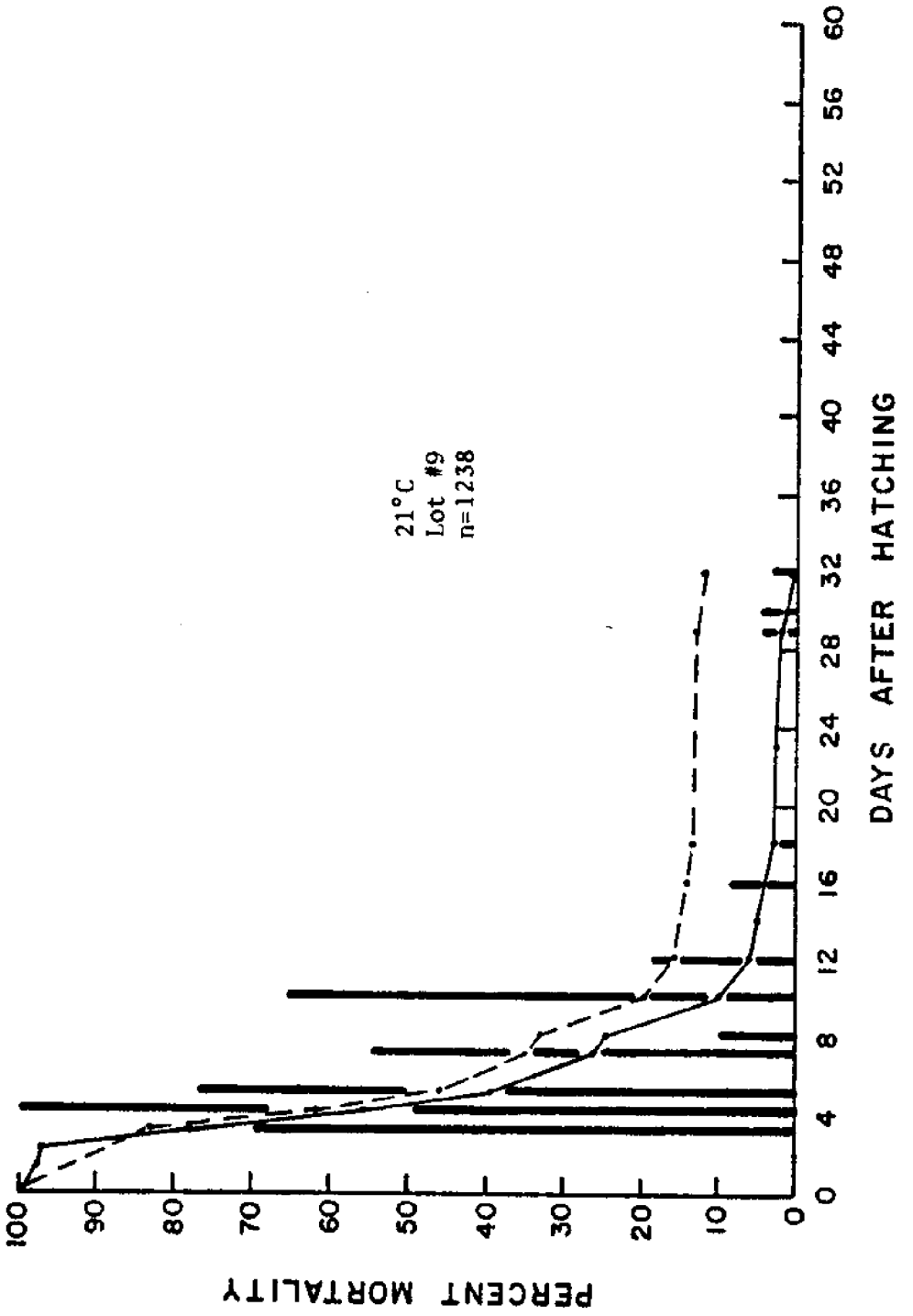
24
28
32
36
40
44
48
52
56
60
DAYS AFTER HATCHING


21°C
Lot #9
n=1238
PERCENT MORTALITY
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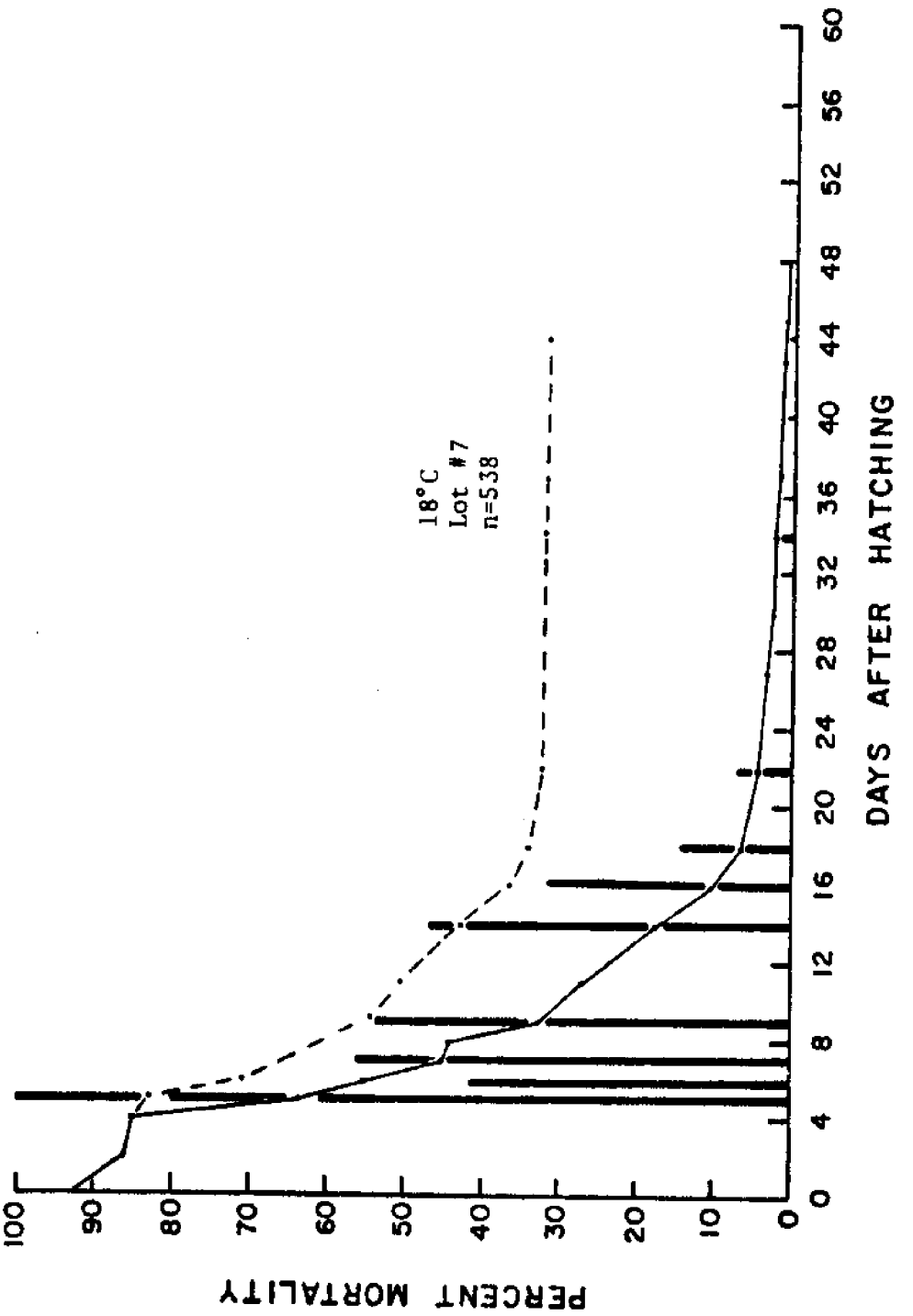
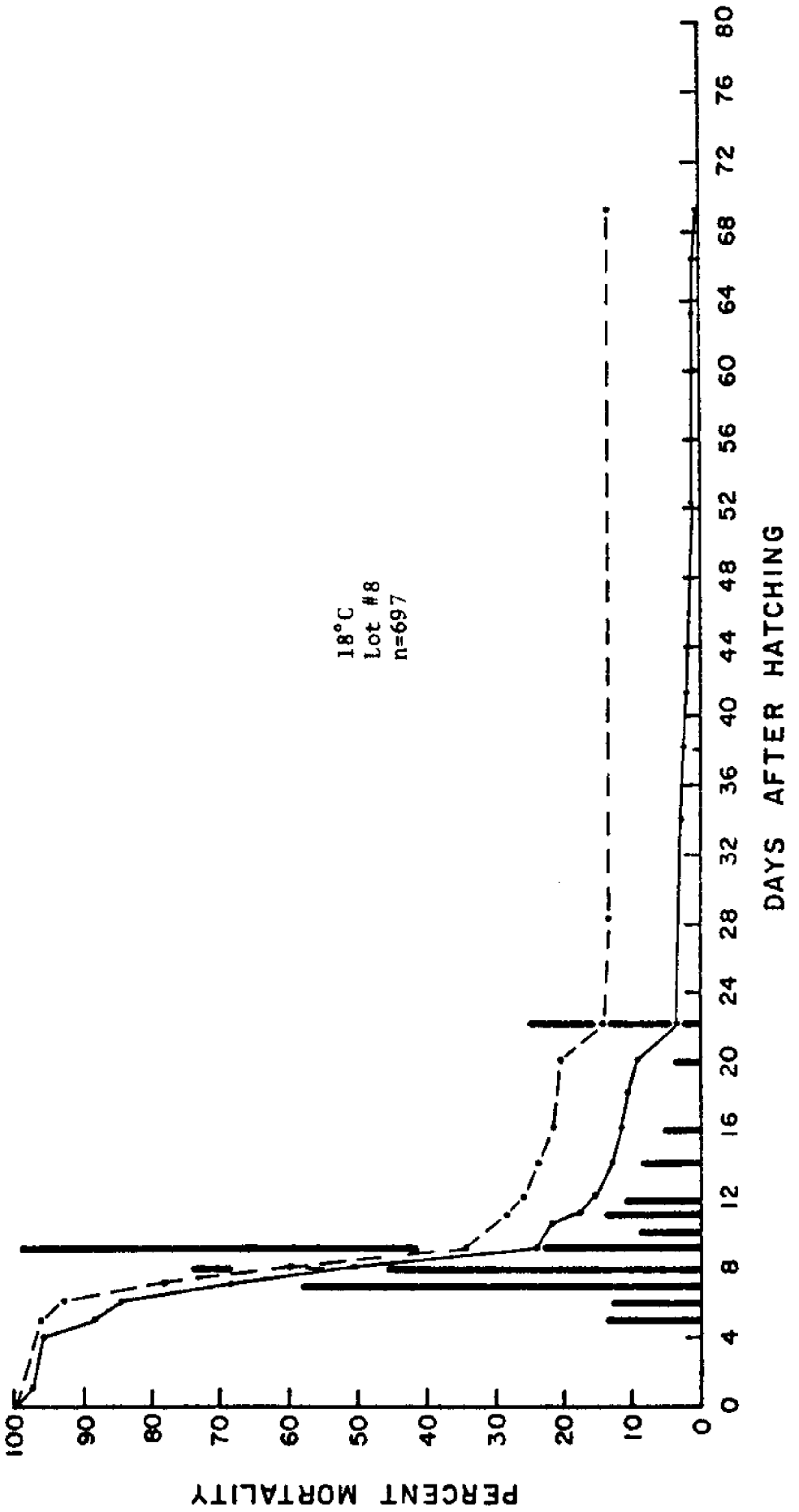
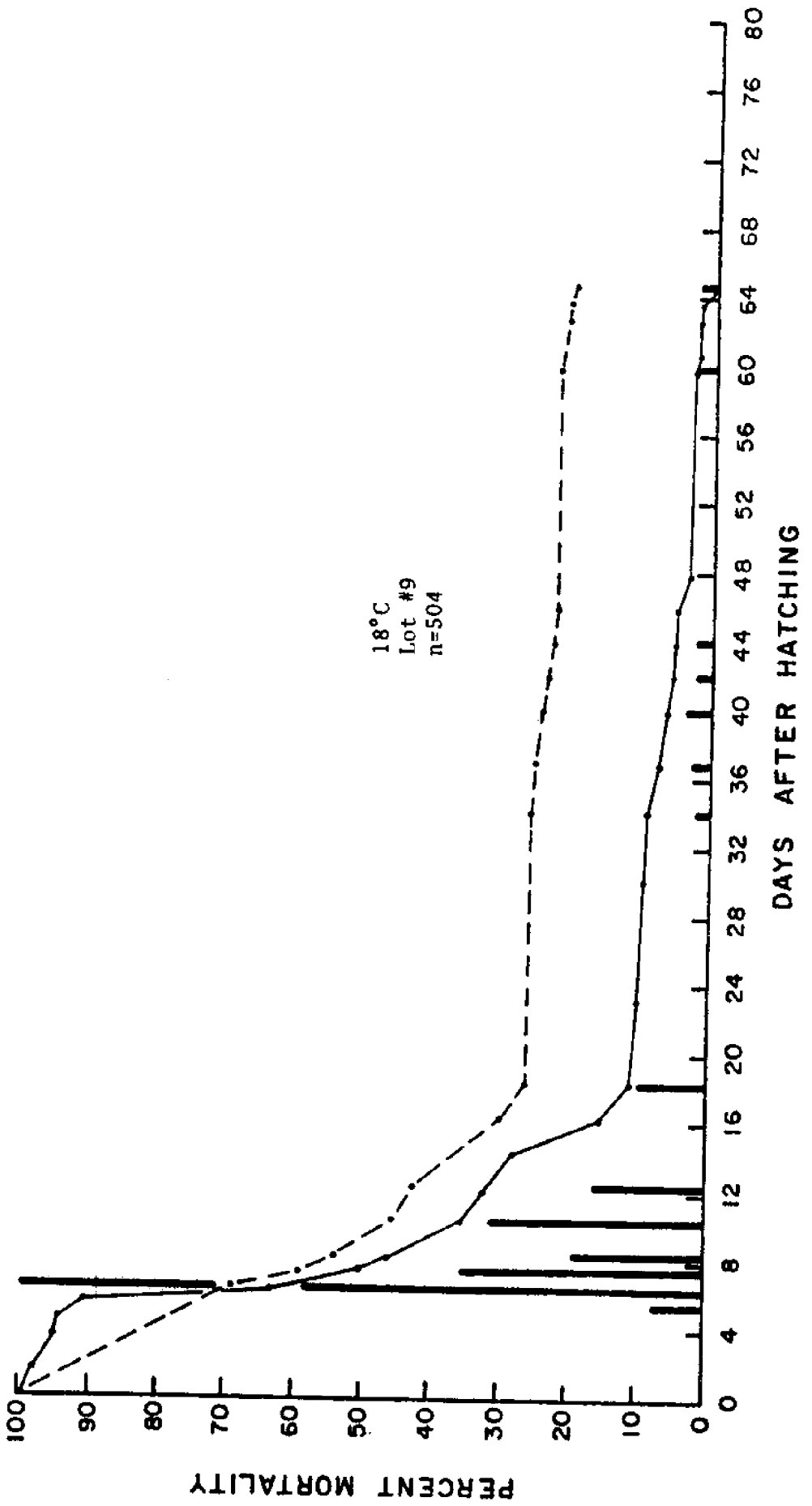
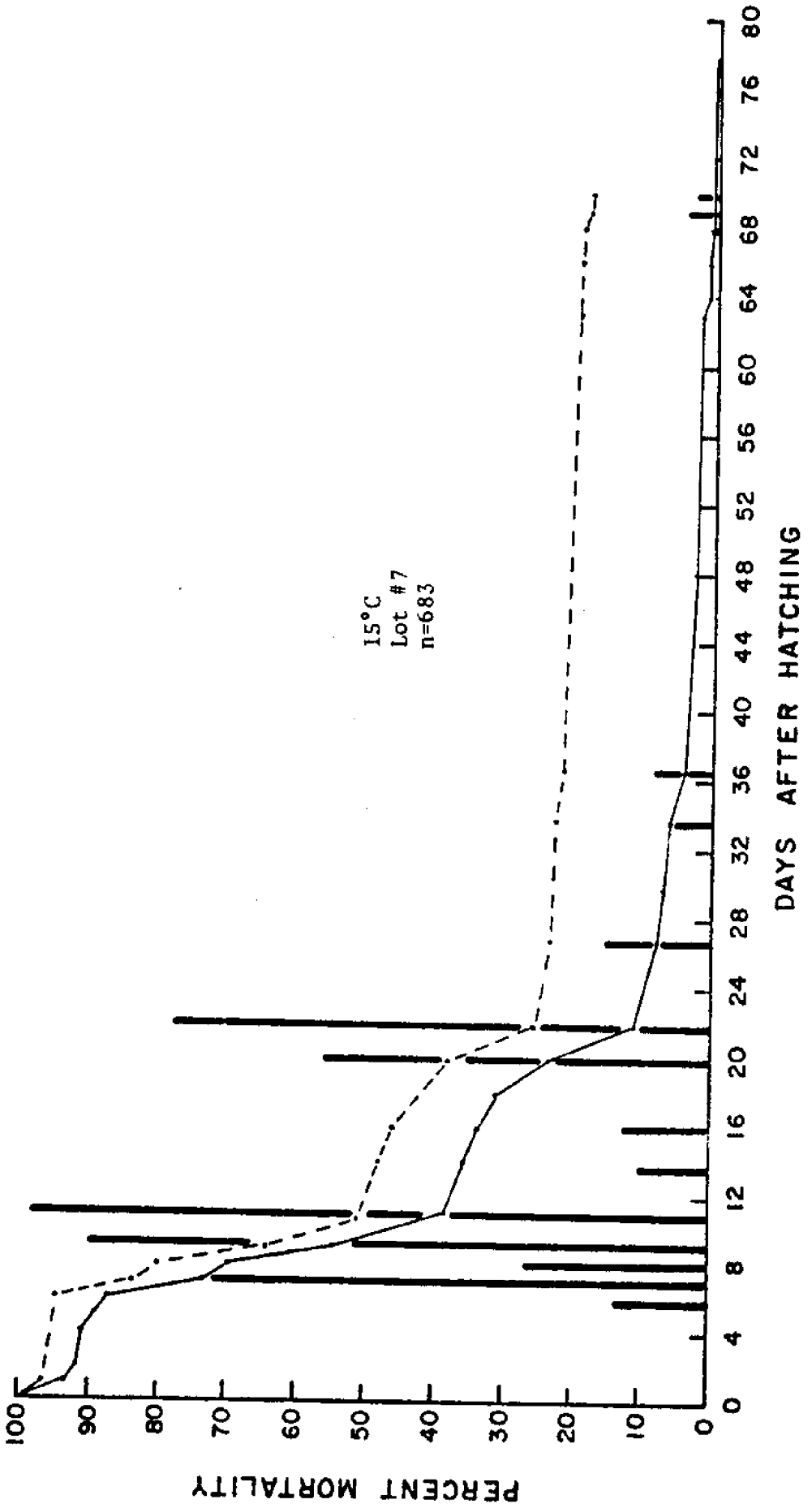
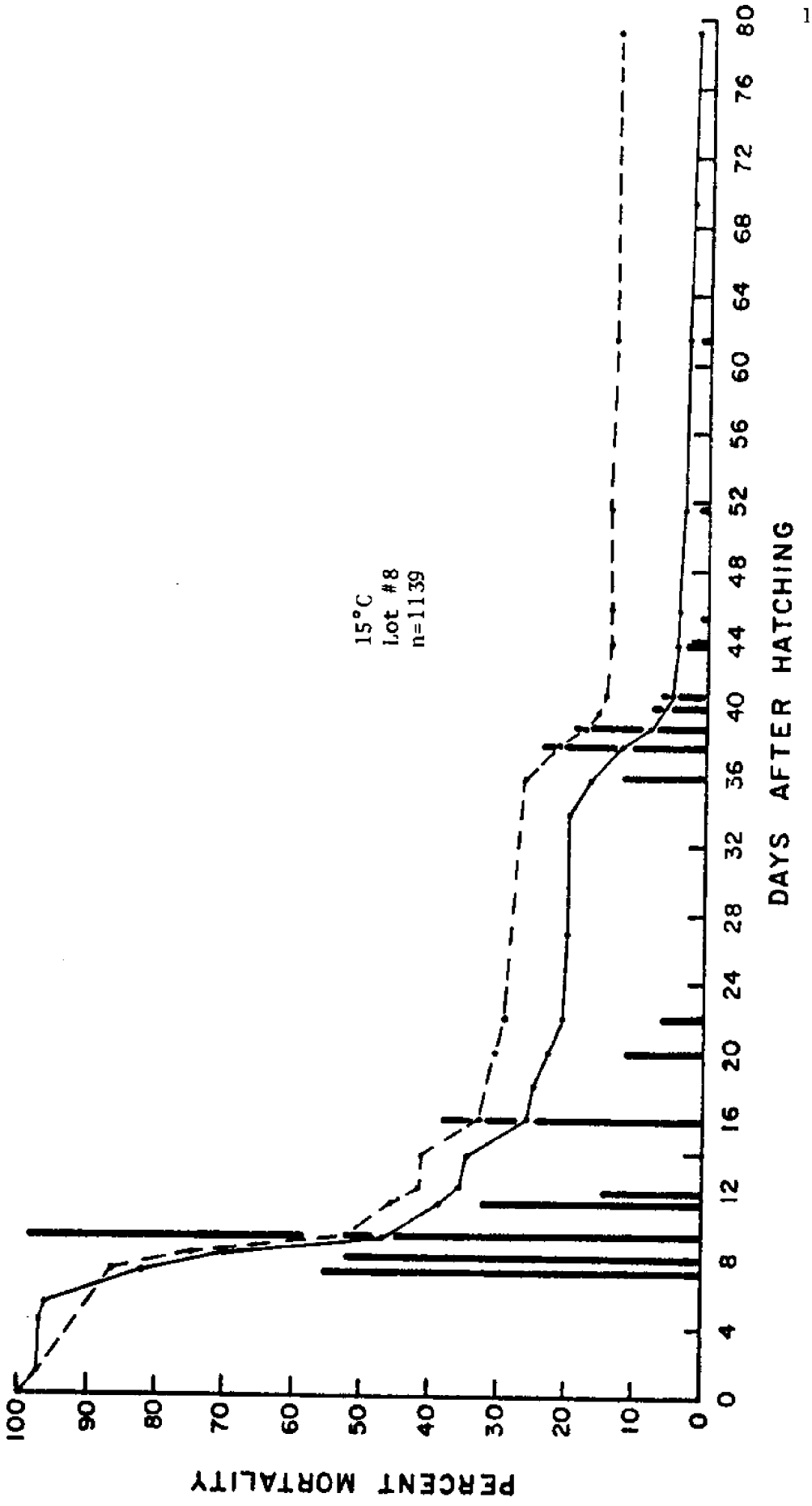
90
80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
DAYS AFTER HATCHING


18°C
Lot #7
n=538
PERCENT MORTALITY
DAYS AFTER HATCHING
0
10
20
30
40
50
60
70
80
90
100
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60


18°C
Lot #8
n=697
PERCENT MORTALITY
DAYS AFTER HATCHING
0
10
20
30
40
50
60
70
80
90
100
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
64
68
72
76
80


18°C
Lot #9
n=504
PERCENT MORTALITY
100
90
80
70
60
50
40
30
20
10
0
DAYS AFTER HATCHING
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
64
68
72
76
80


15°C
Lot #7
n=683
PERCENT MORTALITY
100
90
80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
64
68
72
76
80
DAYS AFTER HATCHING


15°C
Lot #8
n=1139
PERCENT MORTALITY
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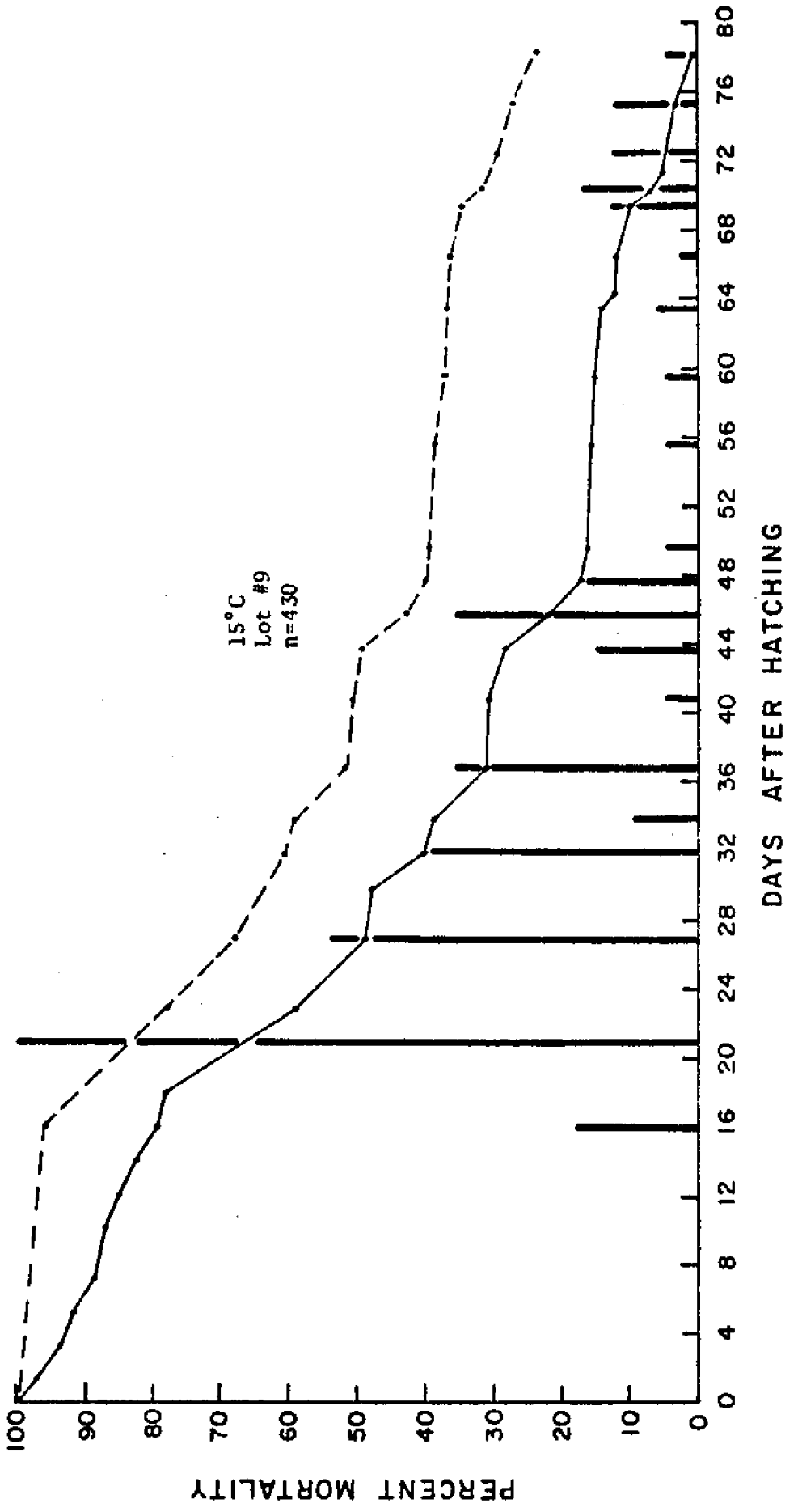
80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
64
68
72
76
80
DAYS AFTER HATCHING


15°C
Lot #9
n=430
PERCENT MORTALITY
DAYS AFTER HATCHING
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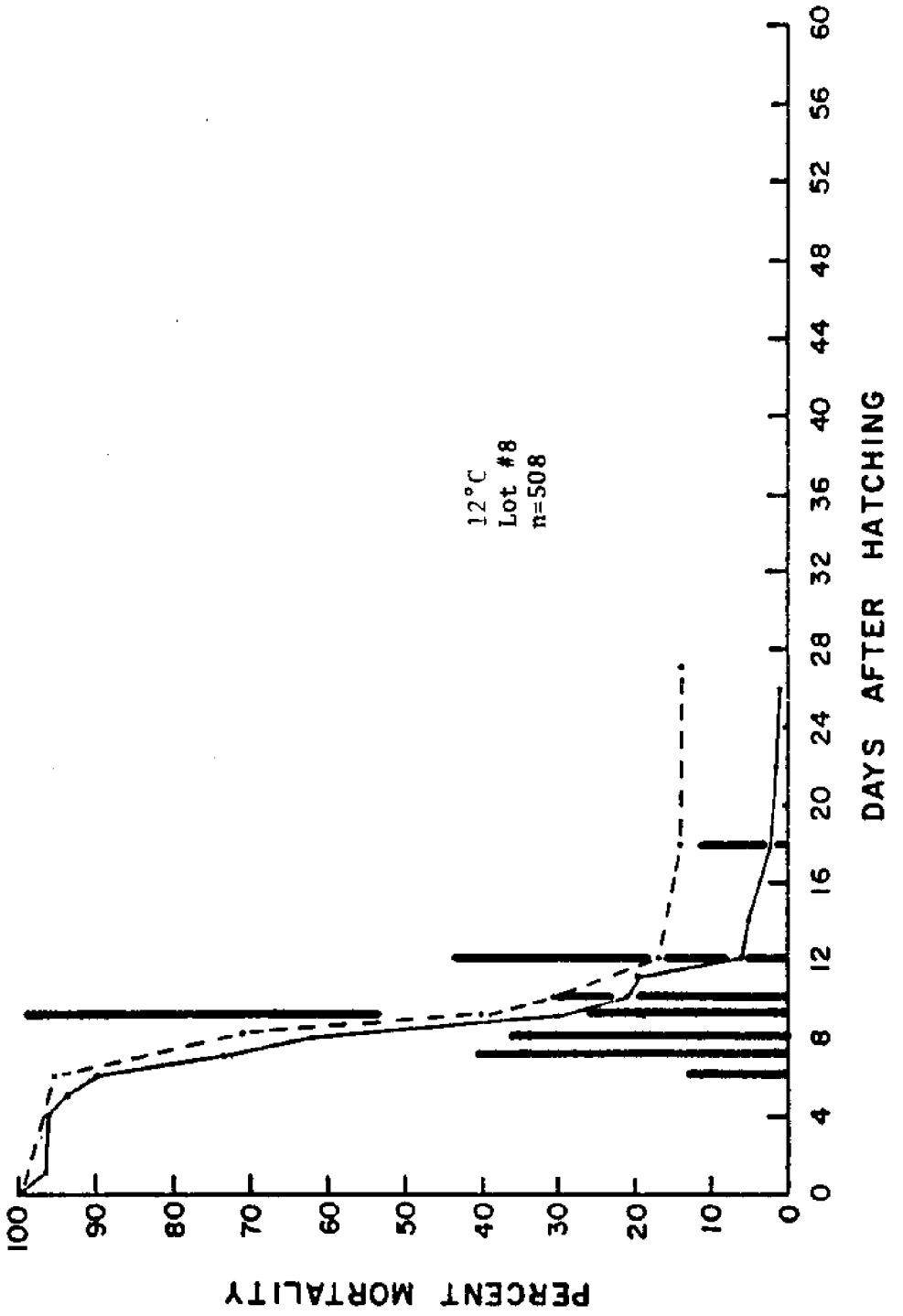
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
64
68
72
76
80
10
20
30
40
50
60
70
80
90
100


12°C
Lot #8
n=508
PERCENT MORTALITY
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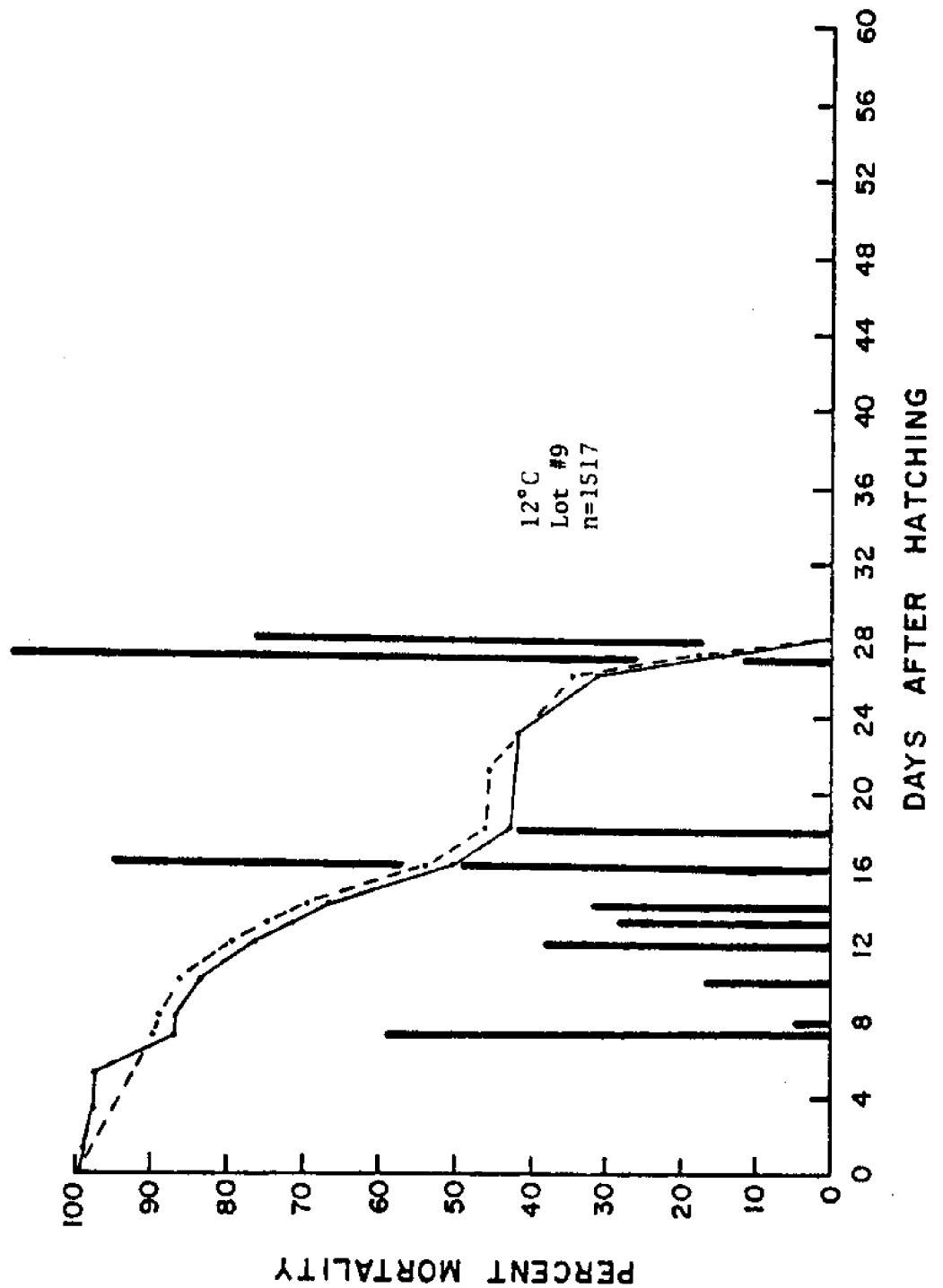
90
80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
DAYS AFTER HATCHING


12°C
Lot #9
n=1517
PERCENT MORTALITY
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80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
DAYS AFTER HATCHING