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

Final Report

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for

Consolidated Edison Company of New York, Inc.
4 Irving Place
New York, New York 10003

Purchase Order Number 5-05666

September, 1976

8111100405 760930
PDR ADOCK 05000247
P PDR

GRADUATE SCHOOL OF OCEANOGRAPHY

NARRAGANSETT MARINE LABORATORY

Contract #50-241/286
Control # 11852
Date 11-18-76 of Commerce
REGULATORY DOCUMENTS

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SUMMARY AND CONCLUSIONS

The effects of rearing temperature on the life stage durations of embryonic and larval striped bass, *Morone saxatilis*, were determined experimentally. Striped bass eggs, prolarvae, and postlarvae were maintained in the laboratory at five fixed temperatures of 12°, 15°, 18°, 21° and 24°C. The temperatures spanned the range encountered by these stages in their natural environment.

In all the stages studied, stage duration decreased with increasing temperature. The time from fertilization through hatching was related to temperature by:

$$\text{time to hatching (hours)} = 258.5e^{-0.0934\ (\text{Temp. } ^\circ\text{C})}$$

The duration of developmental events prior to hatching was related to temperature in much the same way as was the time to hatching. The duration of the prolarval and postlarval stages decreased with increasing temperature. However, differences in the pattern of growth among the progeny of different matings resulted in marked variability in response among the stages examined. Under laboratory conditions, mortality at all stages increased with increasing temperature. There was heavy, largely unexplained mortality among the prolarvae in all lots.

It is concluded that while many factors affect larval survival and stage duration in nature and in the laboratory, the effect of temperature is important and should be taken into account in the preparation of life history models for the striped bass.

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).

A number of simulation models have been devised for 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 early life stages of fish can be improved by incorporating relevant specific biological 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. These are based on the degree of structural development and the mode of larval nutrition (Hubbs, 1943).

Eggs, prolarvae or yolk-sac larvae, and the postlarvae can be identified in river ichthyoplankton samples. Because each of these stages defines a sequential part of the developing ability of the young fish to avoid 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 ultimately be able to avoid entrainment. The duration of a life stage determines the length of time that these fish will be vulnerable to entrainment.

Knowledge of water movements, avoidance abilities of 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

may accurately predict the extent of losses attributable to 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 of appearance of various stages in plankton and beach seine collections following striped bass spawning has been observed. While this approach has provided good estimates of stage duration under natural conditions, experimental studies provide the best means of isolating the effect of a single given environmental factor from the many conditions that affect stage duration in the river. Although the study of larval fish biology is still in its infancy, it is clear that the pattern of growth seen in the increasing modal size of larvae is a result of the interaction of a variety of factors, including some not yet properly identified. Among factors that have been identified as affecting success and rate of embryonic and larval development are: temperature, salinity, dissolved oxygen, water-borne toxicants, food type, food abundance, density of individuals, and disease.

Although it is impossible to take all factors into account, some can be systematically varied and the results observed. This experimental approach permits the identification of particular factors, but introduces a measure of simplicity which does not exist in nature. This simplicity is due to elimination of the influence of other factors and factor interactions. The value of this approach is that it helps to identify 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 every 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. Temperature affects the maintenance energy requirements of the embryo. Hence the efficiency of conversion of yolk to embryonic tissue is affected. After the change from endogenous to exogenous energy sources, the nature and abundance of food becomes the primary determinant of larval growth. The larva must receive sufficient food to meet its maintenance requirement. This includes the cost of searching and capturing prey as well as the energetic equivalent of whatever growth in biomass it is able to attain. The energetic costs of activity and maintenance are intimately related to temperature. Hence temperature determines the amount of energy available for growth. When the diet is more than adequate 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 which have been reviewed by Blaxter (1969). The period between fertilization and hatching has received the most attention. This is also the case for striped bass (see Bayless, 1972). The time course of developmental events prior to hatching has been observed at one constant temperature by Bayless (1972) and at a slowly rising temperature by Mansueti (1958). While 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 males and females collected on the spawning grounds in the Hudson River between Cornwall and Croton, New York. Samples of fertilized eggs were provided by Texas Instruments, which operates a striped bass hatchery at Verplank, New York. Ripe adults were captured using haul seine 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. Vital statistics of the brood female 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.

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 with 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.

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.

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

Growth in body weight is continuous throughout all these stages, and growth in body length is continuous from hatching. Concurrent with an increase in size and the passage through these growth phases is an increase in capacity for directed movement. This makes the distribution of the young fish less predictable on the basis of water transport alone.

Of the four major developmental landmarks, fertilization and hatching are fairly 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 our developmental landmarks, 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 our observations of the developmental stage of eggs in our bi-hourly samples were compared to the photographs of a developmental series provided by Bayless (1972). Bayless' hour-

by-hour series permitted identification of these data in terms of equivalent hours of development at 19°C. In Figure 1 actual hours of development against equivalent hours of development at 19°C have been plotted at five temperatures. The time in hours after fertilization is accurate to a few minutes and was considered to qualify as an independent variable. Least-squares regression lines fitted to these observations at each temperature fitted the data well. They suggest 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 hours after fertilization ranged from $r = 0.987$ to $r = 0.997$. 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.

By connecting points representing the time of attainment of several easily 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 does not hatch at the same time. Hatching may last several hours. The estimated time of 50% hatch has been used as a measure of the end of the egg stage, because it was impossible to maintain an accurate cumulative count of emerging larvae within each culture container once hatching had begun.

Hatching is a relatively discrete event, but the assignment of a time of hatching is somewhat arbitrary. The end of the prolarval or yolk sac

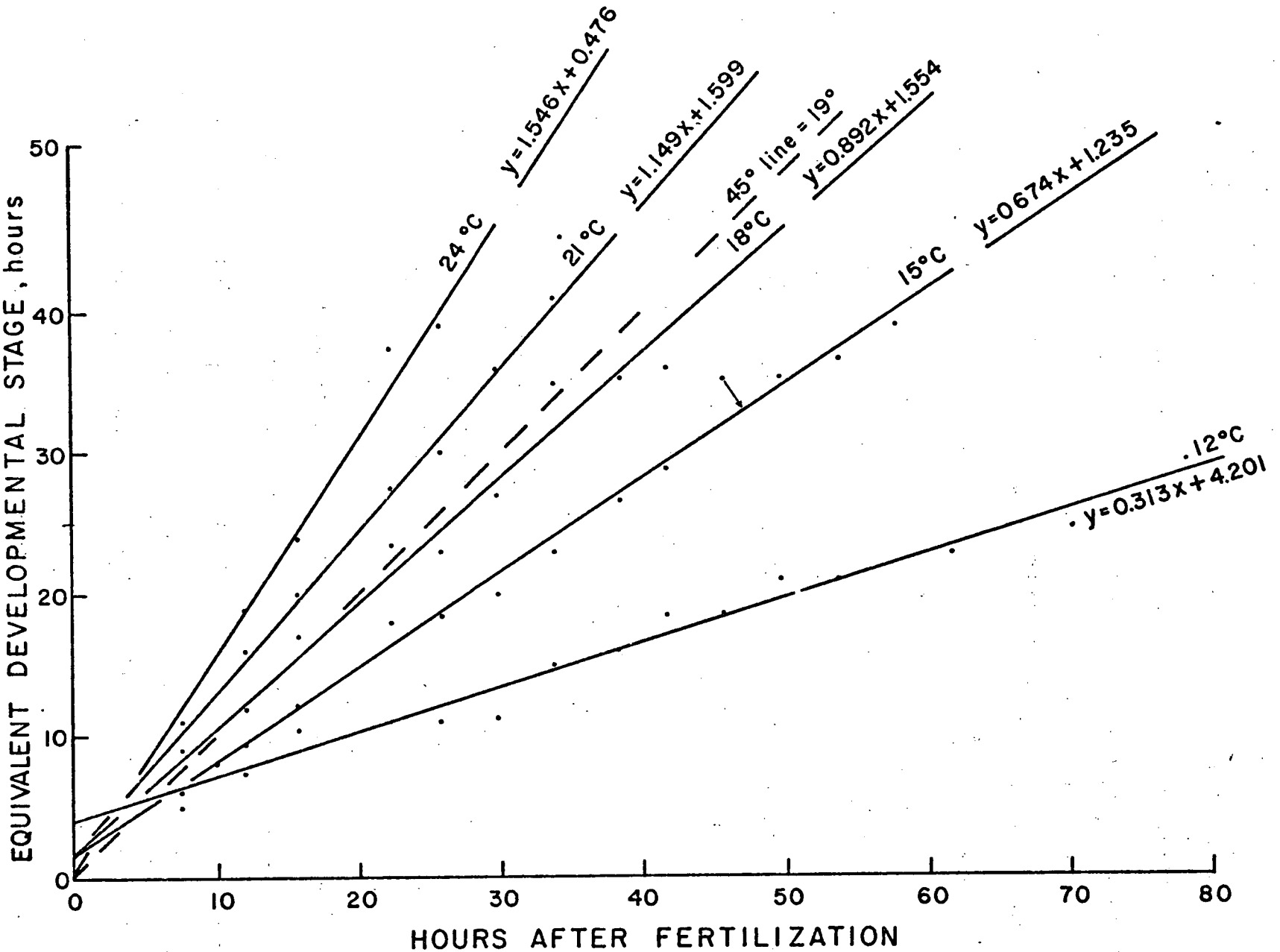

Figure 1
The regression of hours of embryonic development observed in this study at five experimental temperatures against those observed by Bayless (1972) at 19°C for the attainment of equivalent levels of structural development.

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. A number of larvae which appeared to have consumed nearly all their yolk using Mansueti's (1958) figure #21 as a model (Figure 2) were examined. The mean total length of a sample of 32 fish 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 yolks 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.

Like yolk absorption, the point at which metamorphosis occurs is difficult to define. Fully metamorphosed striped bass resemble Mansueti's (1958) figure #27. 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

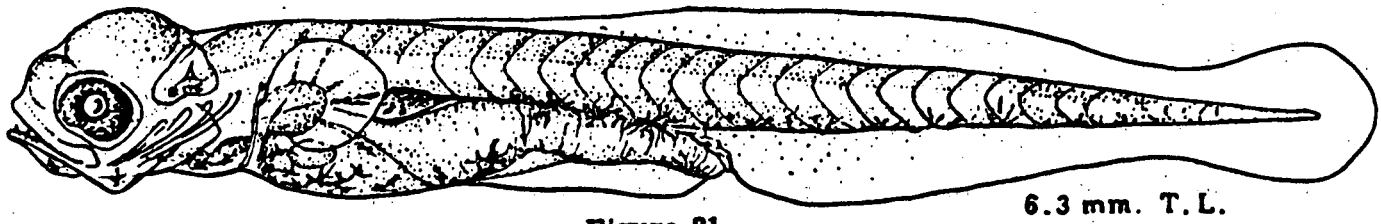

Figure 21

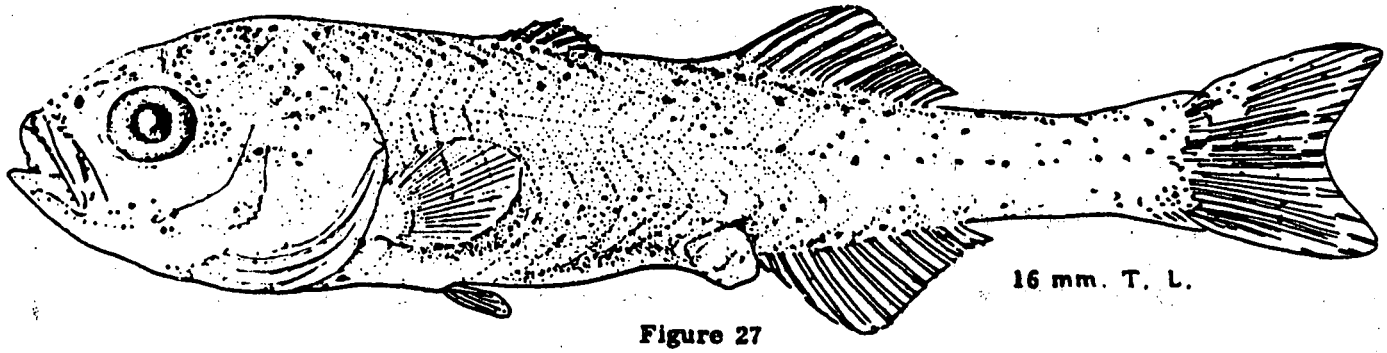

Figure 27

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

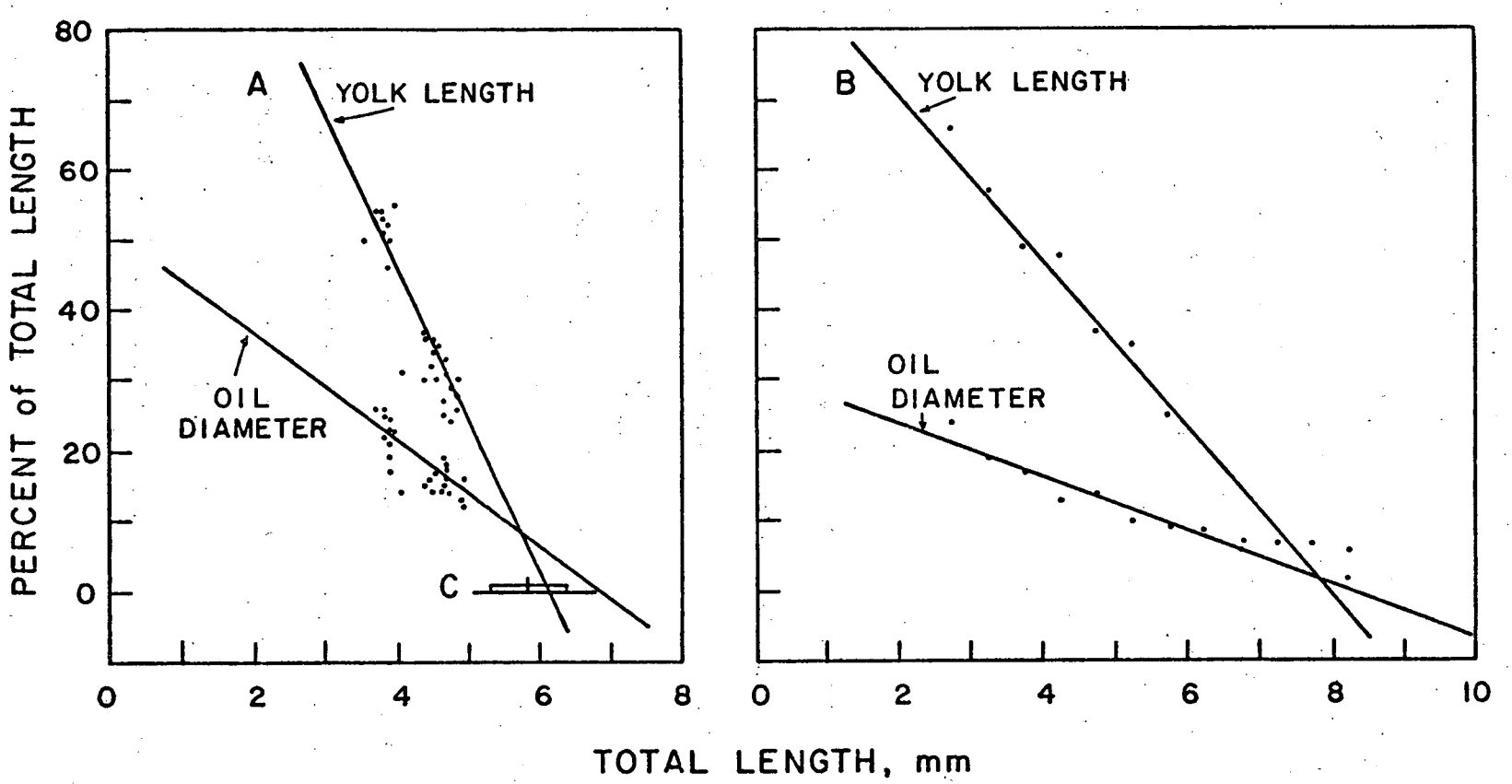

Figure 3. The determination of total length at yolk sac absorption from the regression of yolk length as a percent of total length (y) against total length (x). A. Observations on Hudson River prolarvae for which $y = -21.885\ x + 133.759$ ($r = -0.900$). B. Data from Mansueti (1958) for Chesapeake or 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.

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.

The prolarval and larval stages were defined in terms of the range in lengths attained by individuals. At the beginning and end of each stage 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.

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 provided by Texas Instruments are presented in Table 2. Newly fertilized striped bass eggs water hardened to a slightly smaller

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	11
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)	4.0	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)	0.066	0.048
Mercury (mg/ℓ)	0.0005	0.0008
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)	0.002	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)	0.054	0.048
Potassium (mg/ℓ)	5.00	2.256
Selenium (mg/ℓ)	<0.001	<0.001
Silica, suspended (mg/ℓ-SiO_2)	0.32	0.46
Silica, total (mg/ℓ-SiO_2)	2.46	5.08
Silver (mg/ℓ)	<0.001	<0.001
Sodium (mg/ℓ)	13.88	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)	0.010	0.022

chorion diameter in quarry water than in Hudson River water. In other respects this water supply appeared to be an adequate incubation medium.

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. This salinity prolonged the life of Artemia nauplii between feedings and retarded the formation of filamentous aquatic fungi. These fungi have been observed to ensnarl and kill young larvae. The salinity occasionally exceeded 8 ‰ accidentally when too much brine was added while Artemia nauplii were being fed. There was no evidence that higher salinities adversely affected larval growth or survival.

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 a temperature controlled water bath. Haake (E-50) 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. After June 6 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 quarry 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 5 to 10 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 remainder 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 times 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 heavy incidence of cannibalism. If left unchecked, cannibalism can decimate a treatment population and shorten the observation period.

Our sampling strategy reflected a desire to provide an accurate indication of the size range of the animals in each treatment at a given time within practical limits described above. Samples 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.

The efficiency of yolk utilization was estimated from the formula

$$\text{percent efficiency} = \frac{\text{Dry weight of larva at yolk absorption}}{\text{Average dry weight of unfertilized egg}} \times 100.$$

This ratio suggested by Blaxter and Hempel (1966) does not take into account chorion weight or the contribution of the oil remaining at the time all yolk is absorbed. This technique, while not a rigorous measure of the efficiency with which the embryo uses its stored nutrient reserves, is useful for between-treatment comparisons.

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 first 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.

In comparisons between means a Students-'t' statistic was calculated.

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 overall 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

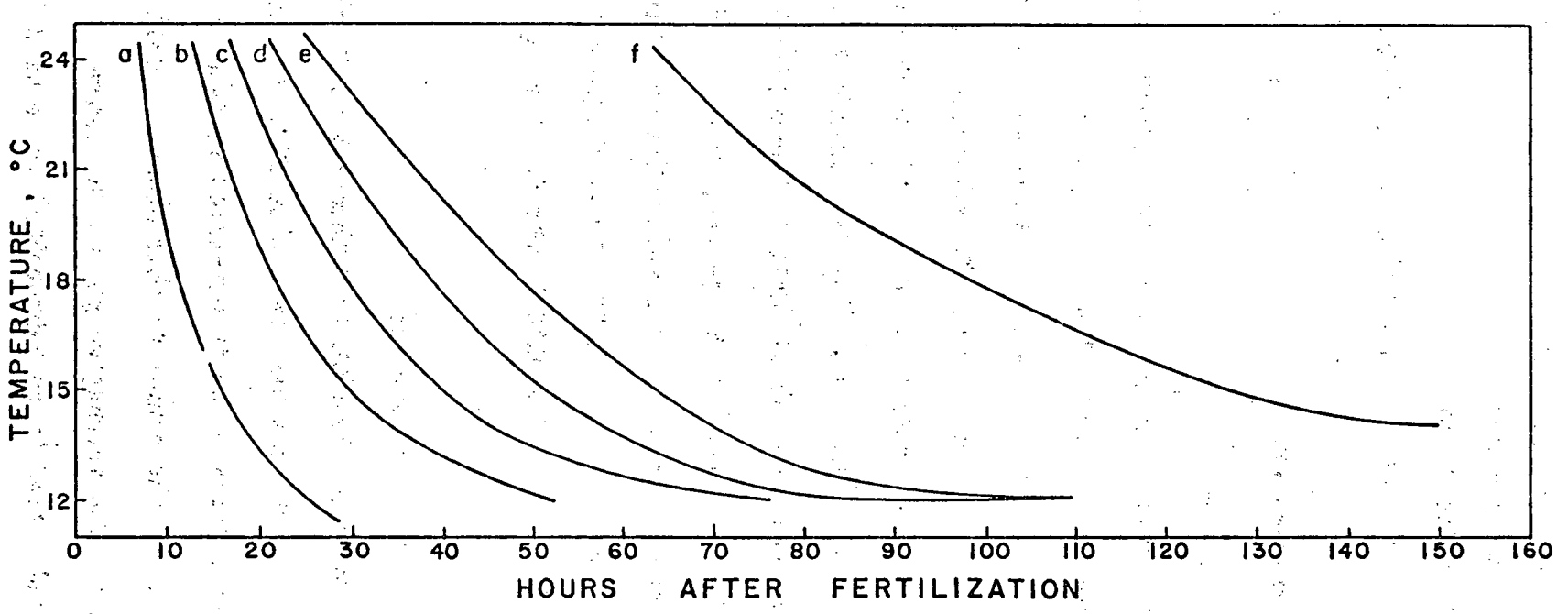

Figure 4A. The effect of incubation temperature on the time from fertilization to selected developmental stages before and after hatching.

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.

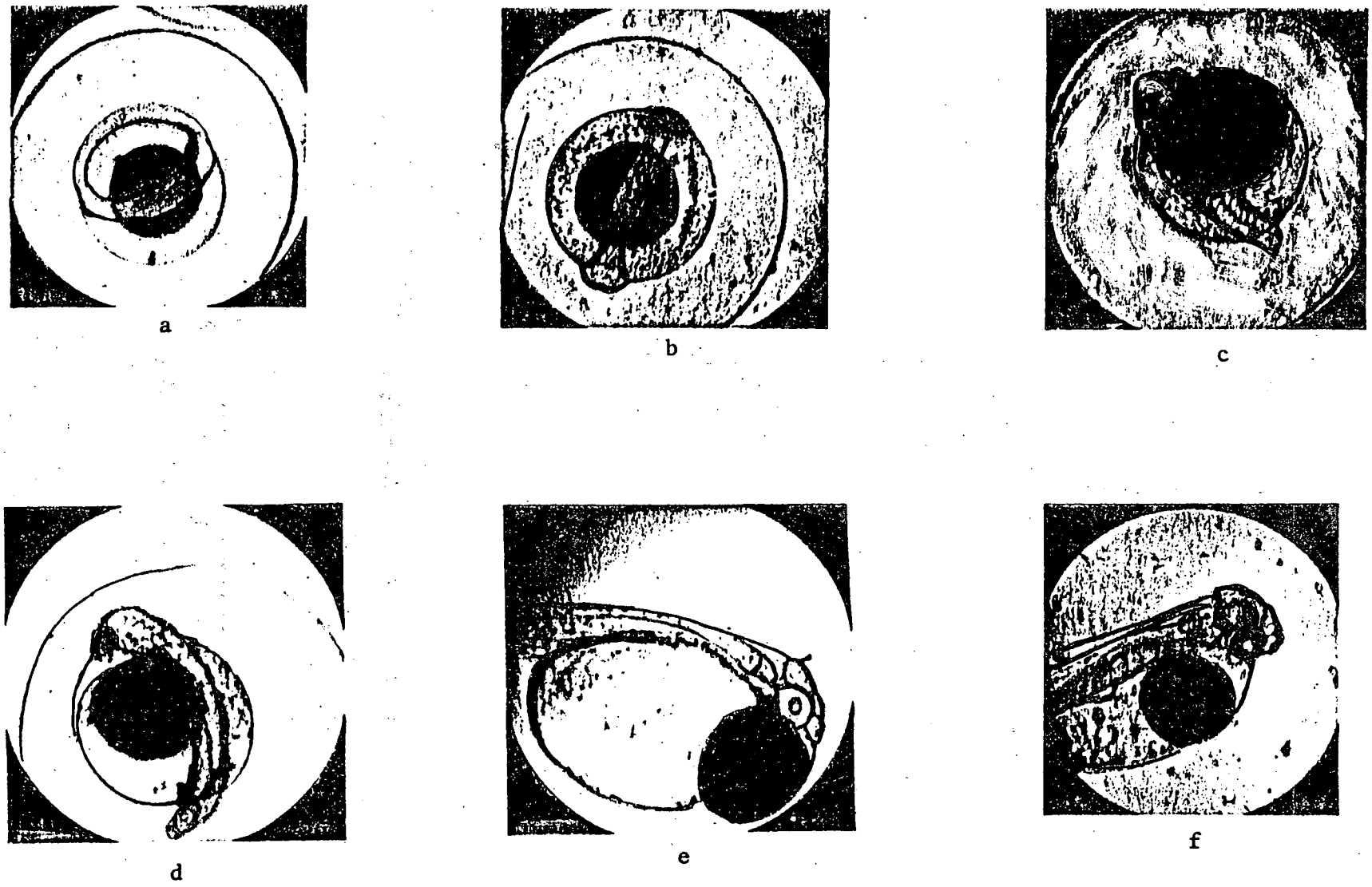

Figure 4B. Illustration of developmental stages described in Figure 4A. Original photographs from Bayless (1972).

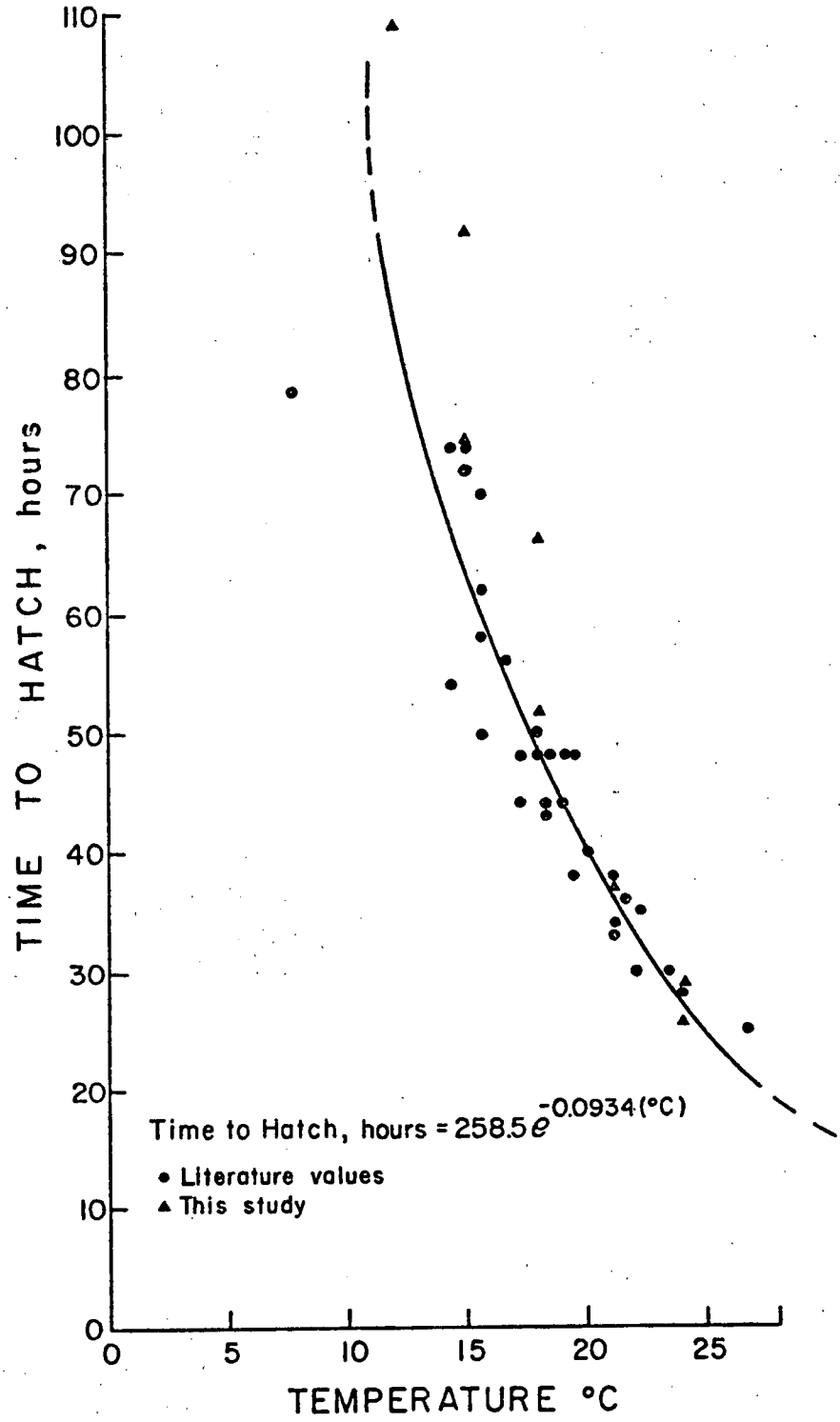

Figure 5. The effect of temperature on the incubation period of striped bass eggs based on observations listed in Table 3.

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

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

with correlation coefficient (r) = 0.93.

The degree of curvilinearity is determined predominantly by terminal observations. Between 15° and 24°C, the range over which incubation most often occurs, incubation time can be predicted as a linear function of temperature by the regression equation:

$$\text{Time to hatching (hrs.)} = -4.616\ \text{temp.}(^\circ C) + 134.310,$$

with correlation coefficient (r) = 0.878.

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 were high and 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 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 and 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° and 18°C.

The Yolk Sac Stage

Growth during the yolk sac stage was divided into two phases. The first 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.

The second growth phase was marked by a drastic decrease in growth rate. This growth plateau began three to four days after hatching at all temperatures and lasted from five days at 24°C to approximately fifteen days at 15°C. At 12°C total mortality occurred before the end of the growth plateau. In some lots growth in length stopped for a period of several days, while in others there was a scarcely discernable increase in length during the entire plateau period. In some lots there was a two to four day period of negative growth. This appeared progressively earlier at higher temperatures. At 24°C the negative growth period occurred five days after hatching. At 12°C negative growth began approximately twelve days after hatching and continued until all larvae had died. During the growth plateau the average larval length stayed below 6 mm. The occurrence of reduced growth during this period was clearly concurrent with the use of the last of larval yolk reserves. The end of the prolarval stage and the attainment of 5.84 mm. total length marked the end of the growth plateau. The length of the yolk sac period as a function of rearing temperature is presented in Table 4. The duration of the yolk sac stage as a whole was directly related

TABLE 4

The range in time (days) between hatching and yolk sac absorption based on mean total length at yolk sac absorption of 5.84 mm ± one standard deviation (SD) of 0.54 mm at four rearing temperatures.

Temperature	Lot	-1 SD (5.84-.54) 5.30 mm	Days to Mean Total Length at Yolk Sac Absorption 5.84 mm	+1 SD (5.84+.54) 6.39 mm
24°C	6	2.0	4.75	12.0
	8	4.0	7.25	11.0
	9	4.0	13.5	23.0
	Mean	3.3	8.5	15.3
21°C	7	3.0	9.75	19.0
	8	4.0	7.0	16.0
	9	5.0	12.5	18.0
	Mean	4.0	9.75	17.7
18°C	6	2.0	10.0	16.0
	7	4.0	13.5	27.0
	8	4.0	6.0	18.0
	9	4.0	17.5	23.0
	Mean	3.5	11.75	21.0
15°C	7	5.0	16.5	27.0
	8	5.0	24.0	34.0
	9	5.0	24.0	30.0
	Mean	5.0	21.5	30.3

to the duration of the period of reduced or suspended growth on the growth plateau.

Mortality During the Yolk Sac Stage

Mortality was higher in all lots during the yolk sac stage than at any other time after hatching. Mortality figures 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 losses was determined.

The sigmoid portion of the time-mortality curve coincided with the length of the yolk sac period as defined. The attainment of an average total length of 5.84 mm. was achieved slightly after half of the total cumulative losses during the period of sigmoid mortality had occurred. The period in days after hatching between the beginning of yolk sac absorption as defined by 5.84 mm. total length less one standard deviation (5.30 mm.) and the end of yolk sac absorption defined by a length of 5.84 mm. plus one standard deviation (6.39 mm.) encompassed slightly more than 100% of the period of sigmoid mortality at all temperatures. The percent of the original population at hatching which died each day during this stage appeared to be temperature related (Table 5). Daily percentage losses ranged from 4.0 to 20%, with the highest mean daily percentage mortality at the highest temperature.

TABLE 5

Larval mortality by developmental stage, expressed as the percentage of the number of larvae at the beginning of each stage which died each day during the course of that stage.

Temperature (°C)	Lot	Yolk Sac Stage (%)	Yolk Absorption to Metamorphosis (%)
24	6	20	4.3
	8	14	4.8
	9	8	10.0
	mean	14.0	6.37
21	7	10	4.5
	8	14	4.2
	9	8	5.6
	mean	10.67	4.7
18	7	7	3.8
	8	17	2.9
	9	6	4.3
	mean	10.0	3.7
15	7	6	1.8
	8	4	2.2
	9	4	1.6
	mean	4.67	1.7
12	8	6*	*reflects losses up to point of complete mortality yolk sac stage not completed
	9	4*	
	mean	5*	

For prolarvae at all temperatures for all lots:

$$\text{daily \% mortality} = 0.955\ (\text{temp.}^\circ\text{C}) - 8.800$$
$$r = 0.639$$

The Larval Stage (Yolk Sac Absorption Through Metamorphosis)

Growth rate increased during the larval stage from a low level at the end of the yolk sac stage growth plateau to a rate of increase in size which was strongly related to rearing temperatures. Growth during this stage can be approximated by an exponential model (Table 6). 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 6B):

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

As a result, stage duration is a direct function of rearing temperature (Table 7). There were fewer differences between lots in the growth response within given temperature treatments during this stage than were observed during the yolk sac stage.

Mortality Between Yolk Sac Absorption and Metamorphosis

A period of significantly reduced mortality followed the sigmoid portion of the mortality curve which characterized the yolk sac stage. In treatment populations periodic sampling for growth measurements was the major source of mortality during the larval period. Each population had been reduced to 10 to 40% of the population originally present at hatching by the time this growth stage had begun. Mortality during the larval stage attributable to causes other than sampling ranged from 1.6 to 10% of the number alive at the beginning of the stage per day. The mortality rate again increased with increasing temperature. For postlarvae at all

TABLE 6

Total length versus days after hatching. Regression equations by life stage where:
y = total length (mm)
x = days after hatching
r = correlation coefficient.

Temperature and Lot		Hatching Through Yolk Sac Absorption		Yolk Sac Absorption Through Metamorphosis		Early Post-Metamorphosis	
			r=		r=		r=
24°C	Lot 6	$\log_{10}y = 0.007x + 0.714$	0.581	$\log_{10}y = 0.017x + 0.662$	0.938	$\log_{10}y = 0.009x + 0.838$	0.985
	8	$\log_{10}y = 0.008x + 0.682$	0.903	$\log_{10}y = 0.018x + 0.643$	0.971	$\log_{10}y = 0.008x + 0.915$	0.903
	9	$\log_{10}y = 0.007x + 0.682$	0.919	$\log_{10}y = 0.048x + 0.089$	0.983	not available	—
21°C	Lot 7	$\log_{10}y = 0.016x + 0.638$	0.922	$\log_{10}y = 0.024x + 0.491$	0.928	$\log_{10}y = 0.008x + 0.942$	0.981
	8	$\log_{10}y = 0.010x + 0.691$	0.828	$\log_{10}y = 0.024x + 0.496$	0.960	$\log_{10}y = 0.009x + 0.922$	0.868
	9	$\log_{10}y = 0.007x + 0.670$	0.898	$\log_{10}y = 0.028x + 0.352$	0.998	not available	—
18°C	Lot 7	$\log_{10}y = 0.010x + 0.667$	0.915	$\log_{10}y = 0.017x + 0.504$	0.979	$\log_{10}y = 0.013x + 0.638$	0.942
	8	$\log_{10}y = 0.013x + 0.679$	0.912	$\log_{10}y = 0.012x + 0.672$	0.961	$\log_{10}y = 0.005x + 1.002$	0.894
	9	$\log_{10}y = 0.005x + 0.681$	0.891	$\log_{10}y = 0.017x + 0.472$	0.984	$\log_{10}y = 0.009x + 0.750$	0.897
15°C	Lot 7	$\log_{10}y = 0.009x + 0.629$	0.824	$\log_{10}y = 0.007x + 0.679$	0.977	not available	—
	8	$\log_{10}y = 0.005x + 0.684$	0.838	$\log_{10}y = 0.007x + 0.652$	0.989	not available	—
	9	$\log_{10}y = 0.003x + 0.674$	0.850	$\log_{10}y = 0.007x + 0.565$	0.994	not available	—

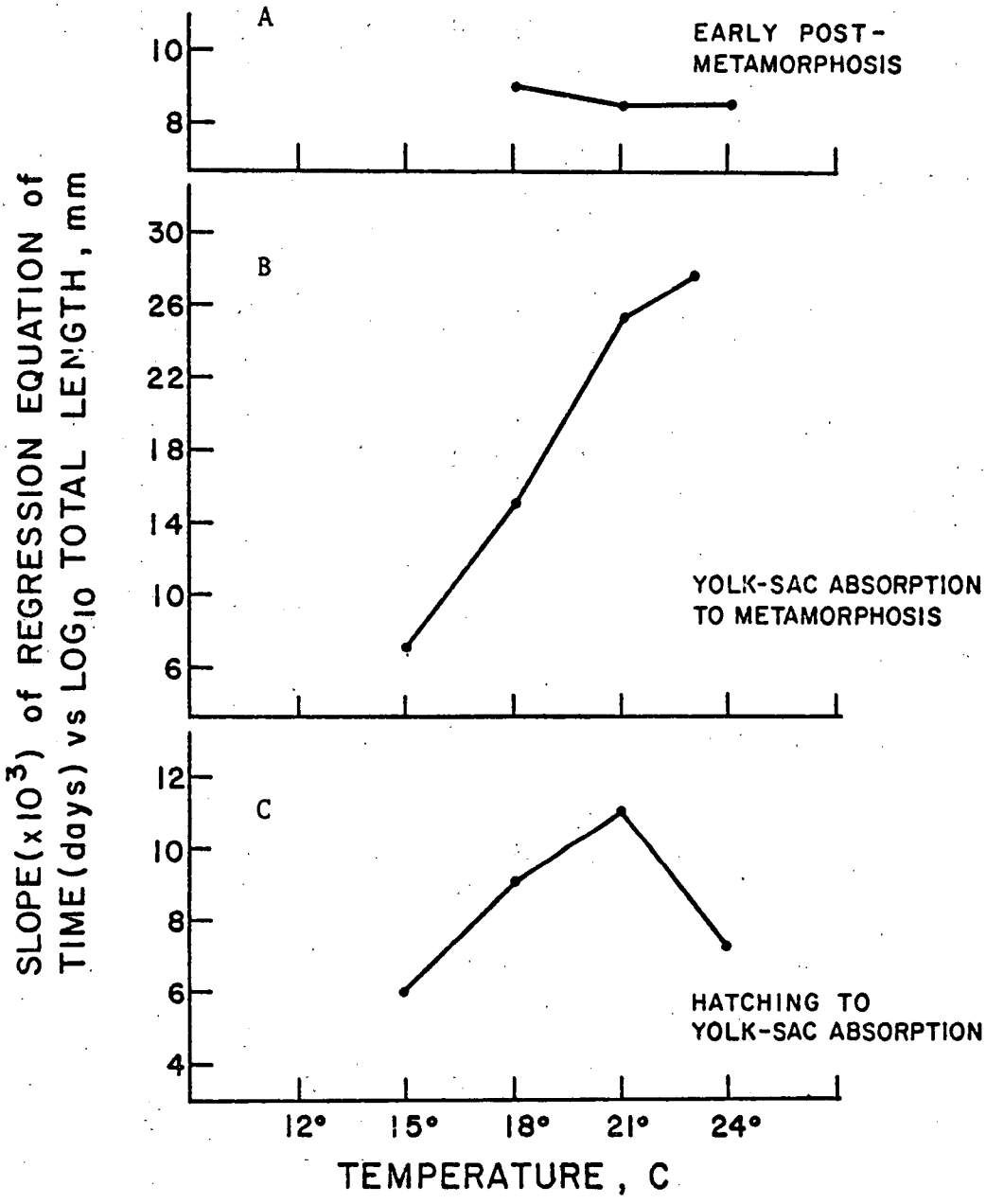

Figure 6. The effect of temperature on the mean slope, b ($x10^3$) of the regression equations of total length against days since hatching for each growth stage. The regression equations were in the form $\log_{10}$ length = b(days) + a.

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) 14.90 mm	Days to Mean Total Length at Metamorphosis 16.32 mm	+1 SD (16.32+1.33) 17.60 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	28.0	32.0	36.25
	8	28.25	31.0	33.75
	9	29.0	30.5	32.75
	Mean	28.4	31.2	34.3
18°C	7	38.25	40.0	44.0
	8	38.0	40.5	43.0
	9	39.0	41.0	45.0
	Mean	38.4	40.5	44.0
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*

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

temperatures and all lots:

$$\text{daily \% mortality} = 0.486\ (\text{temp.}^\circ\text{C}) - 5.323$$
$$r = 0.766$$

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 published observations have been supplemented, particularly at lower incubation temperatures. These 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). Events early in embryonic development are typically less responsive to temperature than the later stages. 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 our 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).

While these experiments permitted observation of the rate of development at all of the temperatures used, mortality from fertilization through hatching was generally high. Above 12°C no single lot gave a good survival series at all temperatures. Within each lot one or more temperature treatment 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%.

Mortality in these experiments can be attributed to several factors. Eggs were stocked into their rearing containers within 20 minutes following fertilization. Variable proportions of the mortality observed may have been

due to non-fertilization. Hence, these 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 when 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 using this antibiotic on Maryland striped bass eggs held in river water was observed. 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.

Work on other species, and 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 should be a measure of the efficiency of yolk utilization through hatching (Alderdice and Forrester, 1968). The relationship between temperature and calculated length at hatching is presented in Figure 7C. Larval growth after hatching is very rapid at all temperatures. Hence, it is important to define the time at which measurements are taken. The method of back calculation used puts the time at which length at hatching is recorded on a common basis for all treatments. An optimum temperature for embryonic development through hatching of 18°C is suggested. However, these data are too limited to support any meaningful conclusions. Analyses of this sort may be confounded by differences in the amount of yolk originally present in the unfertilized egg (Blaxter and Hempel, 1963, 1966). Among striped bass the average dry weight of unfertilized eggs is a linear function of the weight of the female producing them (Rogers, unpublished data). In Figure 7C the amount of yolk originally present in eggs in lot 8 was greater than that in eggs from lot 7, based on dry weight measurements.

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, the rate and duration of which appeared to be independent of temperature; and (2) a period of depressed growth, the duration of which was

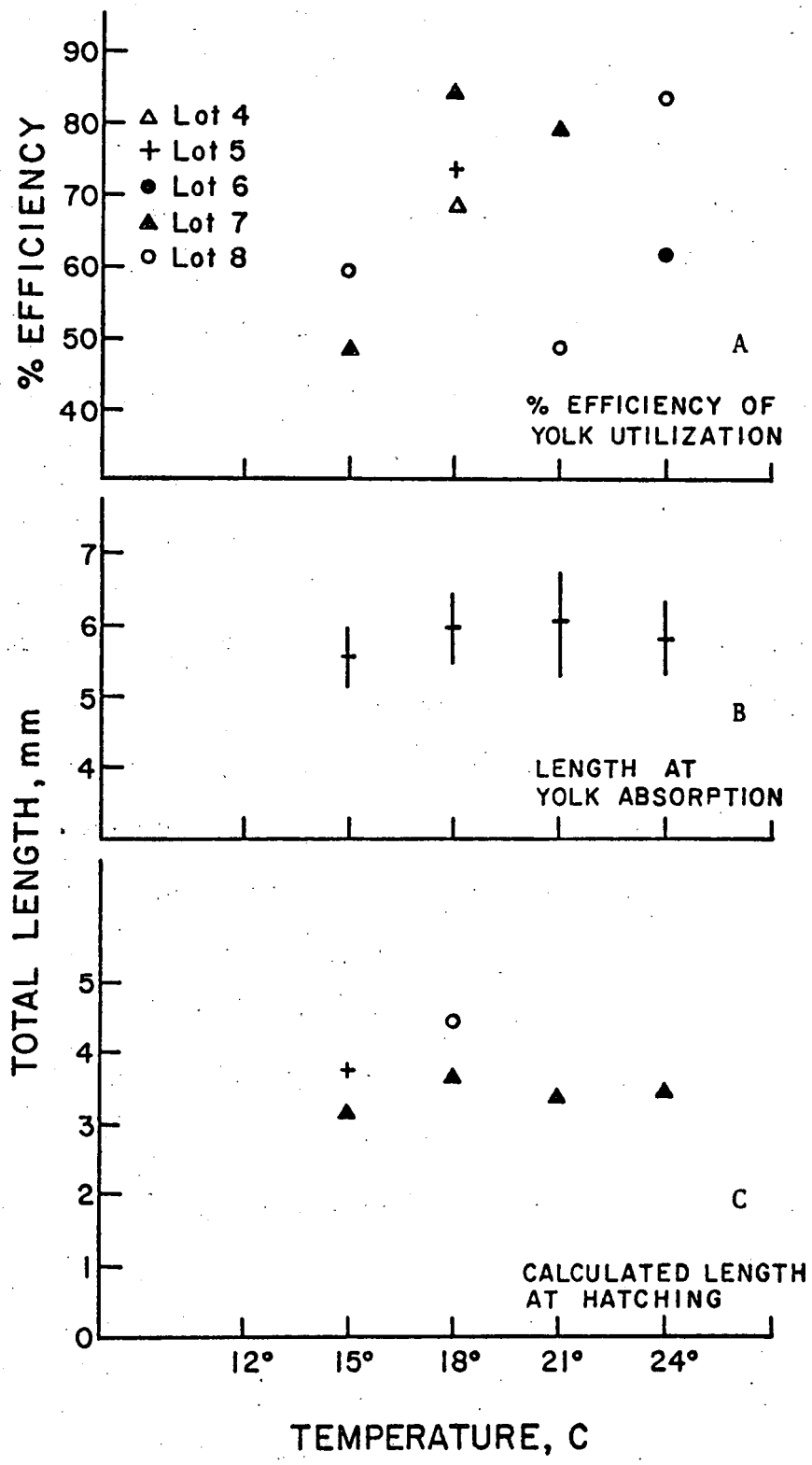

Figure 7. Estimates of the temperature optimum for growth through yolk absorption using three techniques.

directly related to rearing temperature. 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. The period between the end of linear growth and the disappearance of the yolk sac as a structure may last from 2 to 28 days depending on the temperature.

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 length and weight ceases 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 at two to five days after hatching at 17°-18°C. These observations correlate well with the timing at the beginning of the growth plateau in our experiments. 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 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 larval development it probably increases the level of forced activity.

The growth plateau we observed in most of our treatment populations coincides with Farris' section B (Farris, 1959) which was characterized by a period of reduced growth rate. Kuznetzov (1972) noted a similar marked reduction in larval growth before yolk absorption which he associated with the period of transition between an endogenous and exogenous food source.

Mortality curves for all of our experimental treatments are found in Appendix B. A common characteristic of nearly all treatments is a sigmoid pattern in the reduction in numbers. The majority 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. The sigmoid nature of the mortality curve suggests a dose-response curve. 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 quality 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. Based on the average time to complete yolk absorption (Table 4) food became available after a small fraction of larvae had already absorbed all of their yolk. Feeding typically begins before all yolk is absorbed. Larvae which have exhausted their yolk reserves and have begun to resorb their body tissue 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. In our experiments the mean time to yolk absorption occurred at 9.75 days at 21°C and 11.75 days

at 18°C. Among Bayless' fish which had undergone irreversible starvation, death followed four to five days after the ability to feed had been lost. If Bayless' observations and ours are combined, it appears that irreversible starvation occurs very near the time of complete yolk absorption in striped bass but that death from starvation takes considerably longer than among Lasker's anchovies.

It seems reasonable to expect that the time between hatching and yolk absorption, yolk absorption and the "point of no return" and between the "point of no return" and death would be compressed into a shorter time period among larvae reared at high temperatures. This is due to the effect of temperature on metabolic rate. The death of larvae which had not begun to feed is assured on or about the time of yolk absorption. If the time from hatching to yolk absorption for a given treatment population has a bell-shaped distribution the mortality pattern one would expect to observe would resemble a cumulative normal distribution or sigmoid. This is the shape approximated by most of the time-mortality curves generated in these experiments. While the progressive occurrence of irreversible starvation followed by death among larvae completing yolk absorption can explain the shape of the mortality curve, it does not explain the timing of heavy mortalities. At the mean time of yolk sac absorption, based on our criteria, the average size of the original treatment populations had already been reduced to 16%, 36%, 53% and 34% of its original complement at 24°, 21°, 18°, and 15°C, respectively.

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 not entirely inadequate. The food concentration required for optimal growth and survival among striped bass larvae is unknown. Our approach in these experiments was to provide an excess ration at the time feeding began in the hope of encouraging a higher proportion of each population to start feeding. It may be that an intermediate food density may be required for best survival as was the case in the experiments of Saksena and Houde (1972) using Harengula.

These estimates of the mean time to yolk sac absorption are too long to satisfy the nutritional hypothesis. If this hypothesis were true and the distribution of lengths at yolk absorptions are as we have indicated, then at higher temperatures yolk is completely consumed among a portion of the population within a day of hatching. In this case provision of food at the second day after hatching at 24°C was clearly too late.

We assigned the time of mean yolk absorption in each lot by looking at the percentage of fish in a series of samples that had attained a total length of 5.84 mm. or greater. The time of attainment of the mean length at yolk absorption was determined by the appearance of larvae of greater than 5.84 mm. among 50% of the fish in each sample. This approach was applied consistently and was effective where there was a continuous increase in length over time. However, within the growth plateau at 24°, 21° or 18°C there appeared cases of negative growth or periods of decrease in length with increasing time. Lasker (1964) noted a similar shrinkage among unfed Pacific sardine larvae. This reduction in length occurs among larvae which are already undergoing tissue resorption, therefore are well past complete yolk

absorption. In treatments where negative growth appears, it usually does so just following the period of major mortality and just preceeding the period of rapid growth associated with the end of the yolk sac period.

That no period of significant mortality follows these periods of negative growth suggests that most of these larvae which had already absorbed all their yolk and some of their body tissues ultimately began to feed and grow rapidly. The time of yolk absorption by this group of larvae would have preceeded the period of negative growth and would have been missed by the interpolation method we used. If this were the case the actual time of yolk absorption for this segment of the population would be as follows, based on inspection of the growth curves in Appendix B.

Temperature (°C)	Lot #	Corrected Estimated Time to Mean Yolk Absorption	Previous Estimate (Table 4)	Difference
		(----------Days	----------)	
24	6	2.5	4.75	-2.25
	8	4.0	7.25	-3.25
21	8	5.5	7.0	-1.5
	7	8.0	9.75	-1.75
18	9	7.0	13.50	-6.50

Larvae reared at 12°C also underwent negative growth but never recovered. Although food was presented, there was no evidence that any larvae at this temperature ever fed.

Even if our estimates of the time of yolk absorption were excessive for treatment populations which underwent negative growth, larvae would have had to die immediately following yolk absorption to account for the timing of the observed mortalities. At least a portion of larvae in each population were capable of satisfactory recovery from tissue depletion. May (1971) noted a similar resistance to food deprivation in Leuresthes. In his experiments starved fish underwent arrested development and reduction in dry

weight during periods of starvation following yolk absorption of up to 16 days. The energy demands during this period were met at the expense of lipid reserves suggesting a similar function for the atypically large oil globule in striped bass.

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 mortalities. We have no explanation why larvae that ultimately survived showed symptoms of food deprivation when food was present in abundance.

The duration of the yolk sac period decreased with increasing temperature. The length of the yolk sac period as a function of temperature for different lots is presented in Figure 8, and summarized in Table 4. There are variations between lots. We have some evidence that the optimal temperature conditions for development occur between 18° and 21°C. In determining the average length of larvae at the point of yolk absorption we examined larvae reared at all temperatures and found that there was no statistically significant difference in length between temperatures. As a result we used the mean length at yolk absorption for larvae reared at all temperatures to define the mean cutoff point at 5.84 mm. Measurements of the efficiency of yolk utilization at different rearing temperatures yielded no meaningful trend (Figure 7A). The range in efficiencies observed fell within the range observed by Blaxter and Hempel (1966), as well as those reviewed by Blaxter (1969). Blaxter (1969) summarized some of the sources of error in efficiency calculations.

Exponential growth equations fitted to our growth data by life stage are presented in Table 6. The exponential approximation of the pattern of growth during the yolk sac stage was used on all lots and temperature treat-

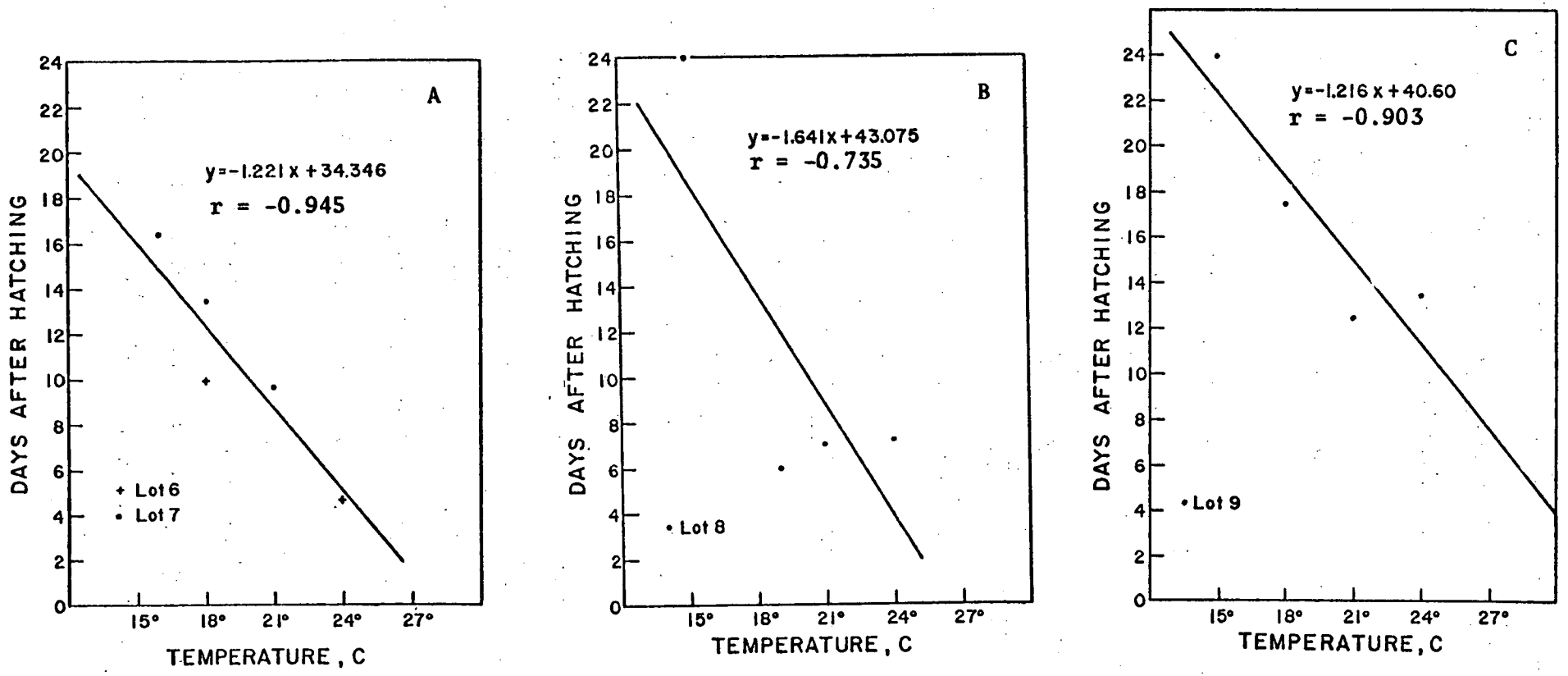

Figure 8. The effect of temperature on the duration of the yolk sac stage by lot.

ments for the sake of consistency. Growth measurements during the first three days after hatching were not used in calculating the growth equation for this stage. There was generally a lower correlation between time since hatching and larval length when prolarval growth was described using an exponential growth function, than was observed when the same function was applied to the growth of later stages (Table 6). This fact undoubtedly contributed to the considerable variability between lots in the slope of the exponential growth function at each temperature. The extent to which the exponential model fails to fit observed growth data is largely a function of the length of the growth plateau and the extent of negative growth in each treatment population. The mean (between-lot) slope for prolarval growth showed an apparent peak at 21°C (Figure 6C), indicating a shorter relative stage duration at this temperature. Empirical growth curves for lots at 21°C revealed no such peak in stage duration estimates (Table 4, Appendix B).

Development Between Yolk Sac Absorption and Metamorphosis

Growth during the larval stage was exponential with the slope of the growth equations increasing with the rearing temperature (Table 6, Figure 6B). 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. For the small samples we were forced to take in the later stages of each treatment the range was used

as a relatively efficient estimator of the standard deviation (Snedecor and Cochrane, 1967). In addition, we felt that removing the largest fish at each sampling prevented a high incidence of cannibalism. 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 half that observed up to yolk sac absorption (Table 5). The daily percentage mortality increased with temperature from a mean of 1.7% at 15°C to 6.37% per day at 24°C. Turner and Chadwick (1972) estimated a daily mortality rate for young bass ranging from 3.0 to 7% per day in the Sacramento-San Joaquin Estuary.

Development After Metamorphosis

Our temperature treatment populations were very much reduced by the time all the remaining individuals had attained metamorphosis. Conclusions

concerning growth of young bass after metamorphosis must be considered at best tentative. Growth curves in Appendix B suggest a reduction in the rate of growth after metamorphosis. Growth curves fitted to the last few samples in each treatment reflect this reduction (Table 6). For those temperatures for which growth observations are available there are indications that past metamorphosis the rate of increase in length is no longer so closely related to temperature as before metamorphosis (Figure 6A).

The rate of mortality after metamorphosis did not appear to change from that before metamorphosis.

Growth Curves

A mathematical function whose form matches the increase in some bodily dimension over time provides a convenient method for describing the growth process and may provide a basis for comparison of growth within the same species under different conditions. This is why we attempted to fit growth curves to our observed growth data. The data in the individual growth figures in Appendix B remain the best representation of the pattern of growth we observed in each treatment.

As is the case with growth functions which are used to describe the growth of adult fish, best fit can be expected when a particular function is applied to a well defined growth stanza, rather than to the entire growth process from metamorphosis to senility. The period of development spanned by our growth figures includes stages marked by different modes of larval nutrition. Hence, there is no reason to expect that a single simple function will adequately describe growth throughout the observation period. Early growth in most aquatic organisms is exponential (Royce, 1972). On this basis we are prejudiced toward the use of an exponential approximation. Kramer and Zweifel (1970) found that this simple relationship described the

growth of the northern anchovy quite well, but warned against the dangers of extrapolation, particularly at higher rearing temperatures.

In Table 8 we summarize the growth equations obtained using linear regression techniques on untransformed and $\log_{10}$ transformed sample means against days after hatching. The mean correlation coefficients (r) for the linear and exponential approximations in Table 8 did not differ significantly at the 0.05 level using a Students 't' test. Both approximations confirm the positive relation between rearing temperature and growth rate, with the slopes of each increasing with increasing temperature. The correlation between temperature and slope of the growth equations was r = 0.908 for its exponential and r = 0.924 for the linear equations. Although larval growth from hatching through metamorphosis appears exponential in form the exponential growth equation consistently fails to describe certain changes in growth rate that occur in experimentally defined growth curves. Figure 9 shows an example of the relationship between the exponential approximation and a curve fitted by eye to sample means. The exponential curve typically underestimates the size at metamorphosis, and the size during most of the yolk sac stage. The growth trajectory implied is misleading and the growth plateau during the yolk sac stage is inadequately represented. The sample data of Kramer and Zweifel (1970) has an early growth plateau like that observed in our experiments which neither the exponential nor the Gompertz model, nor the authors adequately describe.

Farris (1959), Kramer and Smith (1960) and Kuznetzov (1972), among others, have attempted to describe the growth of larval and early juvenile fish one growth stage at a time. We did this and Table 6 summarizes the exponential equations fitted to our growth observations by life stage. We used sample points near the transition between stages to calculate regression

TABLE 8

Total length versus days after hatching regression equations where:
y = total length (mm)
x = days since hatching
r = correlation coefficient.

Temperature		Size Range Total Length (mm)	Linear Growth Equation	r=	Exponential Growth Equation	r=
24°C	Lot 6	4.79-26.20	$y = 0.357x + 3.570$	0.992	$\log_{10}y = 0.013x + 0.711$	0.974
	8	4.86-29.55	$y = 0.403x + 2.781$	0.976	$\log_{10}y = 0.015x + 0.677$	0.978
	9	4.86-21.50	$y = 0.427x + 2.335$	0.822	$\log_{10}y = 0.022x + 0.564$	0.896
21°C	Lot 7	4.71-26.60	$y = 0.428x + 2.095$	0.973	$\log_{10}y = 0.016x + 0.645$	0.956
	8	5.20-29.45	$y = 0.253x + 1.368$	0.544	$\log_{10}y = 0.016x + 0.644$	0.961
	9	4.39-18.00	$y = 0.354x + 2.669$	0.906	$\log_{10}y = 0.018x + 0.595$	0.952
18°C	Lot 7	5.04-26.50	$y = 0.313x + 2.491$	0.956	$\log_{10}y = 0.013x + 0.630$	0.973
	8	5.36-26.15	$y = 0.301x + 3.489$	0.974	$\log_{10}y = 0.010x + 0.690$	0.973
	9	5.04-23.85	$y = 0.290x + 2.662$	0.964	$\log_{10}y = 0.012x + 0.633$	0.972
15°C	Lot 7	4.71-18.90	$y = 0.168x + 3.698$	0.989	$\log_{10}y = 0.008x + 0.673$	0.988
	8	4.88-19.65	$y = 0.172x + 3.283$	0.964	$\log_{10}y = 0.007x + 0.657$	0.990
	9	4.88-16.75	$y = 0.119x + 3.697$	0.947	$\log_{10}y = 0.006x + 0.647$	0.979
12°C	Lot 8	4.88-5.69	$y = 0.015x + 5.244$	0.540	$\log_{10}y = 0.001x + 0.719$	0.540
	9	4.71-5.36	$y = 0.011x + 5.085$	0.536	$\log_{10}y = 0.001x + 0.706$	0.538

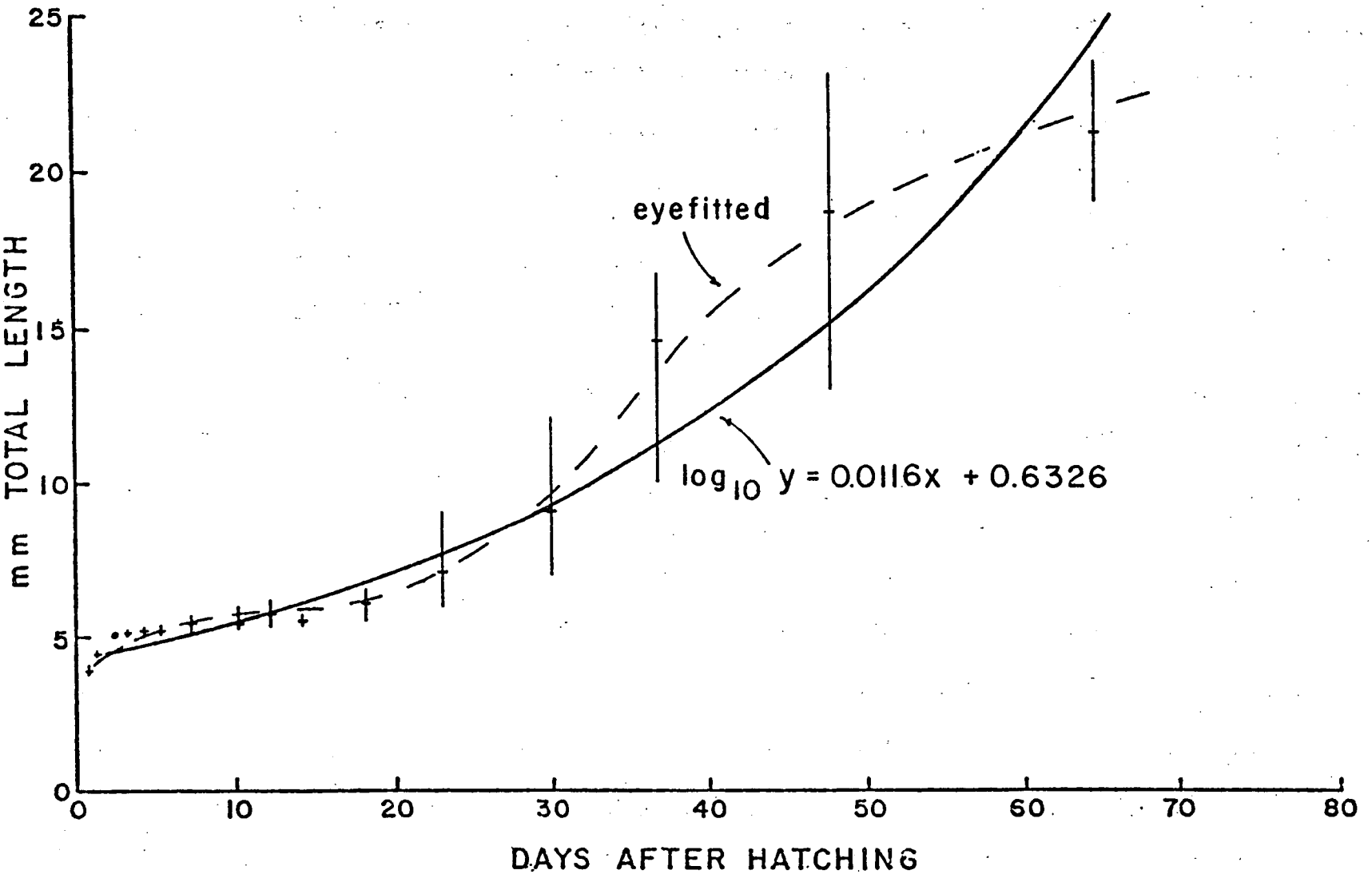

Figure 9. A sample comparison of a least squares exponential growth equation with an empirical growth curve fitted by eye to sample means.

equations for both stages where there was insufficient data. Based on the correlation coefficients the period between yolk absorption and metamorphosis is most adequately described by the exponential curve. The period from hatching to yolk absorption is more correctly logarithmic in nature. Few samples were available after metamorphosis. Describing this stage independently more accurately describes the change of slope that occurs at metamorphosis.

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.

Life Stage:	Stage Duration	
	Lawler et al. (1974)	U.S.N.R.C. (1975)
egg	36-48 hrs.	48 hrs.
yolk sac larva	6-10 days	6 days
post-yolk sac larva	30 days	22 days
	Cumulative Days Since Hatching	
yolk sac larva	6-10	6
post-yolk sac larva	36-40	28

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. According to our results one would expect a yolk sac stage duration of six days at a fixed temperature of 21°-24°C. A ten day yolk sac stage would be expected to occur at a water temperature of between 18° and 21°C. On the basis of our results metamorphosis would be attained in twenty-eight days from hatching at a fixed water temperature of just under 24°C.

Metamorphosis would occur thirty-six to forty days after hatching at a fixed water temperature between 18° and 21°C. 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 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 or later stages.

The pattern of growth defined in this study is compared with previous studies in Figure 10. 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

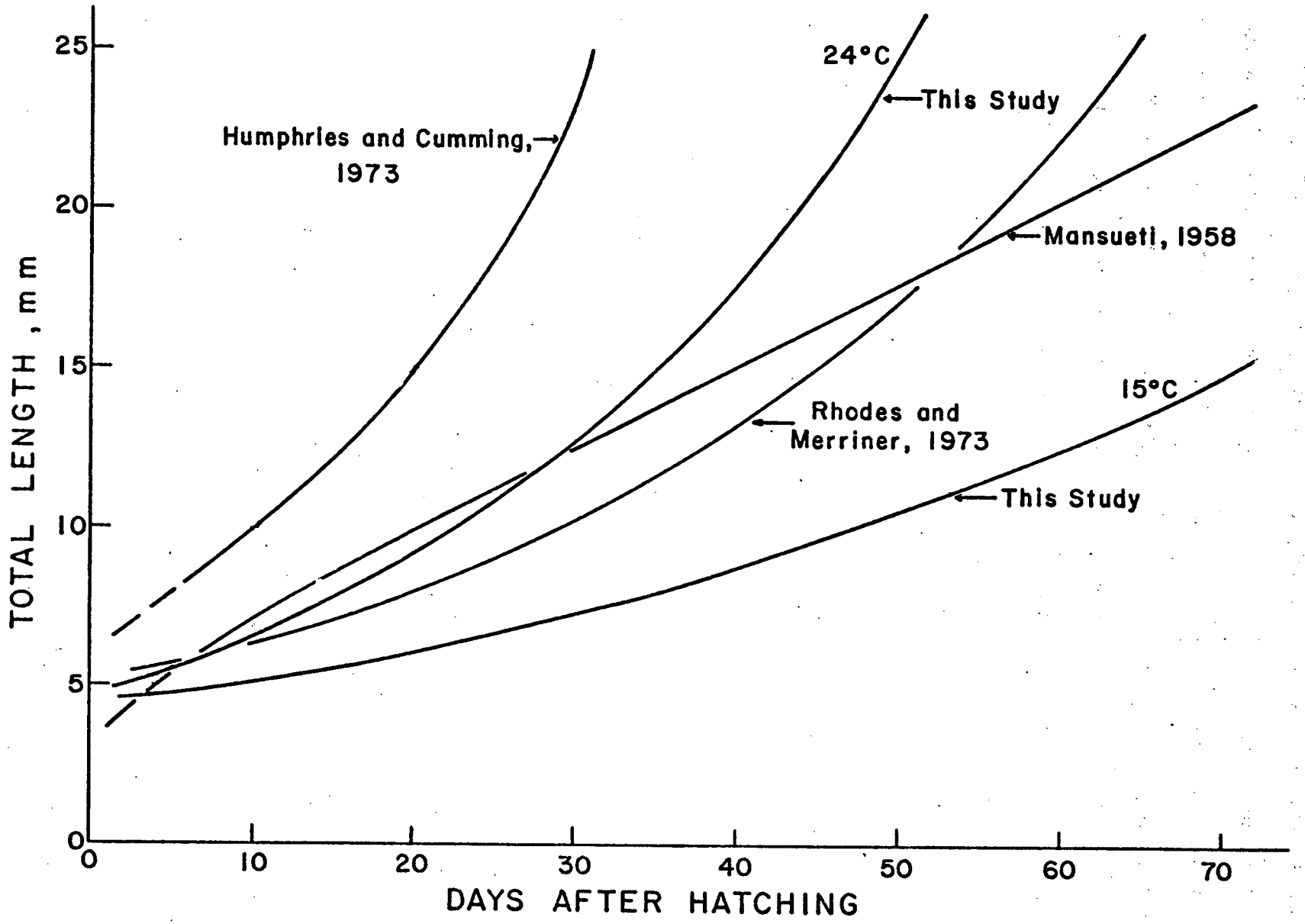

Figure 10. A comparison of growth rates observed under fixed temperature regimes with those obtained in earlier studies under conditions of increasing temperature.

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. If our growth rates are conservative there would be a tendency for the duration of events later in development to be overestimated to a greater extent than events prior to or near hatching.

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APPENDIX A

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Record of observed temperatures in 24° and 21°C design temperature treatments. 62

Record of observed temperatures in 18° and 15°C design temperature treatments. 63

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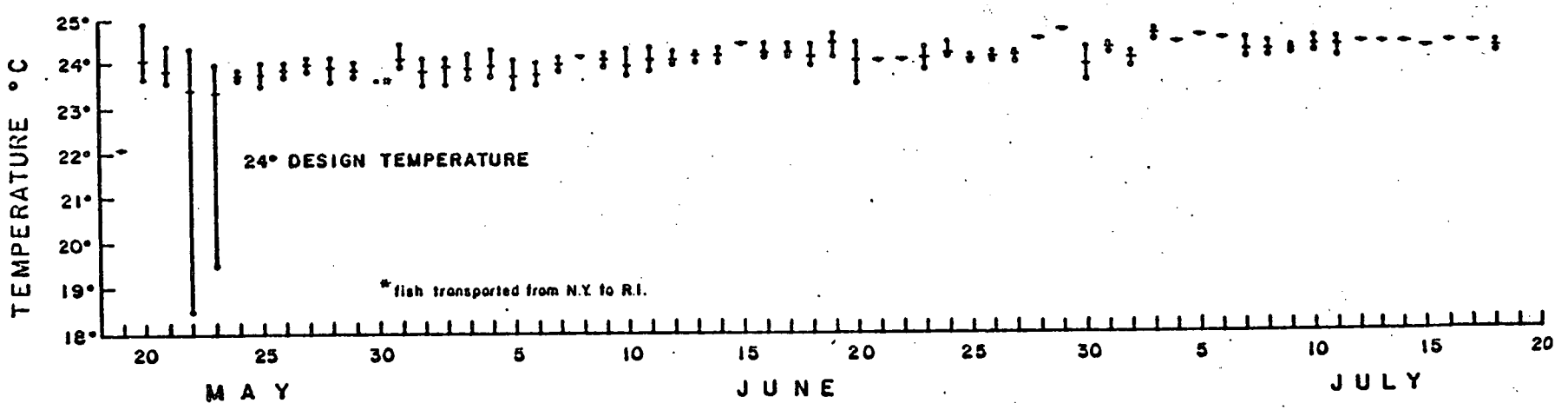
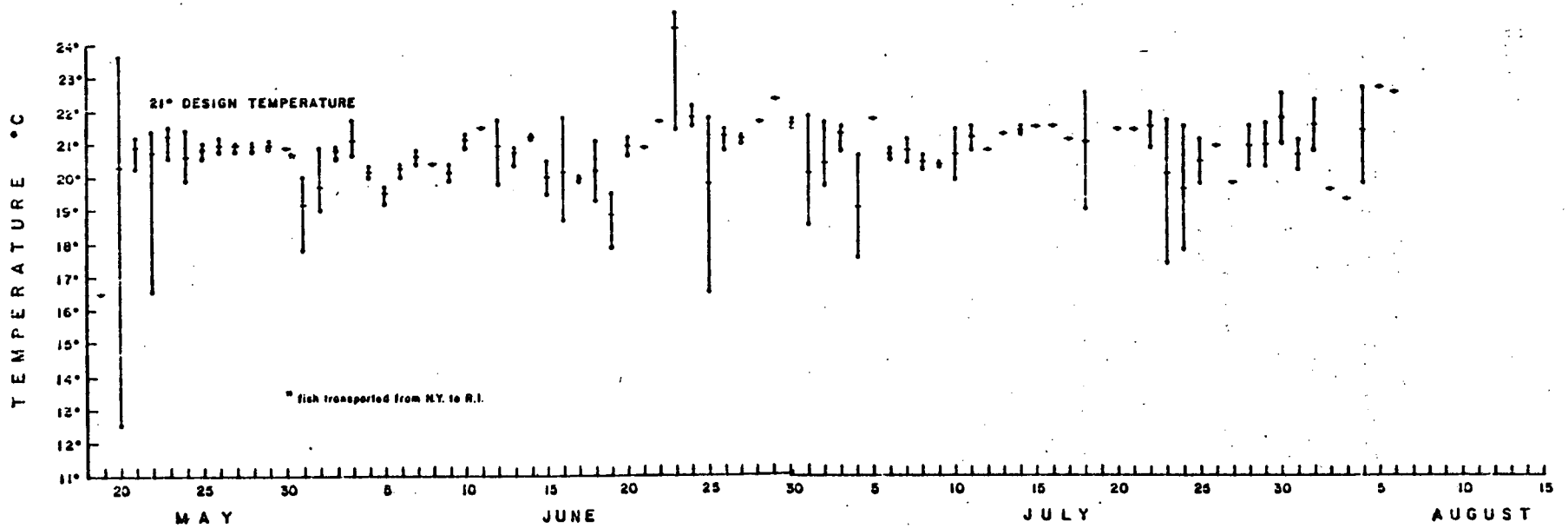
Ammonia concentrations (ppm) before water changes 65

Dissolved oxygen concentrations (percent saturation). 67

pH values 68

Salinity (°/oo) ranges before water changes 69





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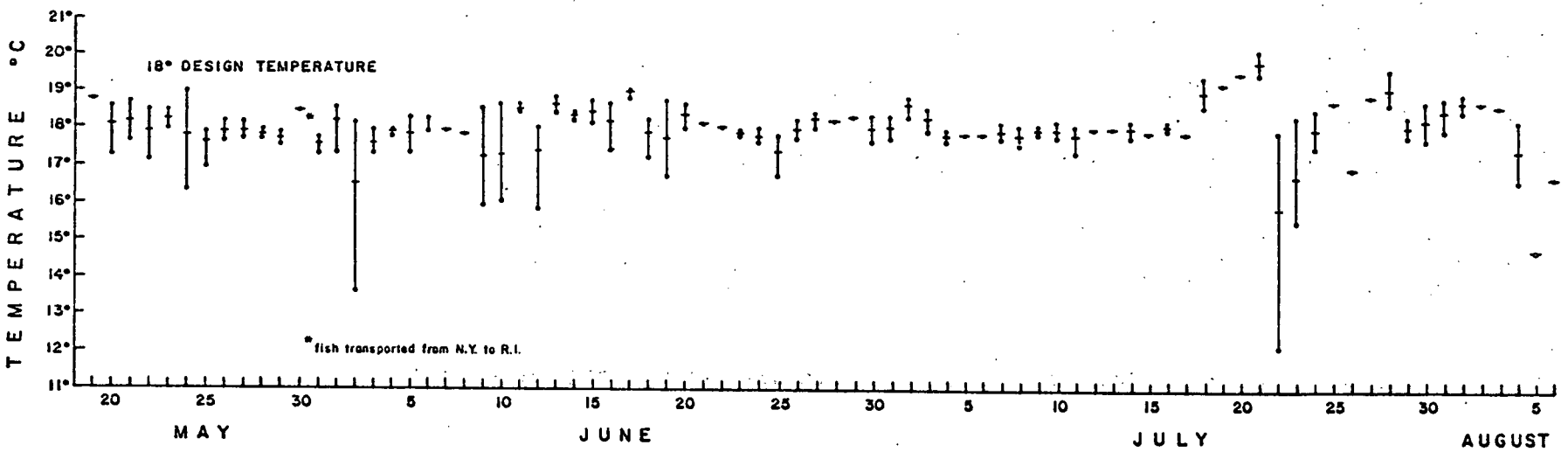

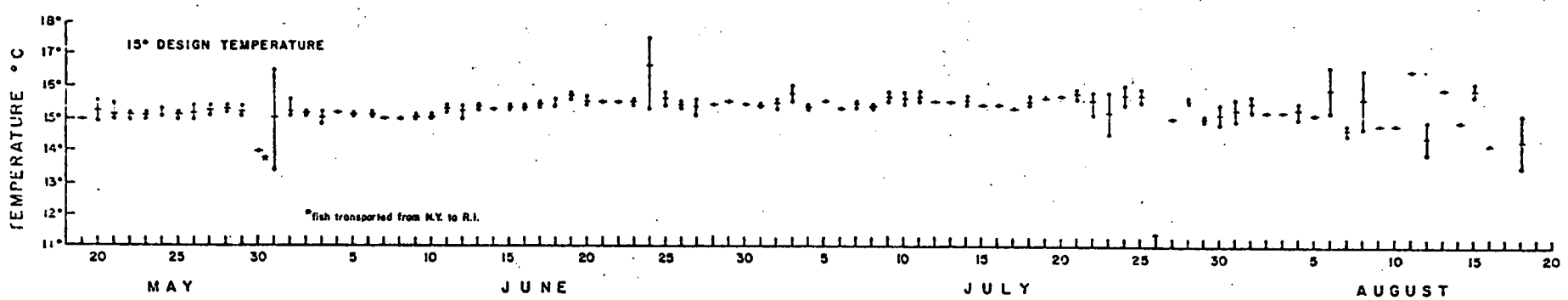

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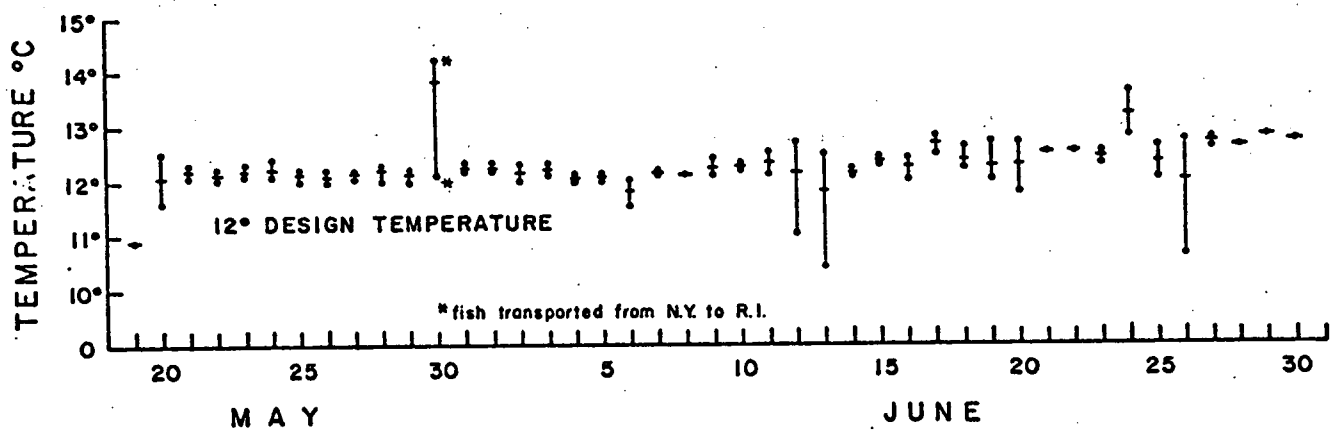


Record of observed temperatures in 12°C design temperature treatment.

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

Pages

Larval Growth Figures. 72

Larval Mortality Figures 87

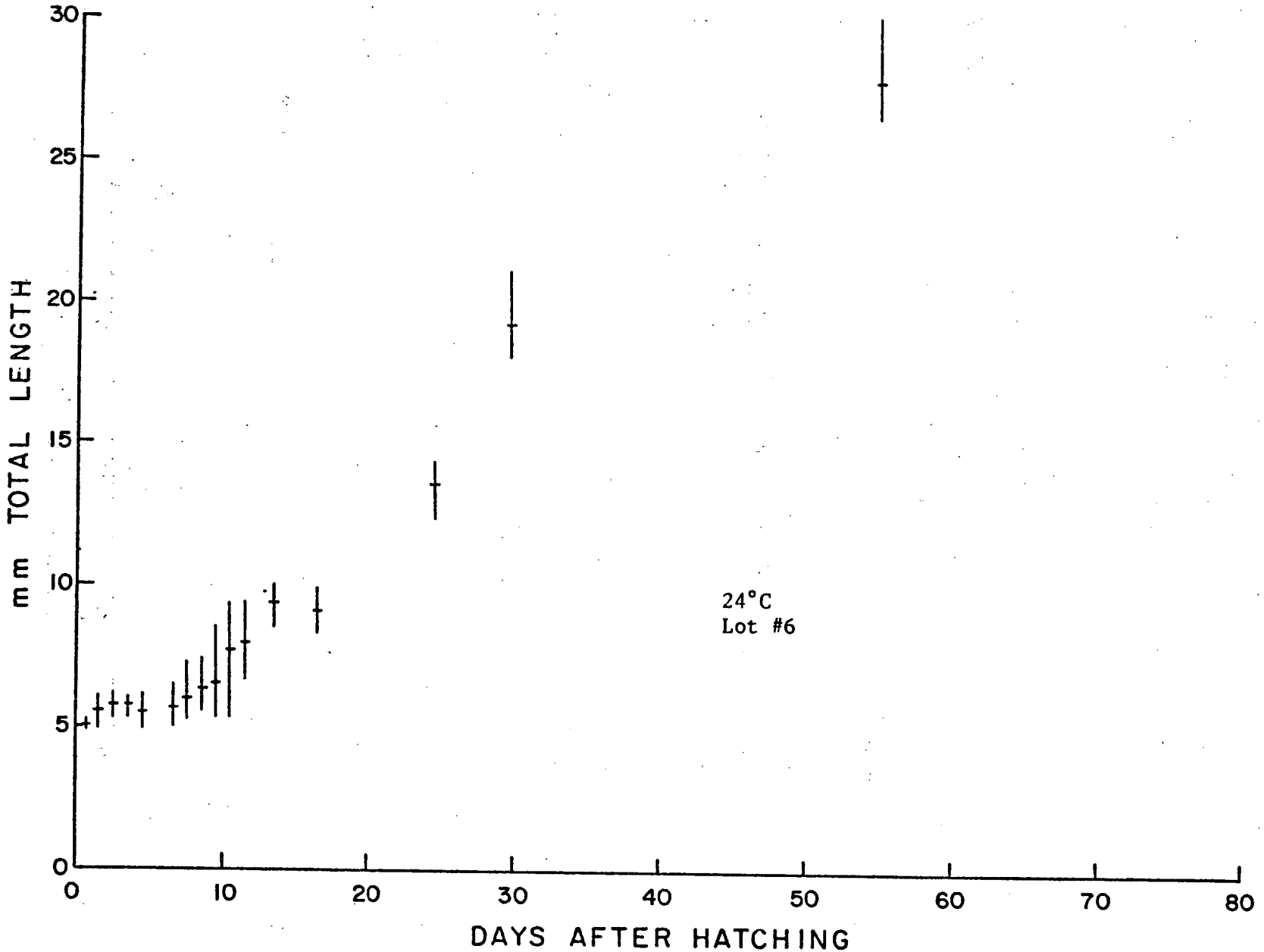
Appendix B

Larval Growth Figures

Legend

vertical bar represents range in length in each sample

cross bar is sample mean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DAYS AFTER HATCHING
24°C
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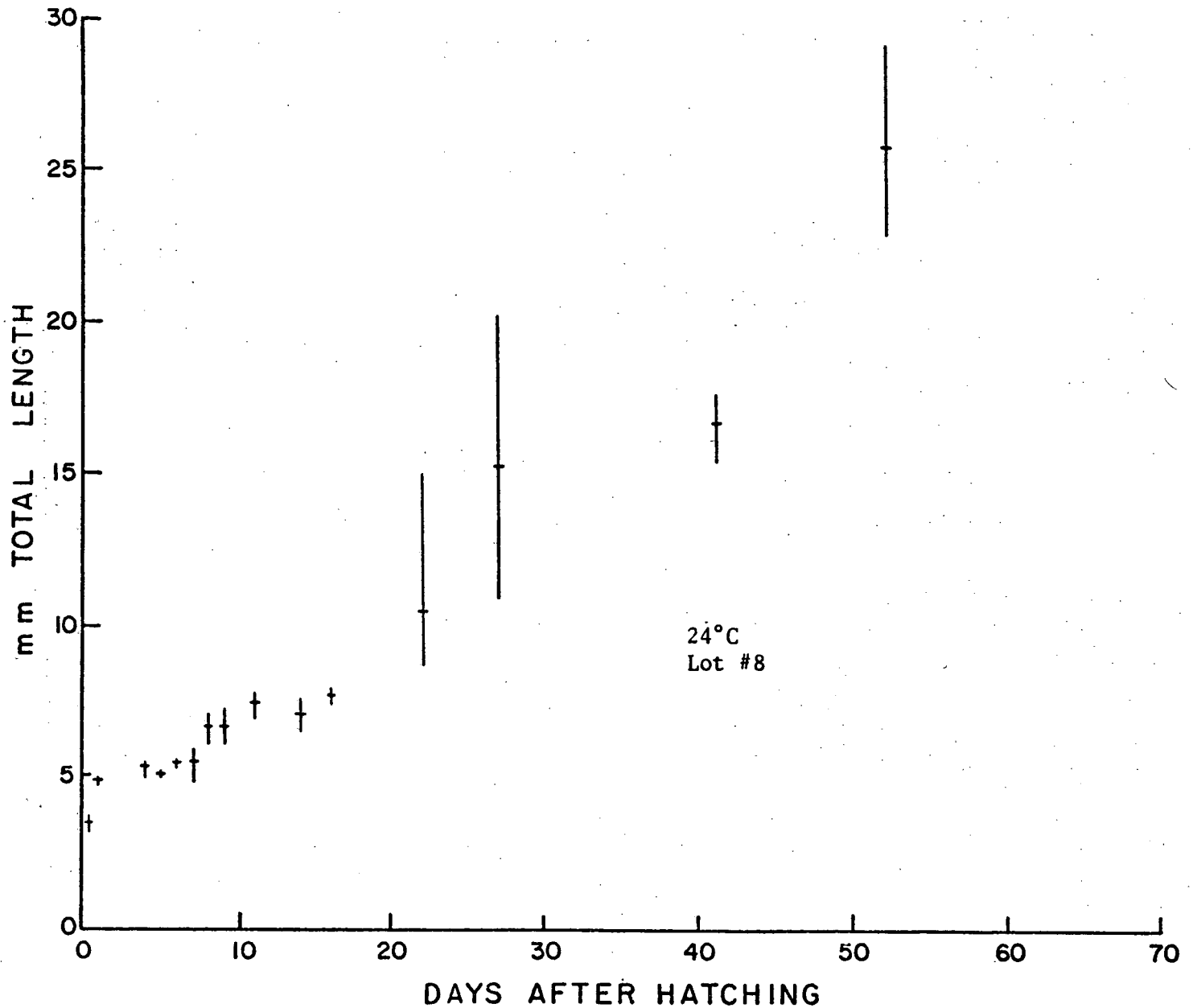
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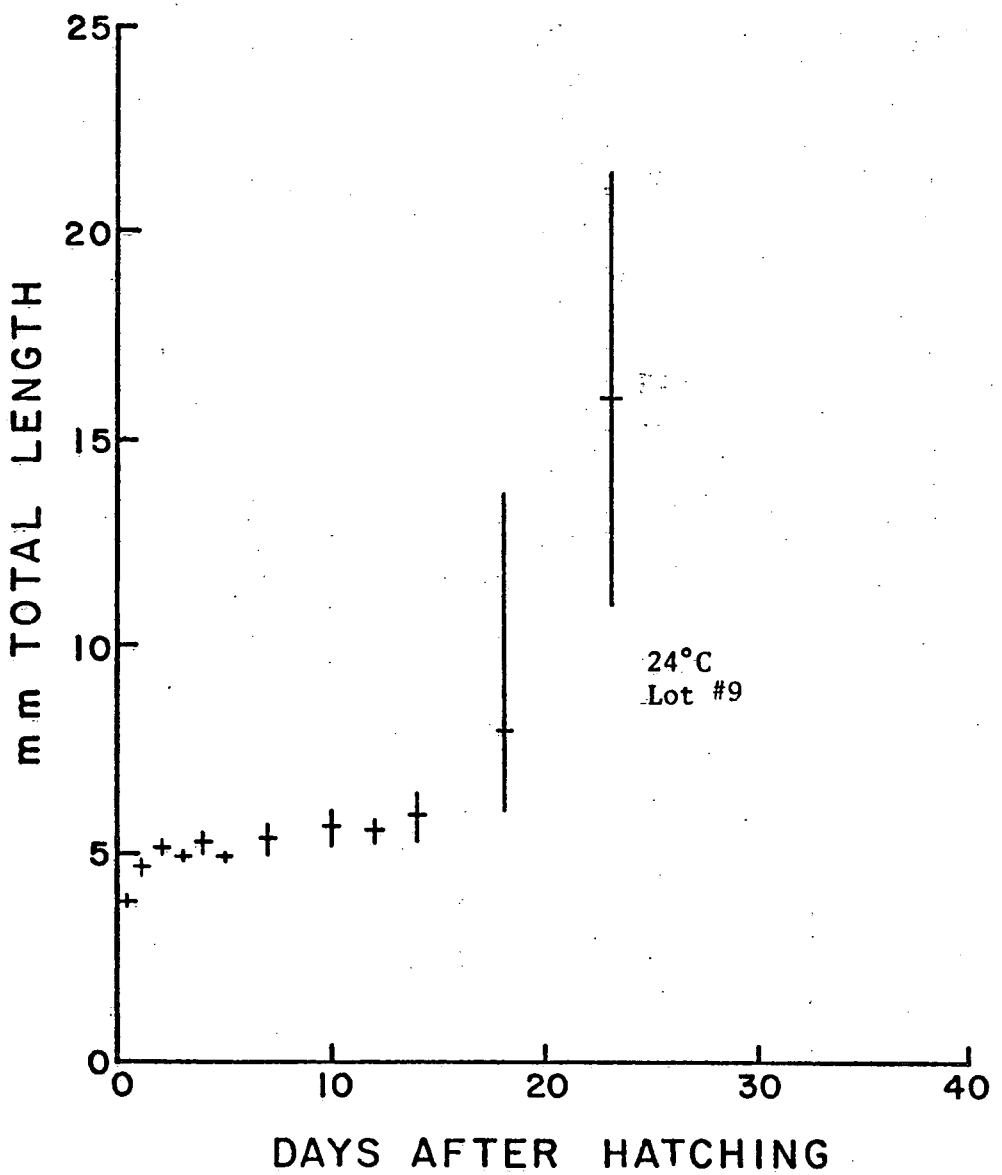
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DAYS AFTER HATCHING
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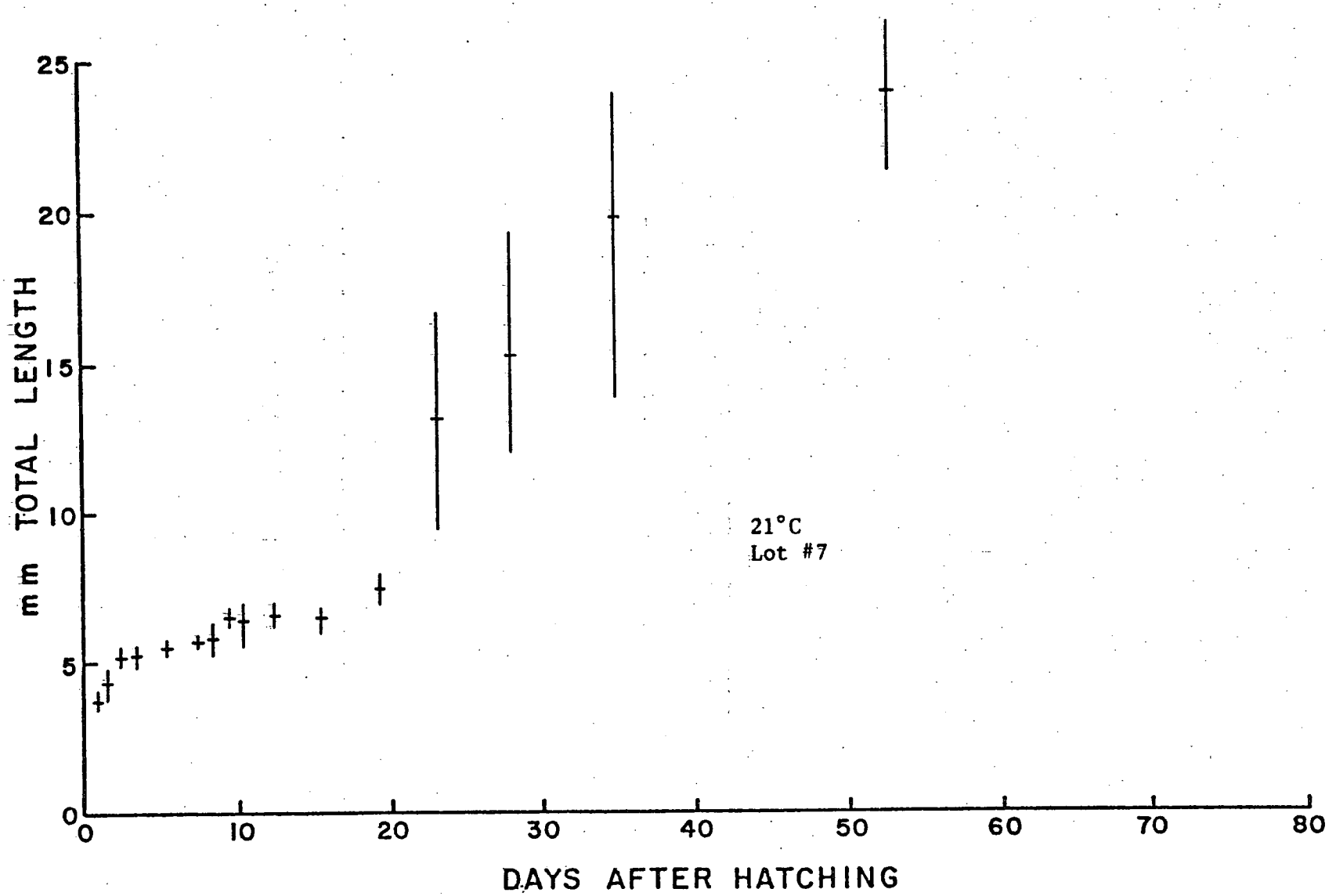
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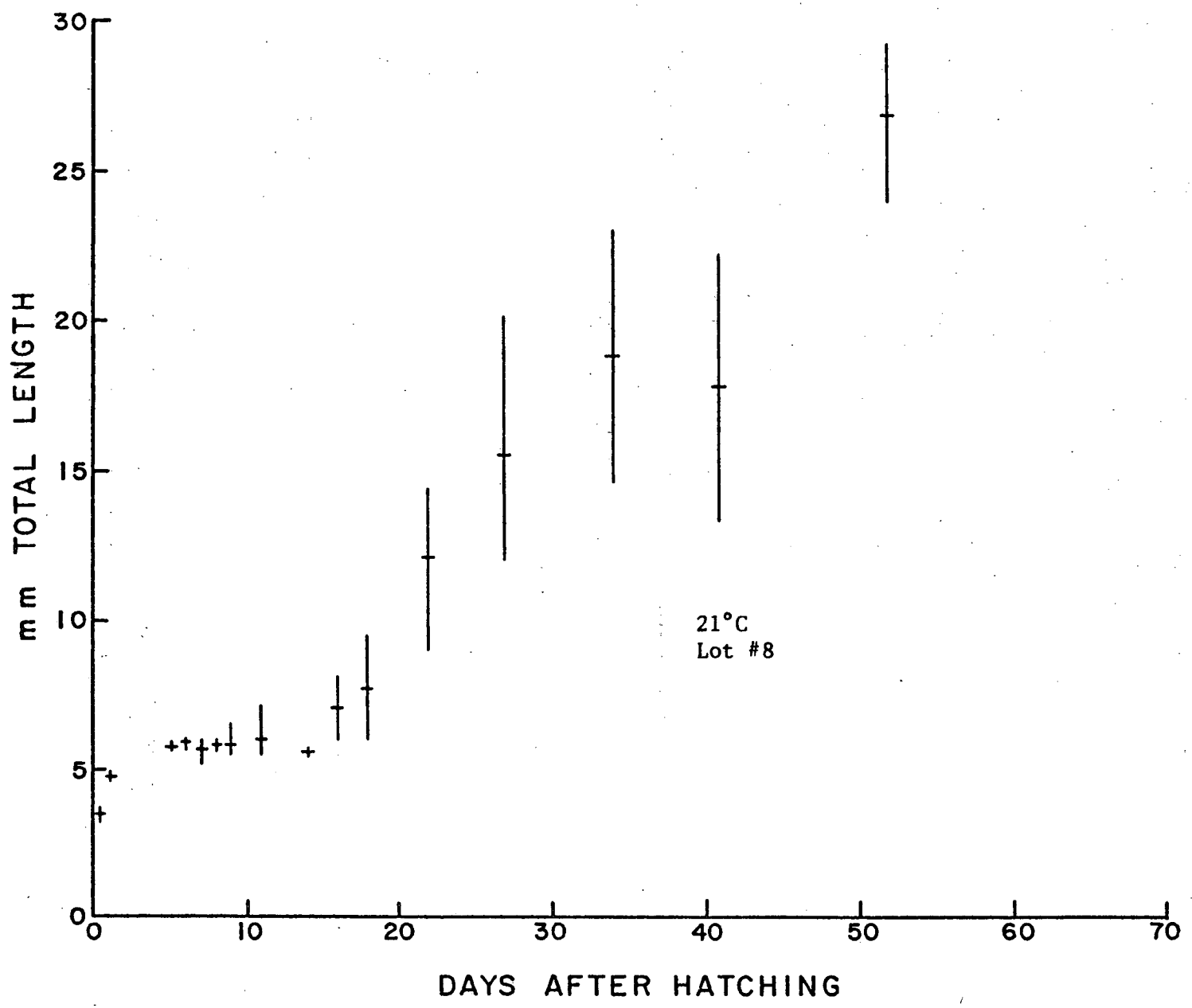
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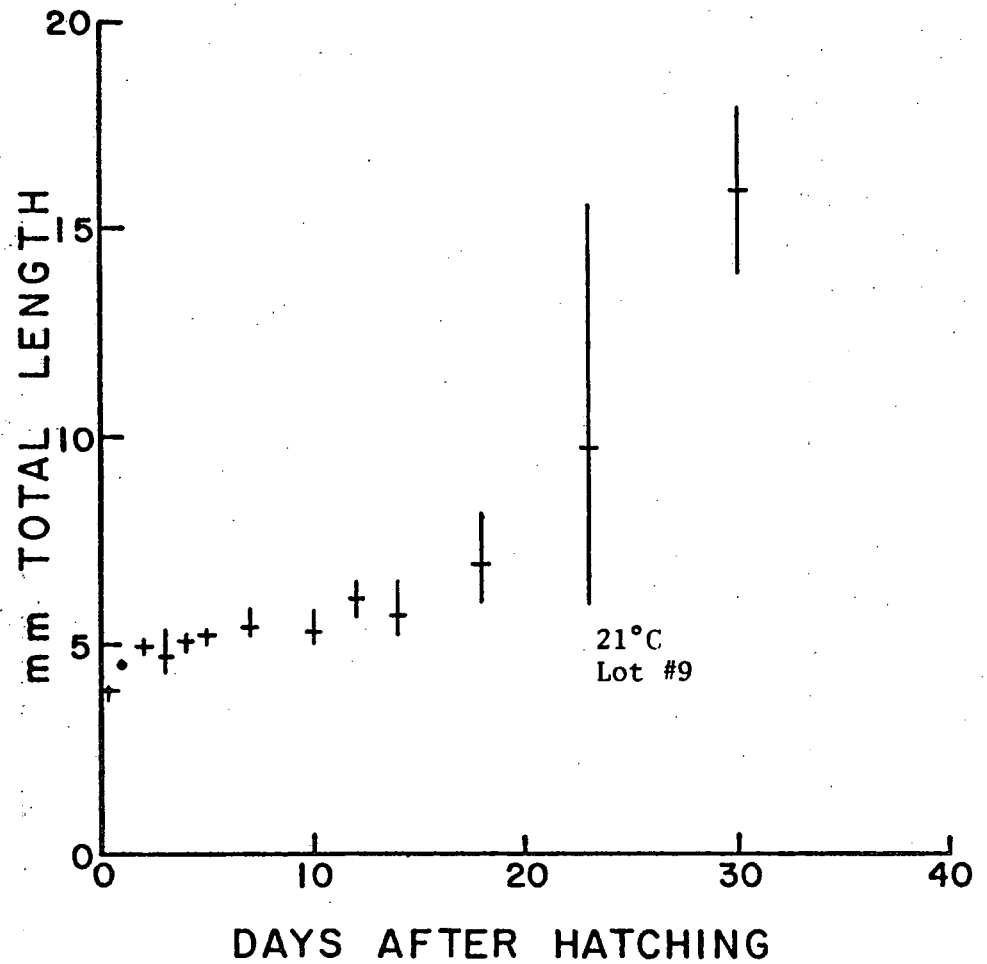
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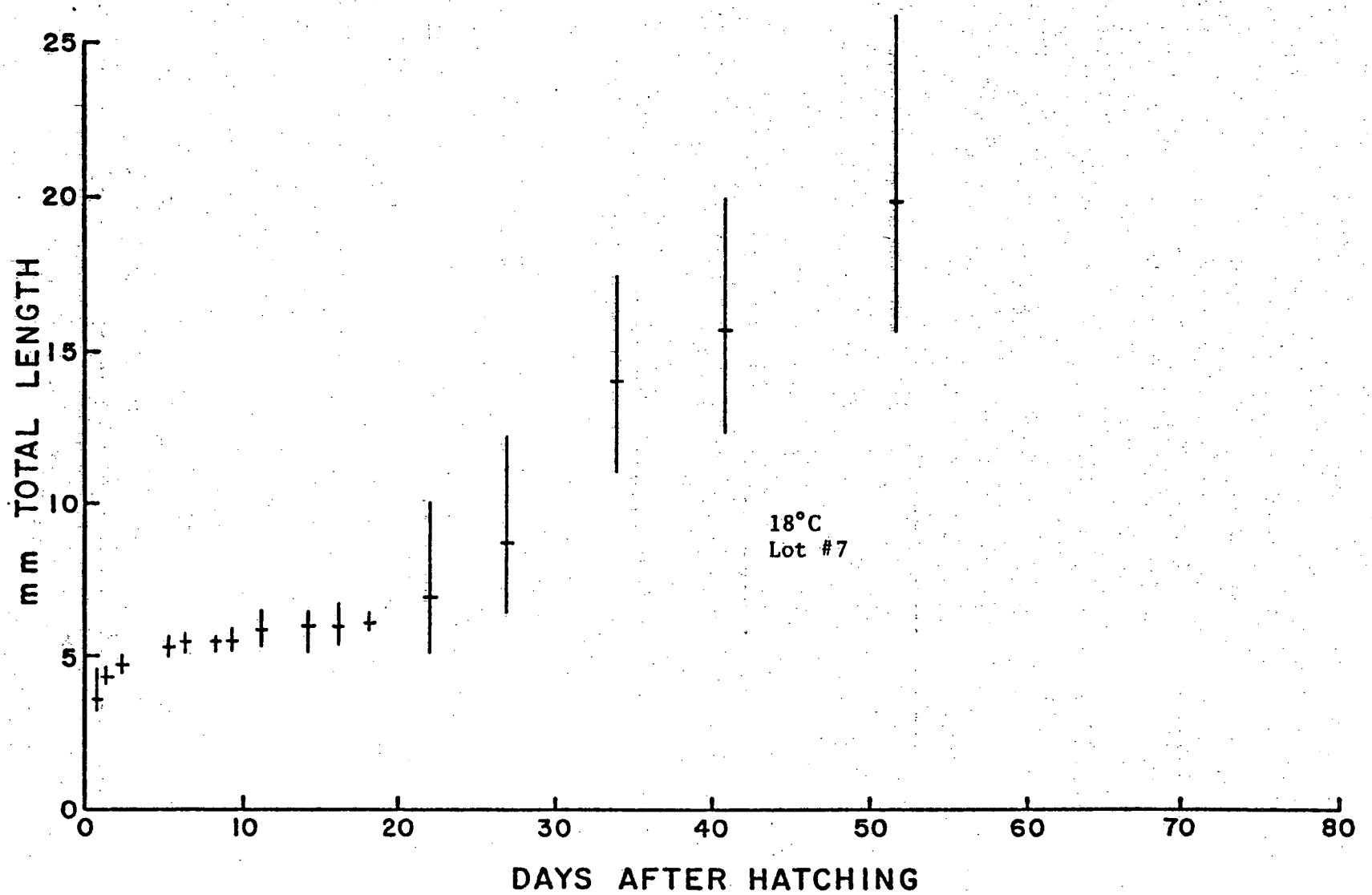
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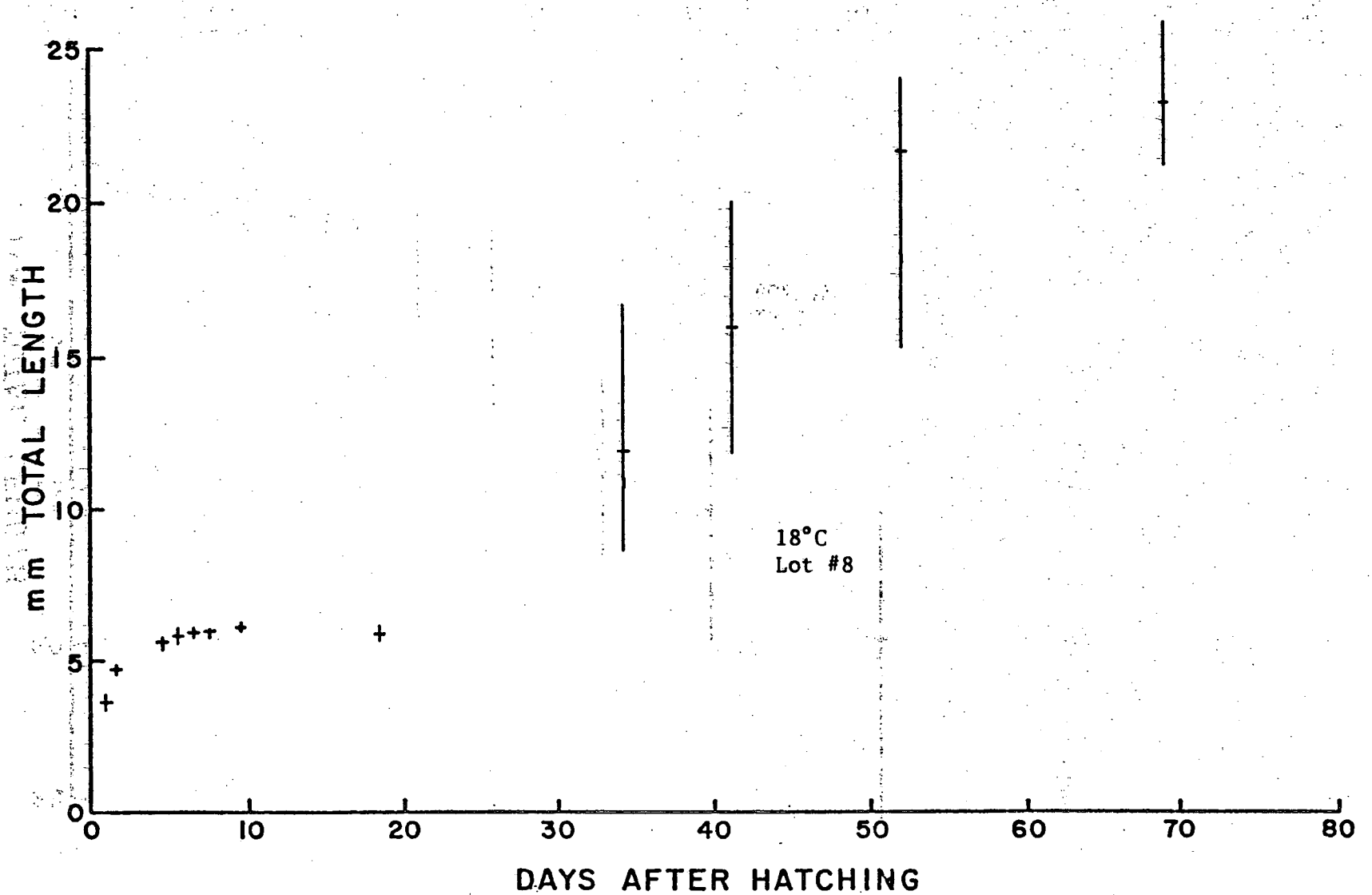
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DAYS AFTER HATCHING
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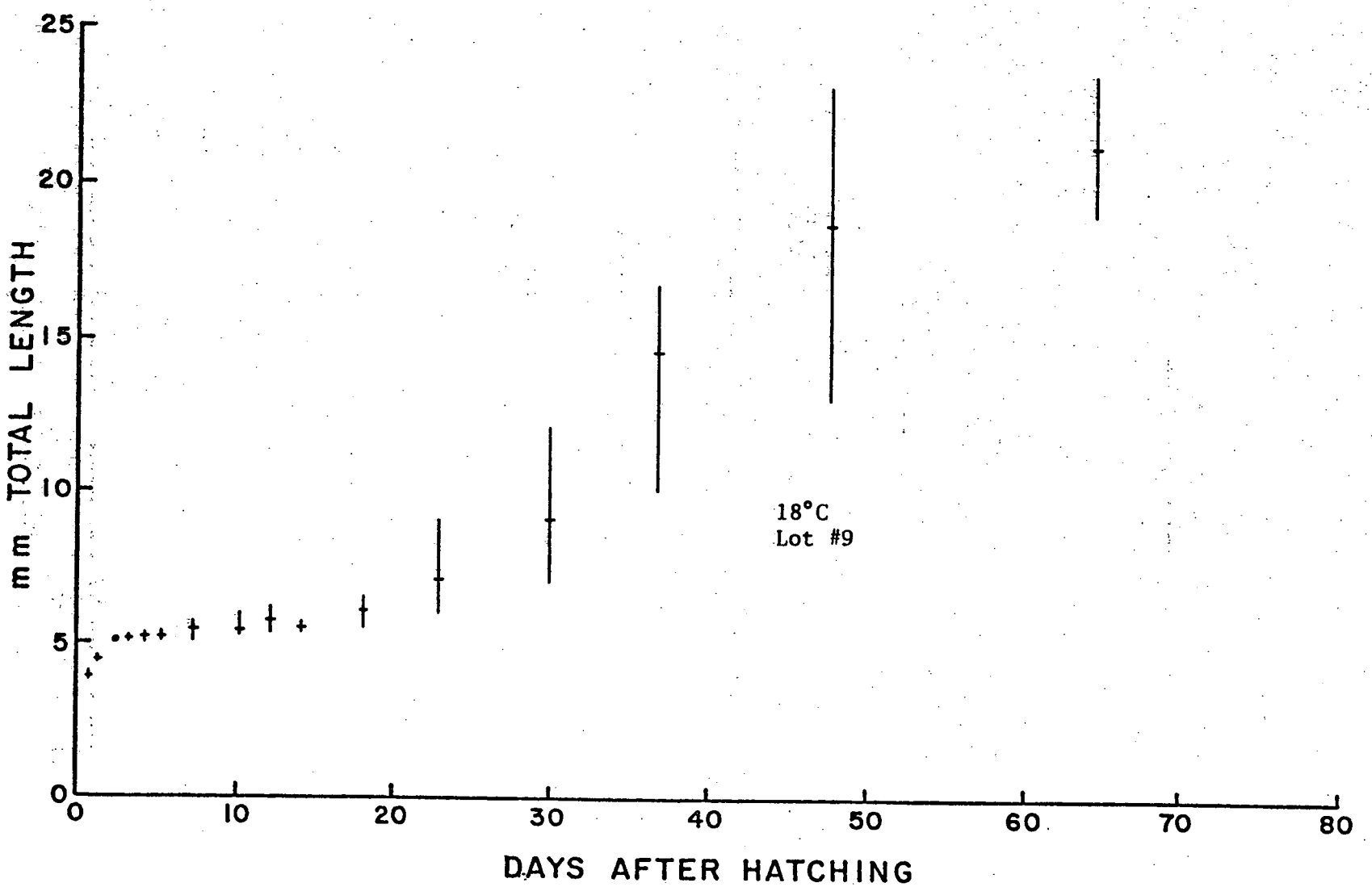
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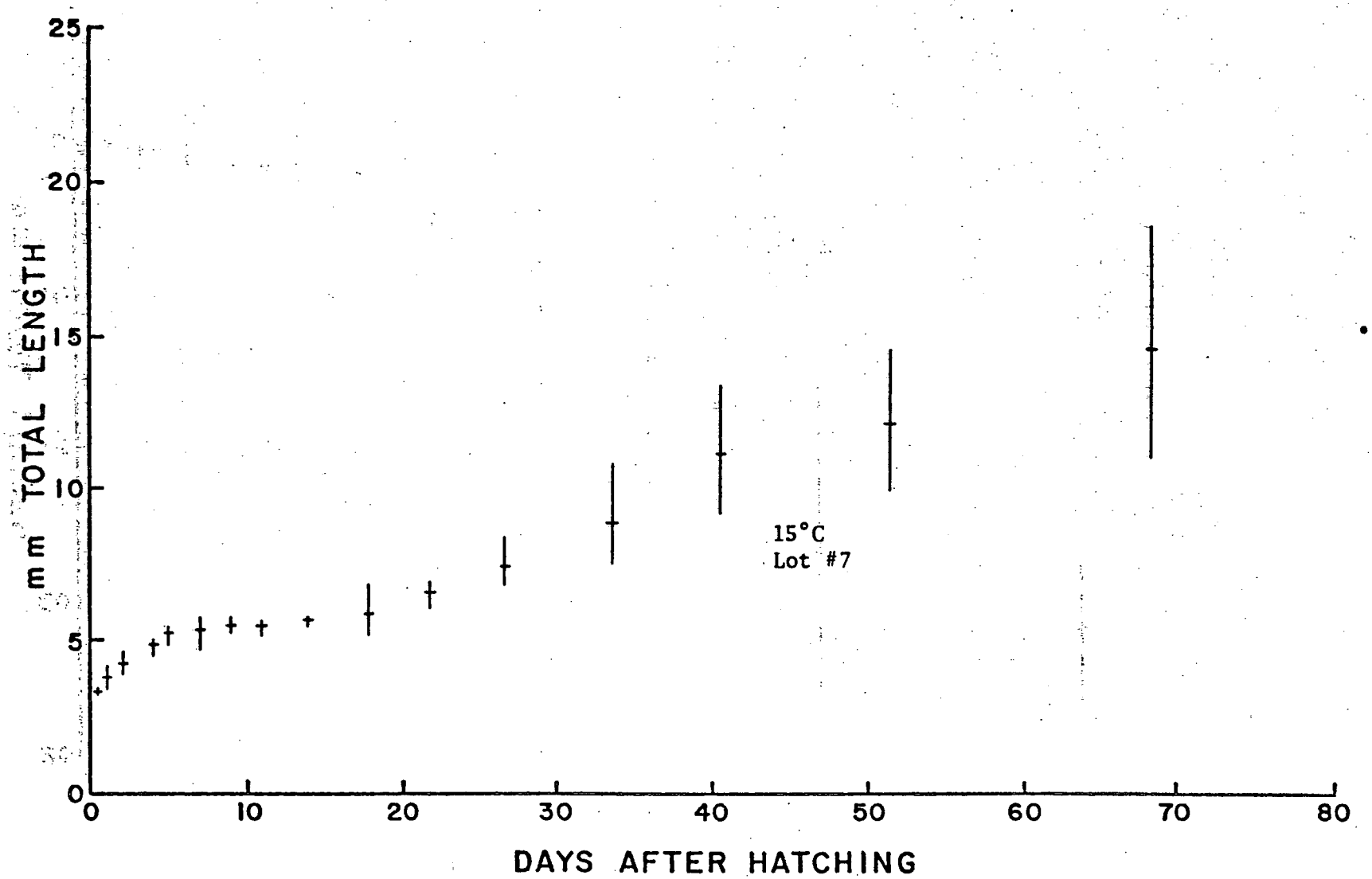
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DAYS AFTER HATCHING
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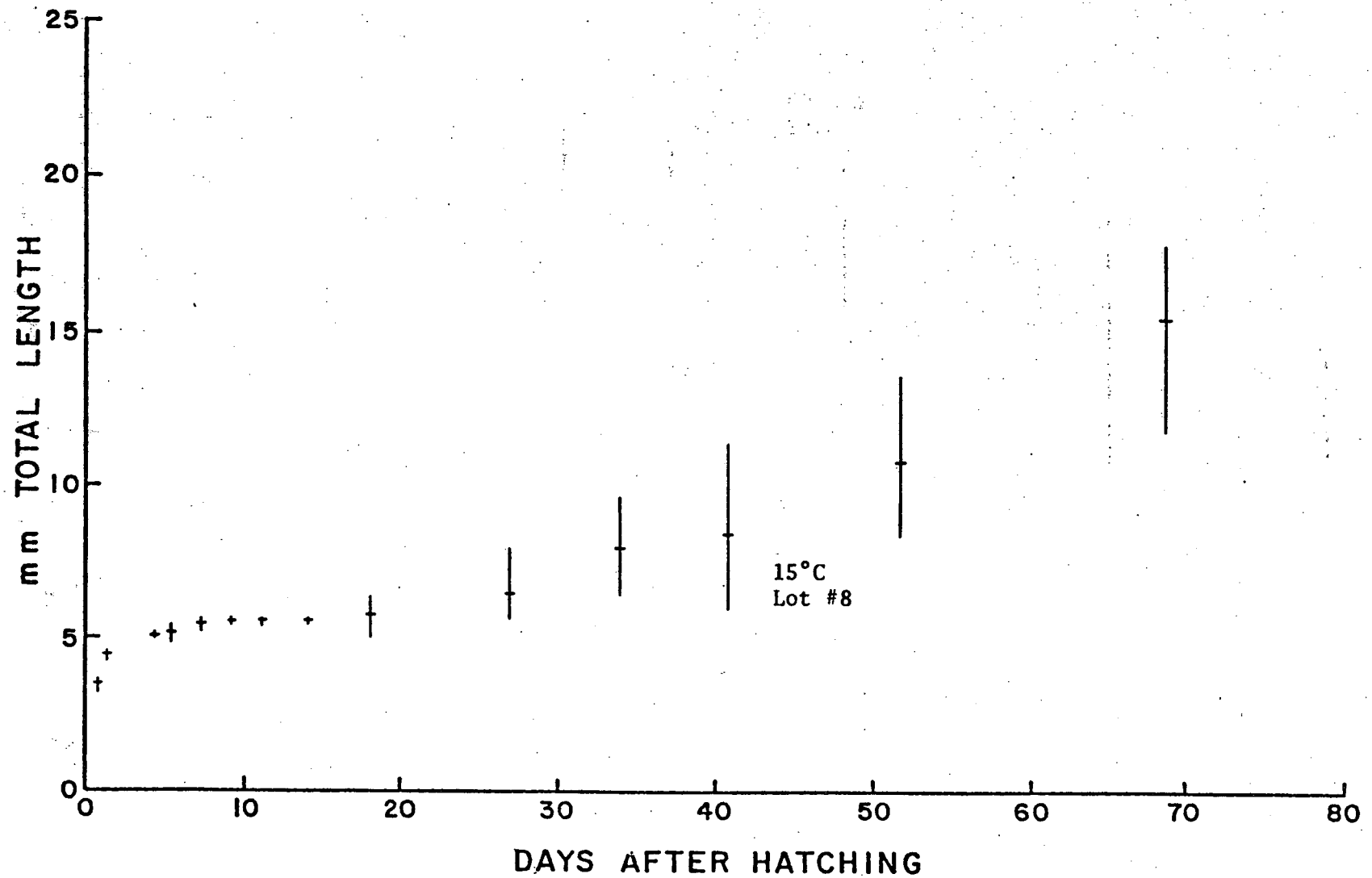
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DAYS AFTER HATCHING
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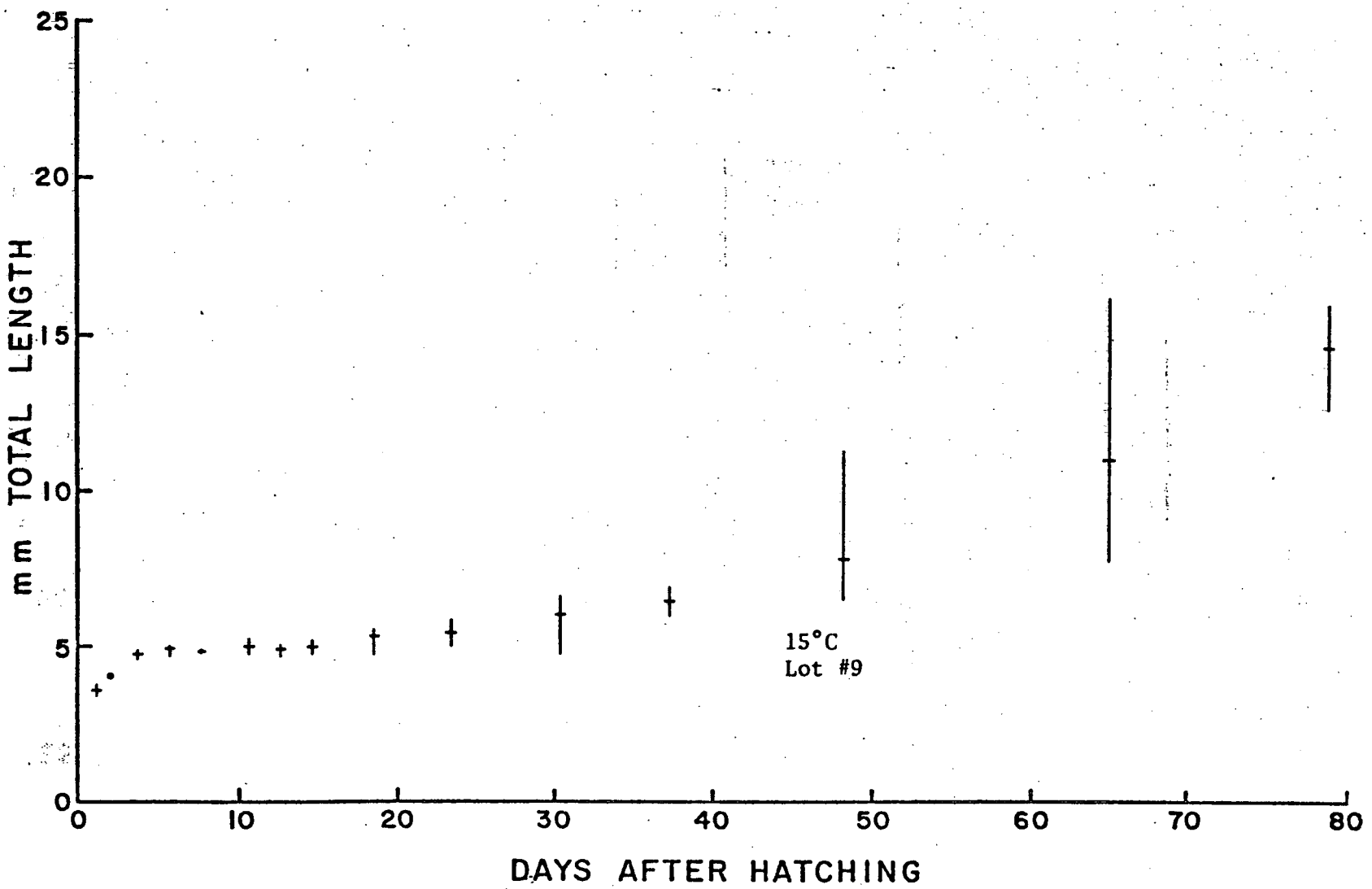
Lot #8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DAYS AFTER HATCHING
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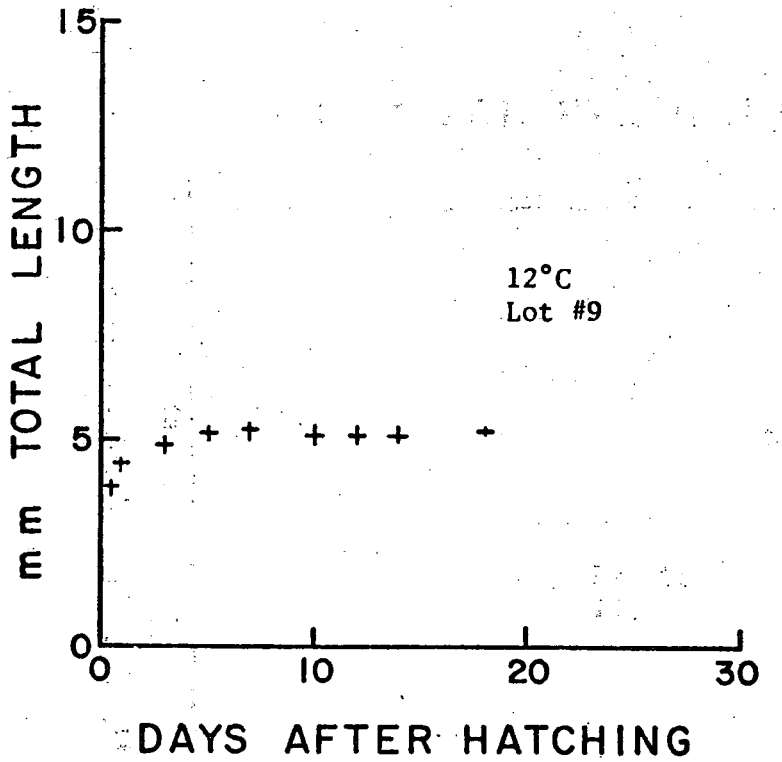
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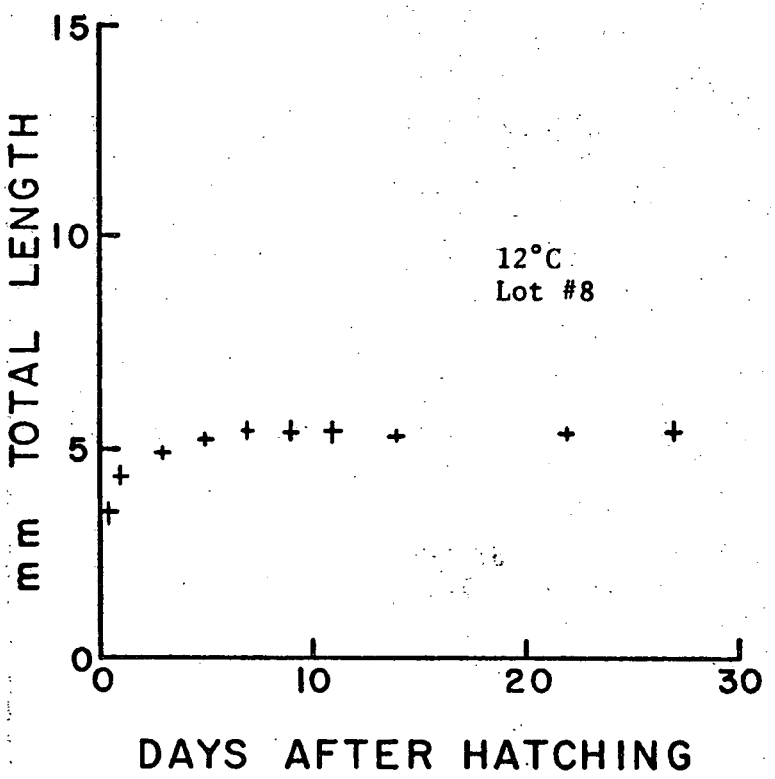
DAYS AFTER HATCHING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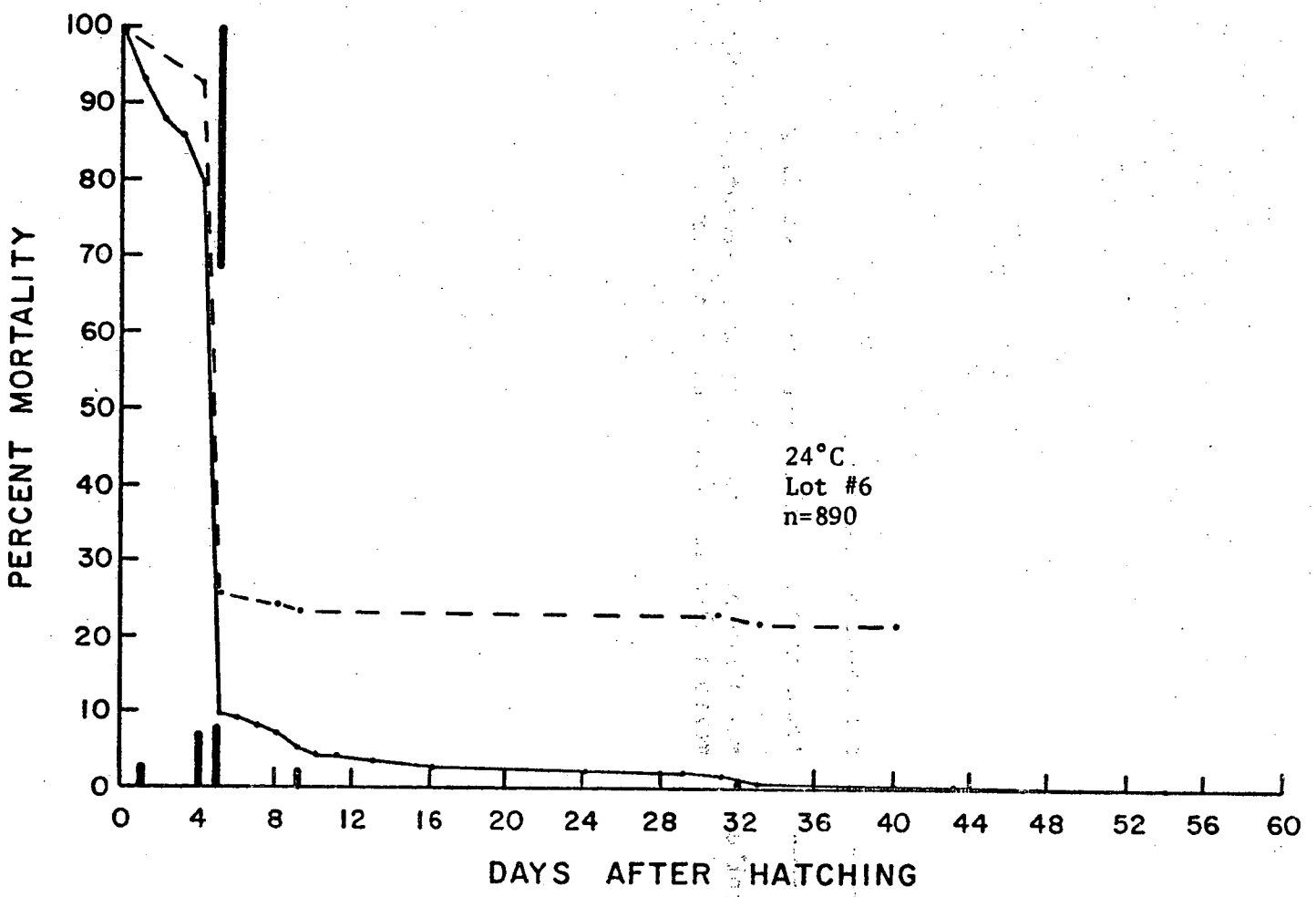
mm TOTAL LENGTH
12°C
Lot #8
0
10
20
30
DAYS AFTER HATCHING

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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4
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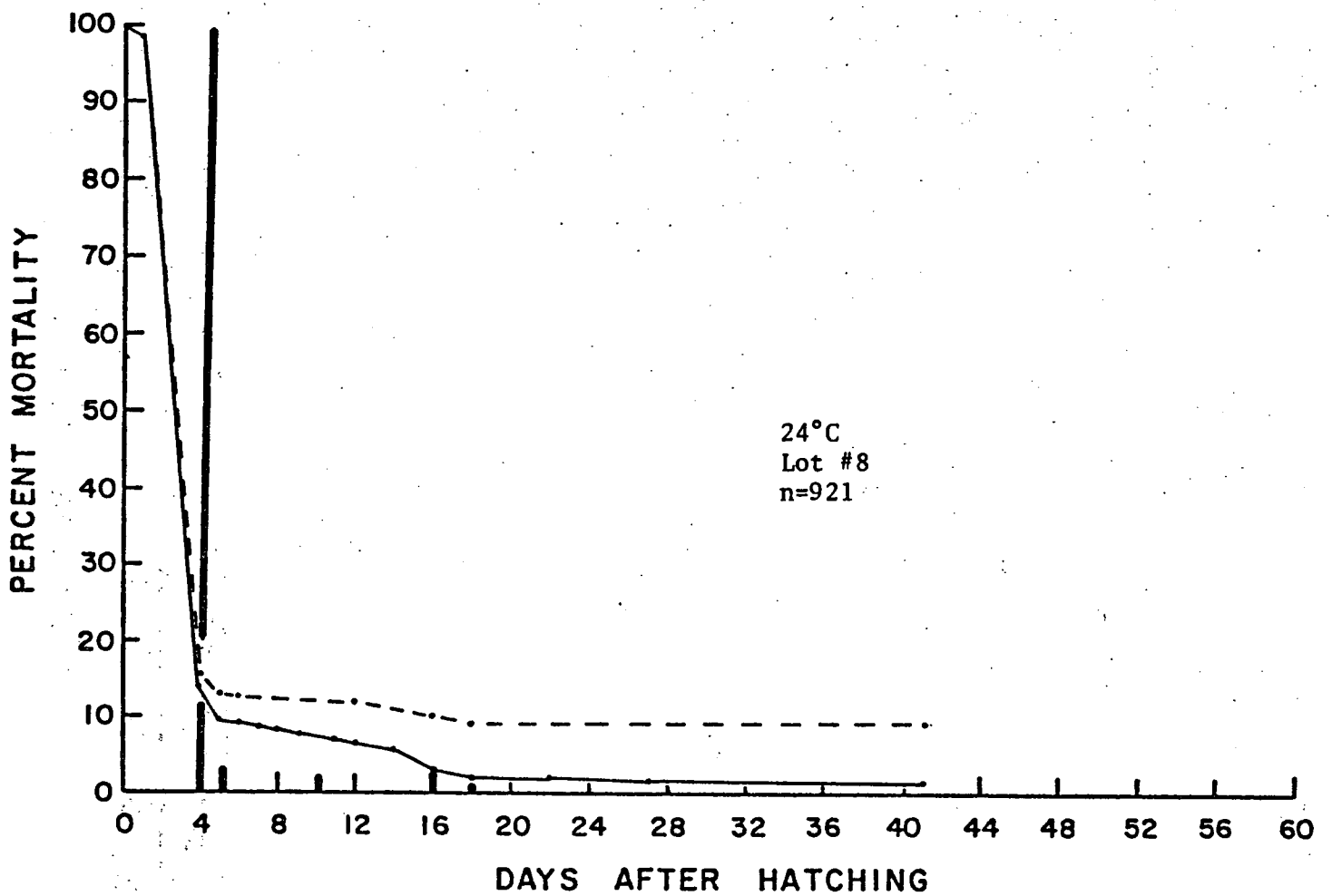
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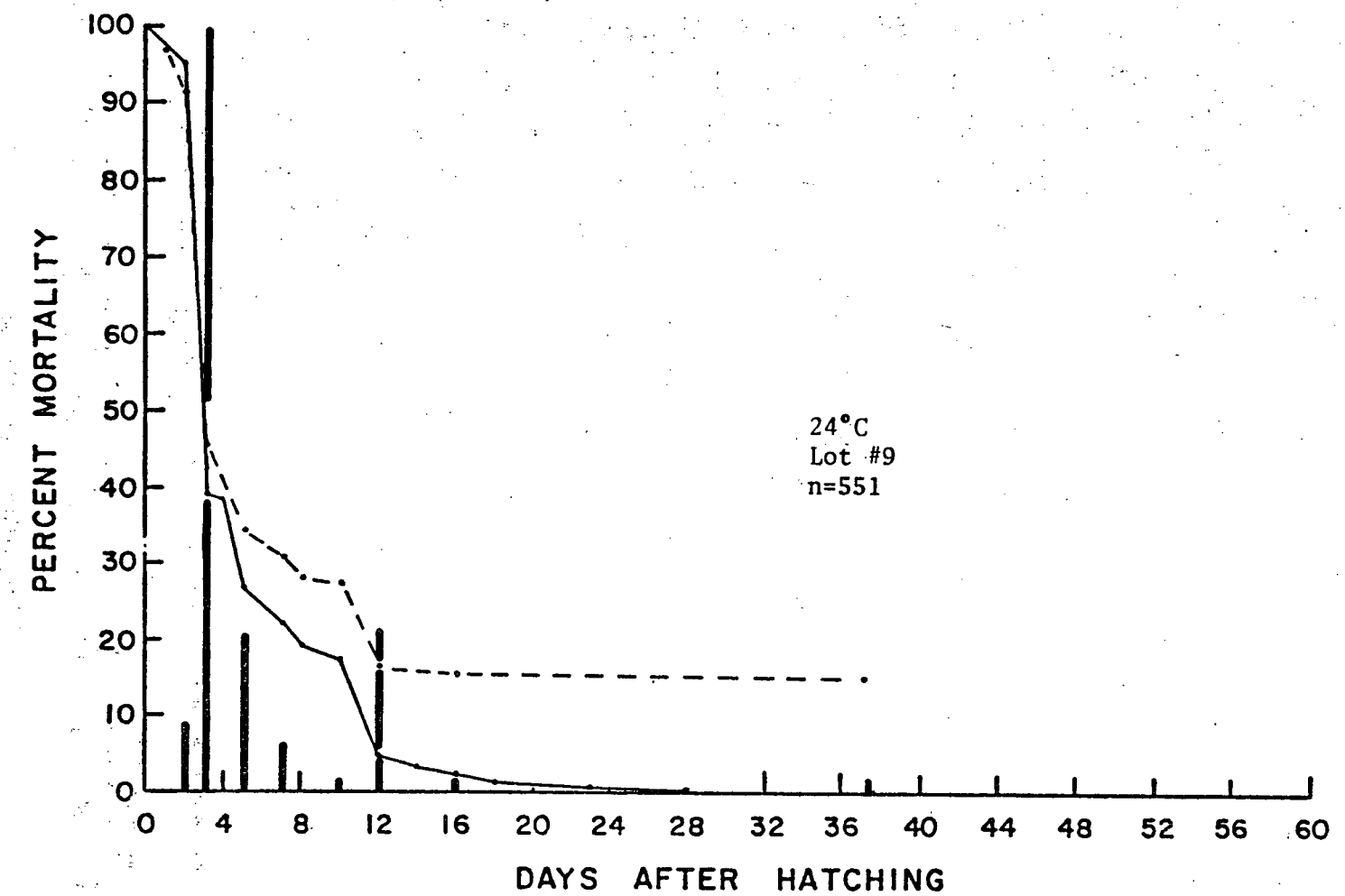
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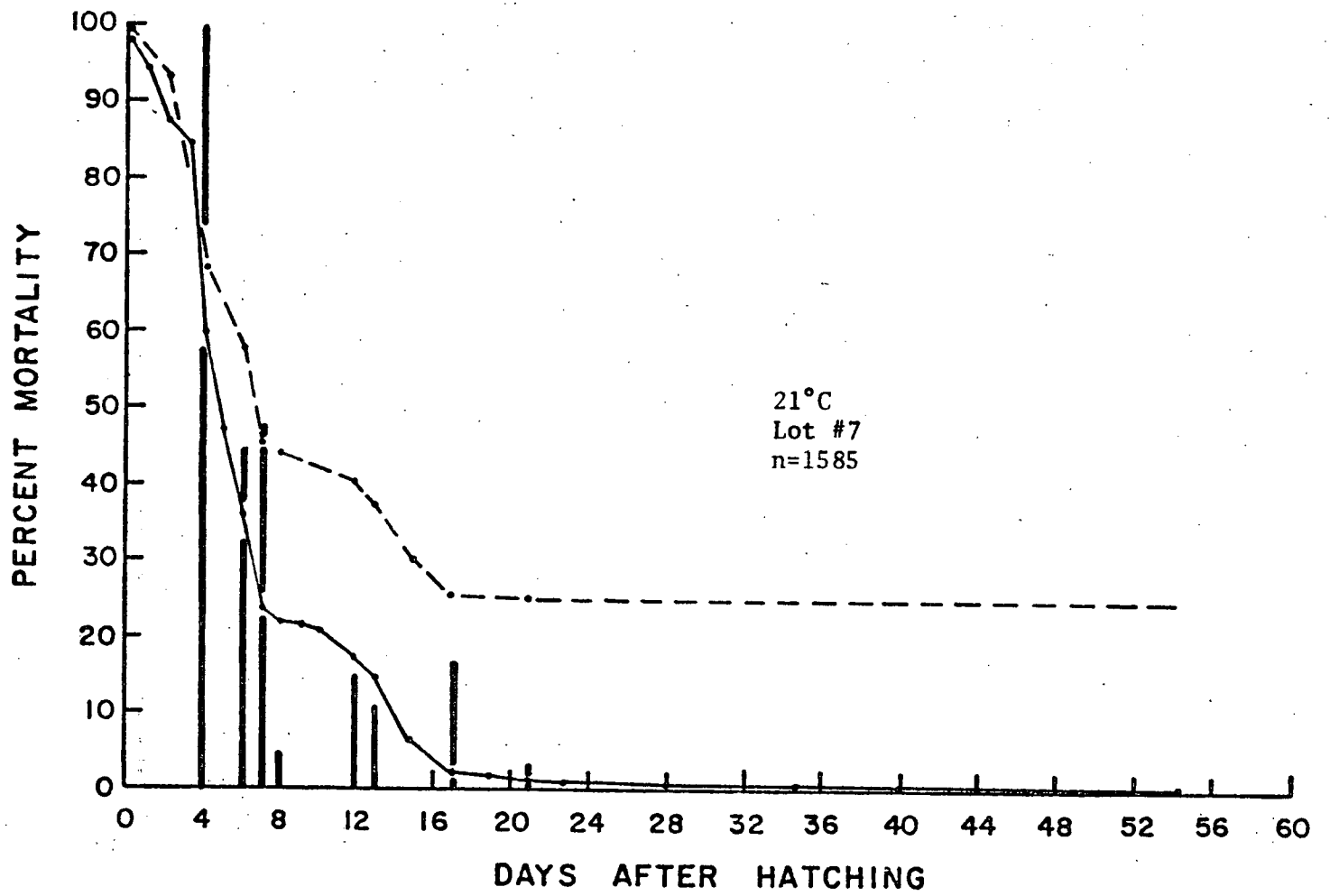
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36
40
44
48
52
56
60
DAYS AFTER HATCHING
21°C
Lot #7
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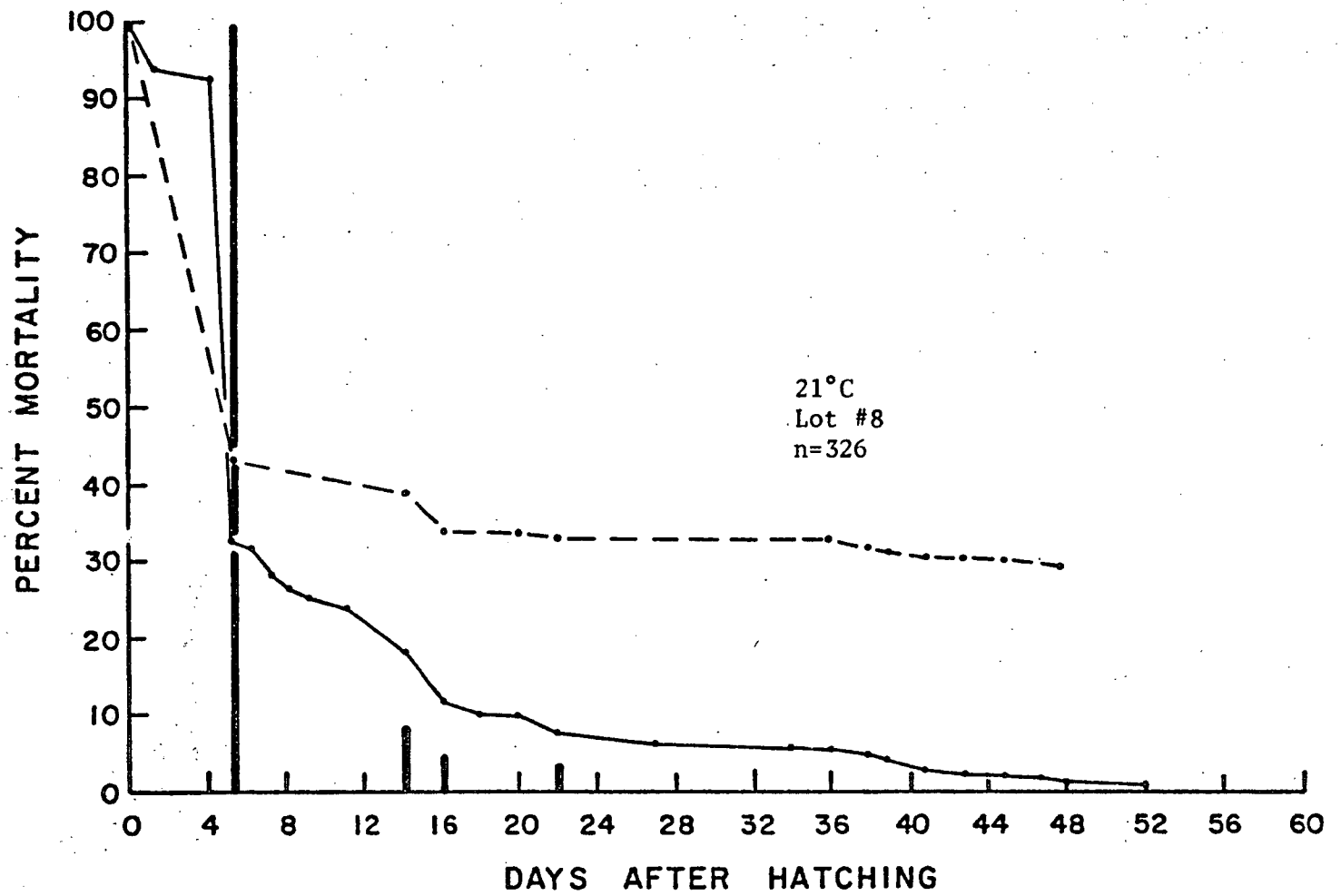
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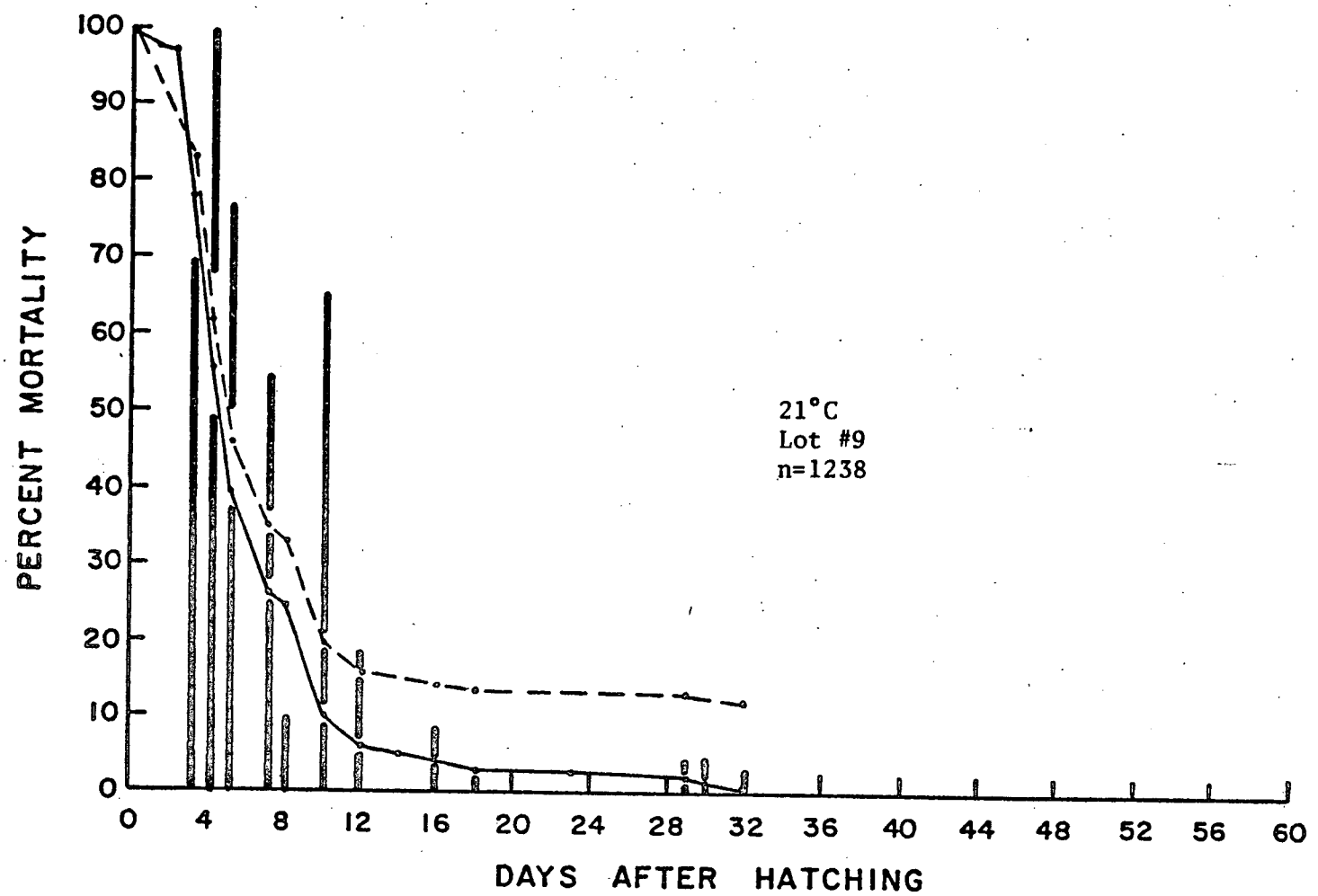
DAYS AFTER HATCHING
21°C
Lot #8
n=326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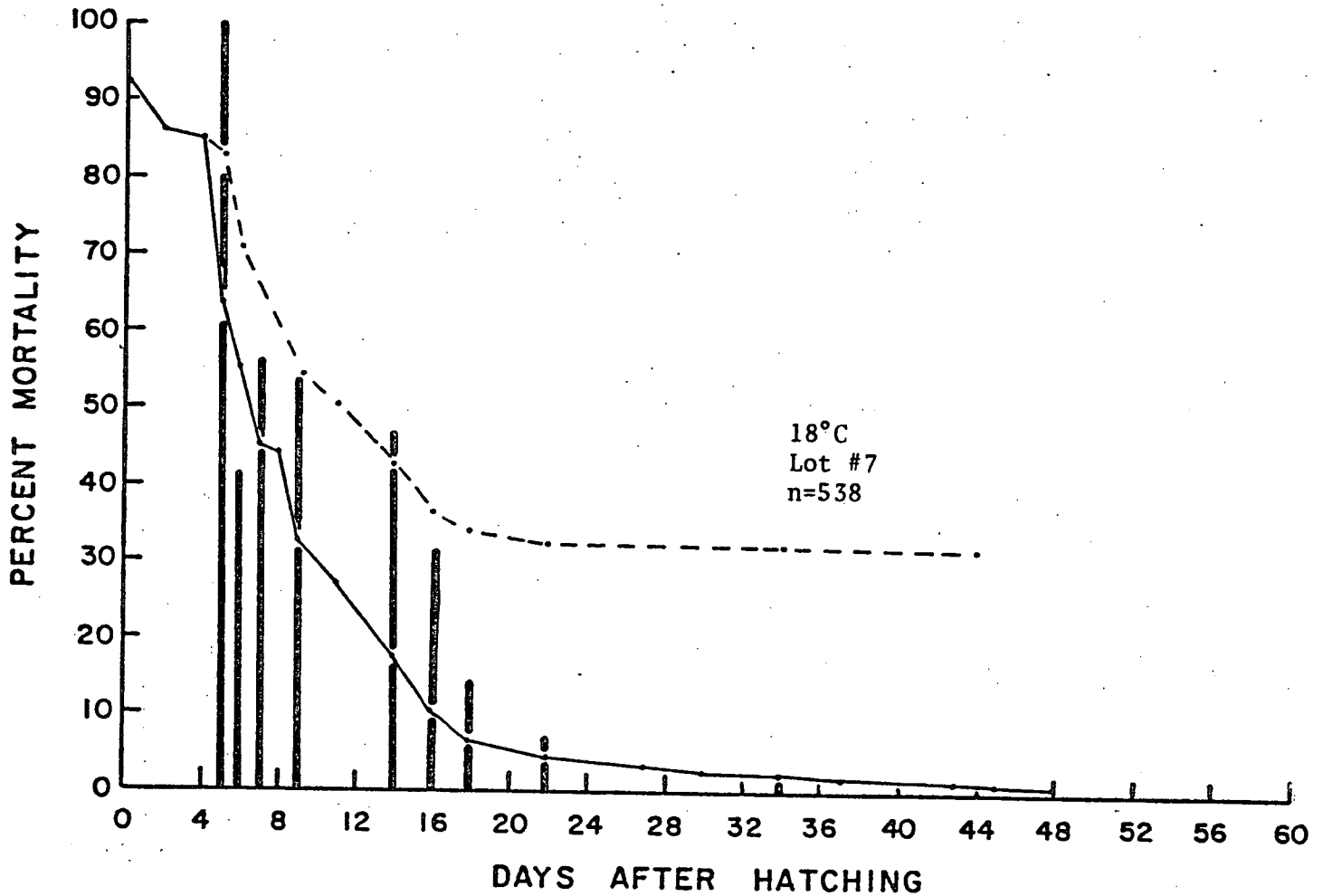
DAYS AFTER HATCHING
21°C
Lot #9
n=1238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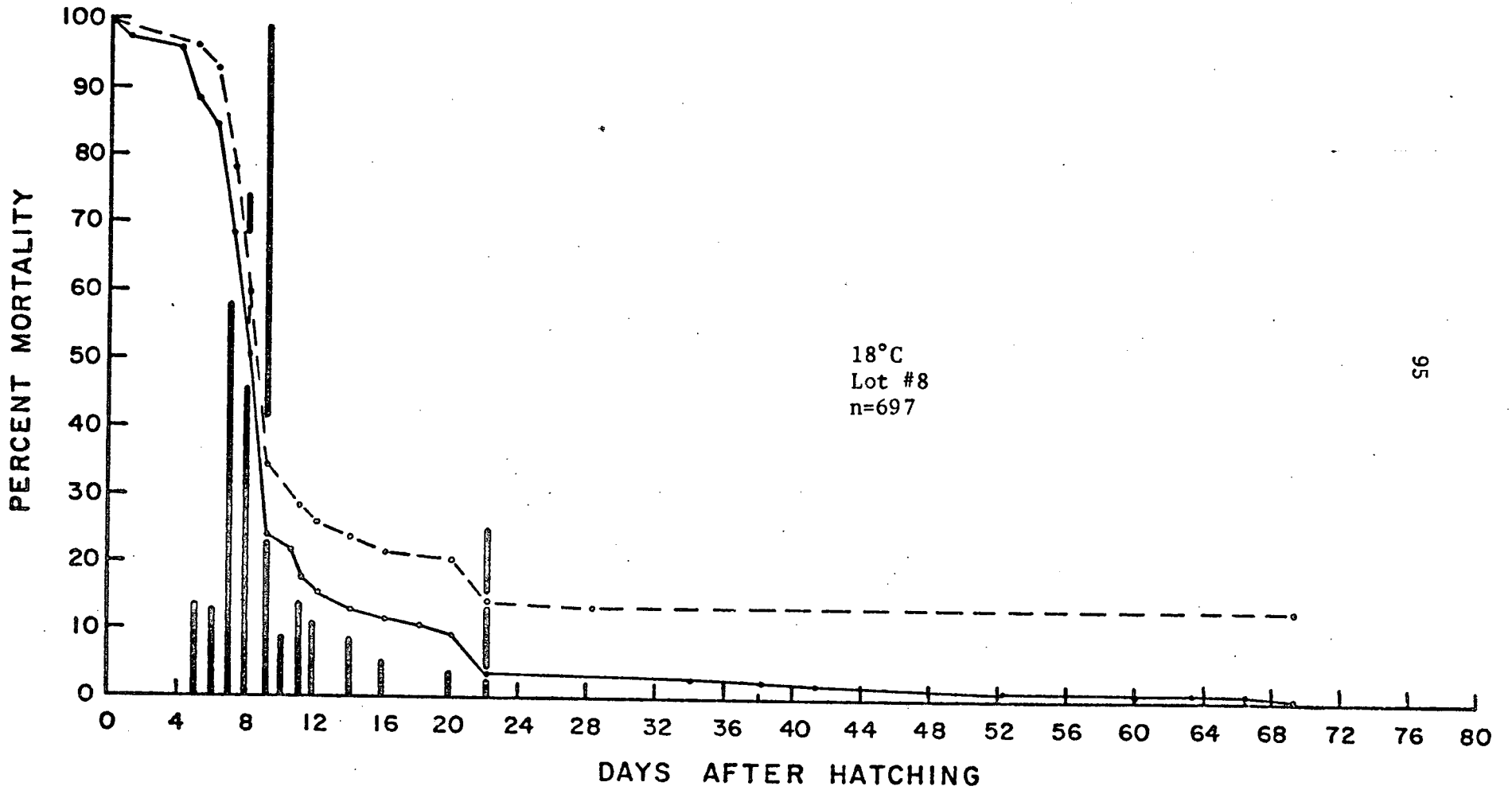
DAYS AFTER HATCHING
18°C
Lot #7
n=538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28
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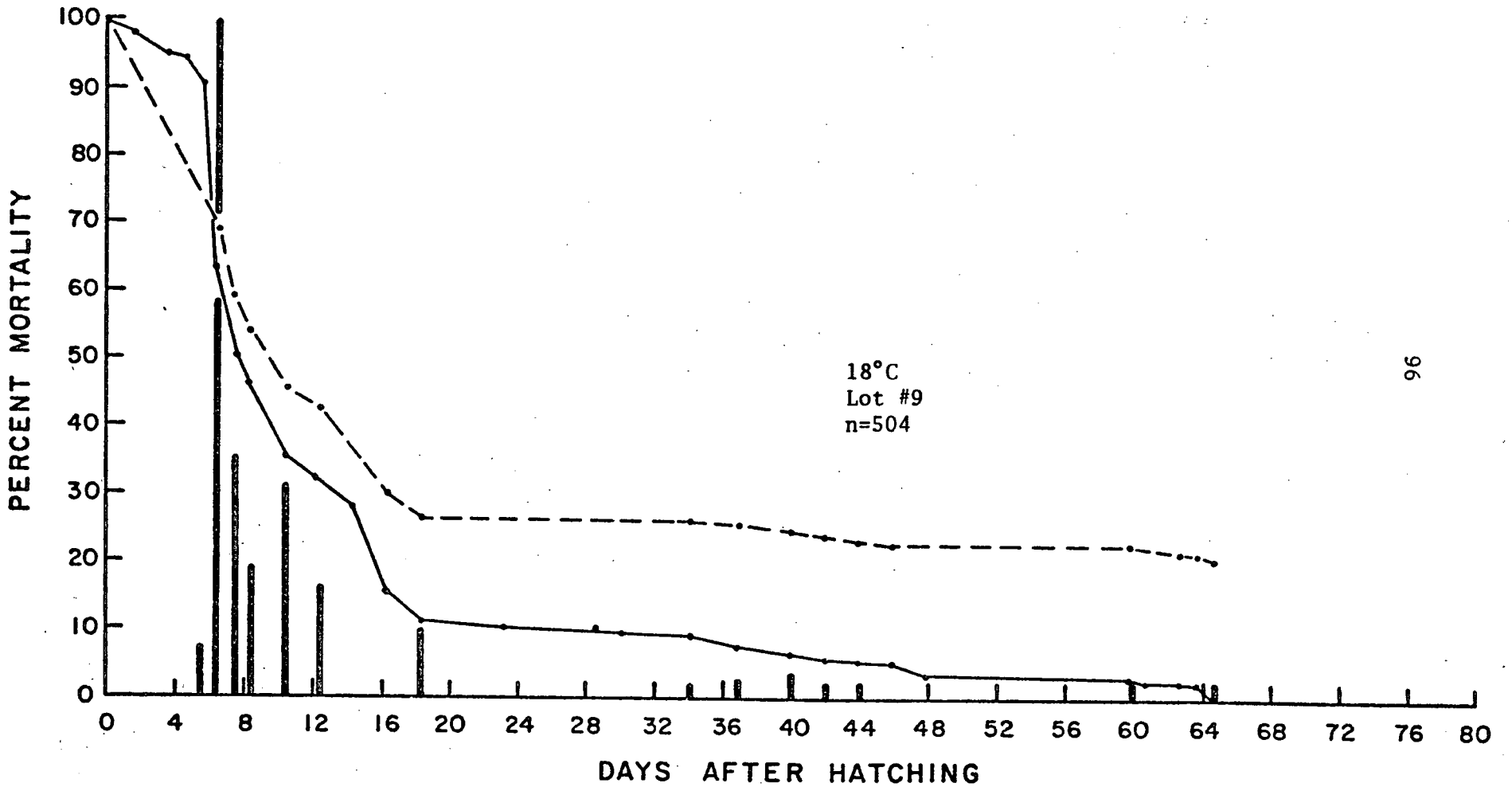
72
76
80
DAYS AFTER HATCHING
18°C
Lot #8
n=697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8
12
16
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24
28
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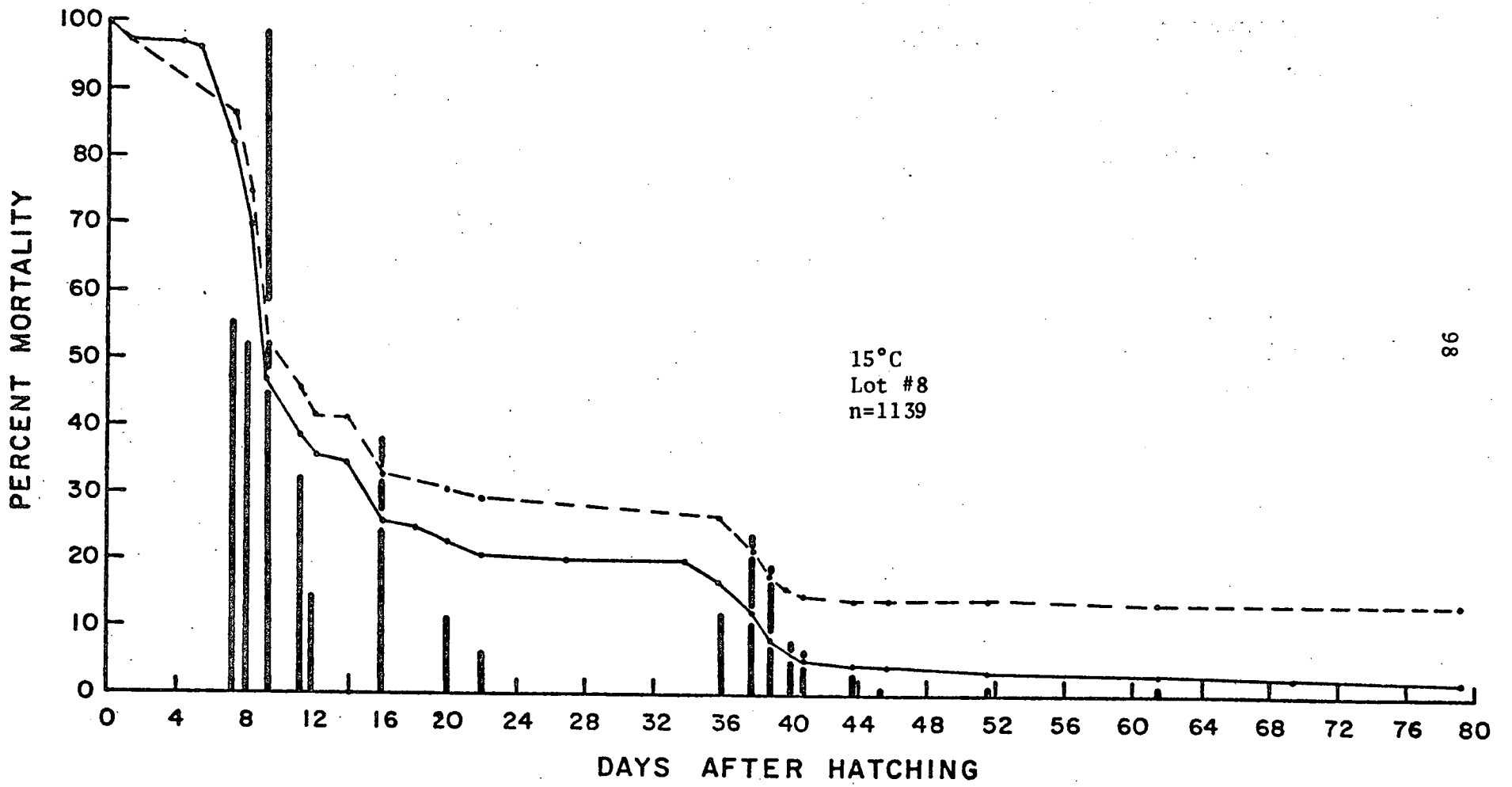
64
68
72
76
80
DAYS AFTER HATCHING
18°C
Lot #9
n=504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28
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76
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DAYS AFTER HATCHING
15°C
Lot #8
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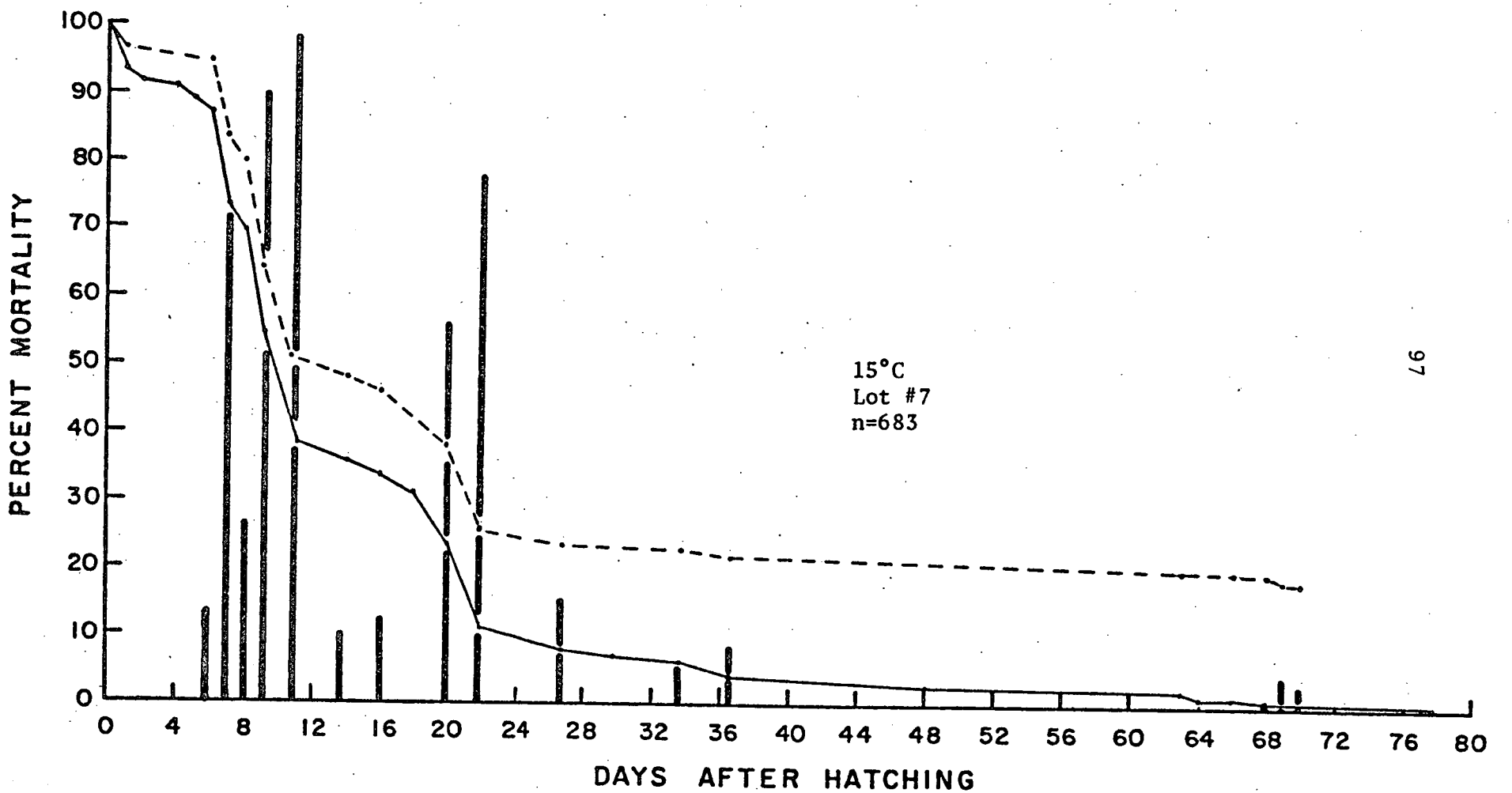
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40
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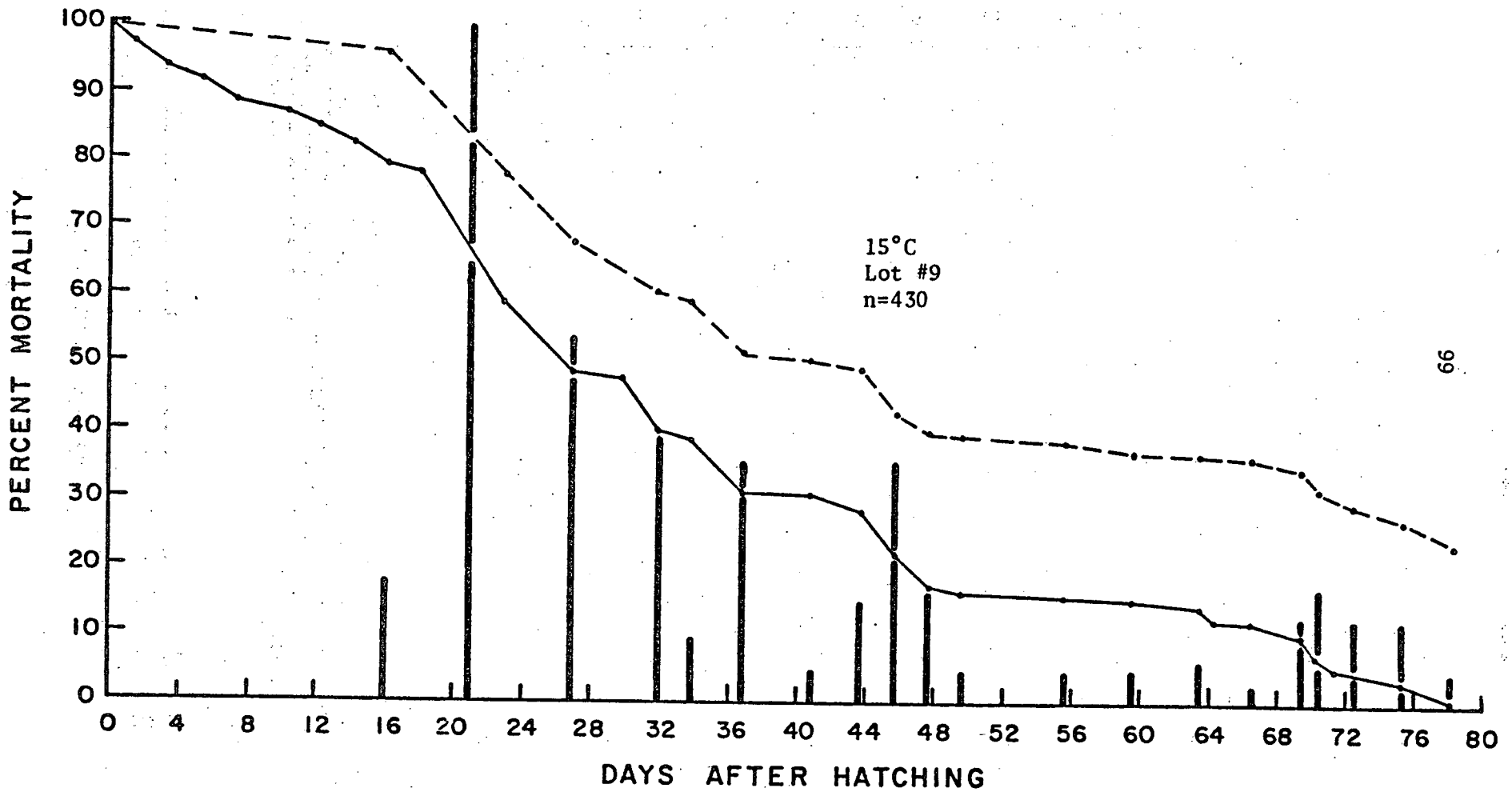
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
64
68
72
76
80
DAYS AFTER HATCHING
15°C
Lot #7
n=683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4
8
12
16
20
24
28
32
36
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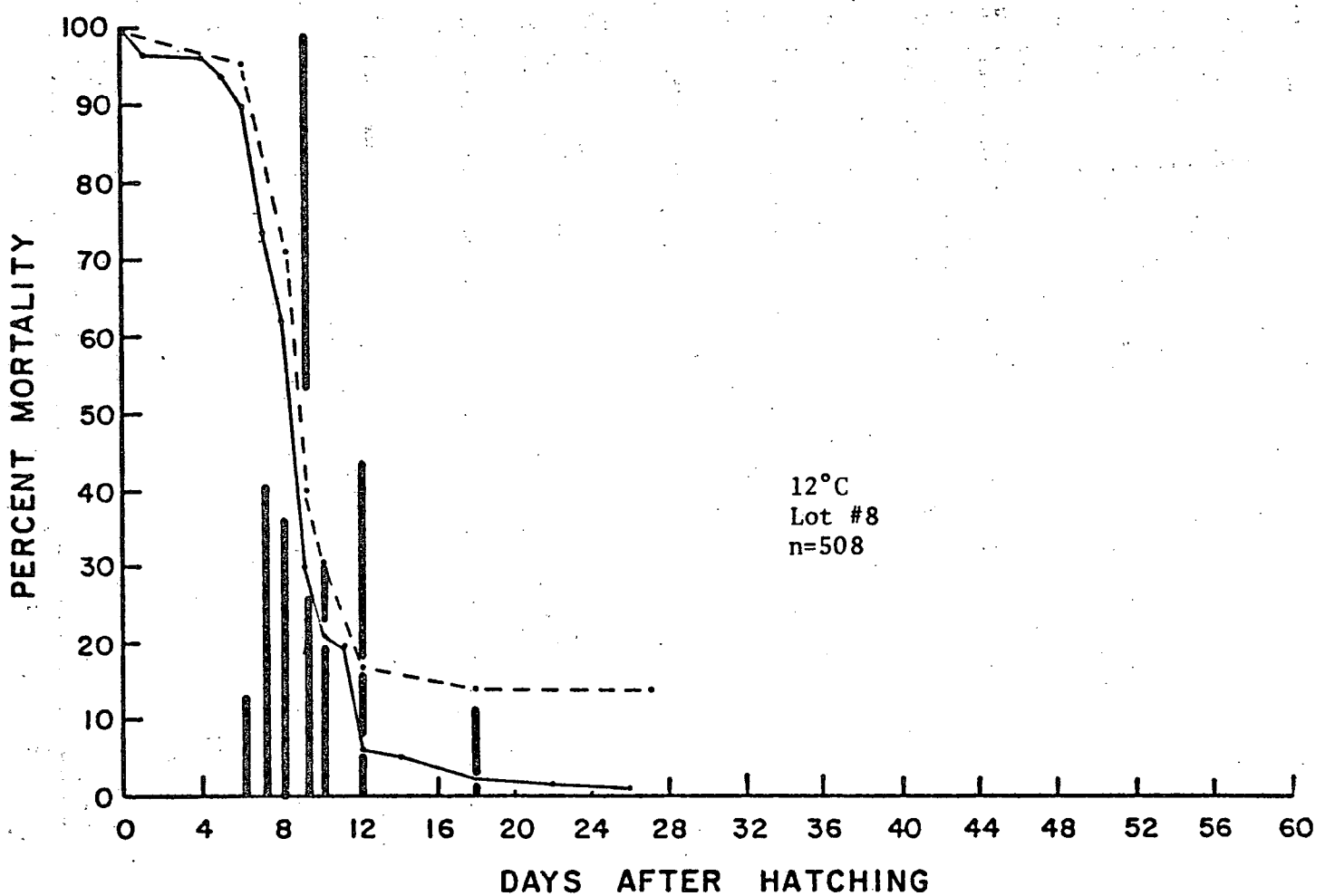
48
52
56
60
64
68
72
76
80
DAYS AFTER HATCHING
15°C
Lot #9
n=430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40
30
20
10
0
0
4
8
12
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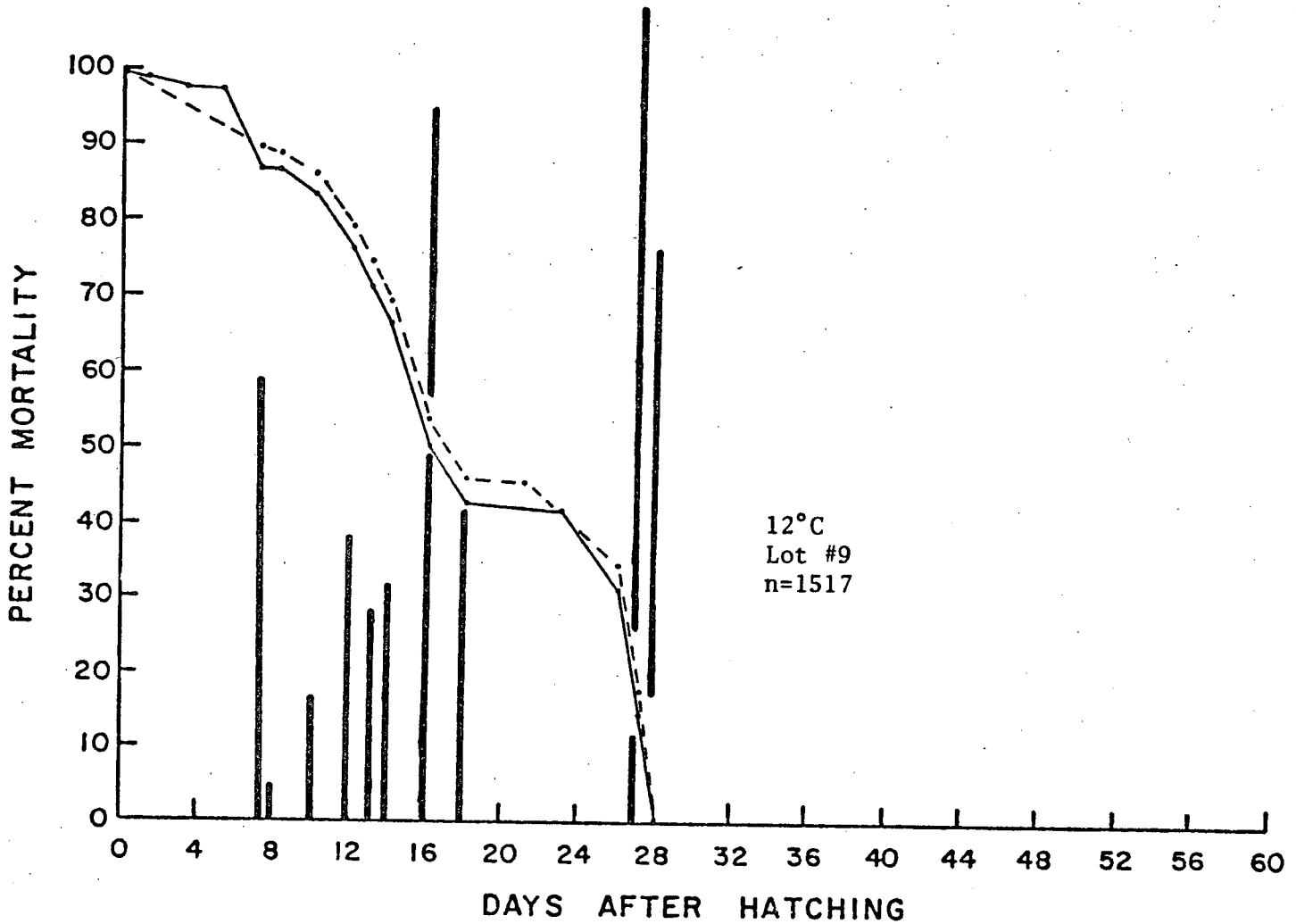
20
24
28
32
36
40
44
48
52
56
60
DAYS AFTER HATCHING
12°C
Lot #8
n=508


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
12°C
Lot #9
n=1517

Appendix C

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Tabulated growth data used in life stage duration studies 103

Tabulated mortality data used in life stage duration studies 131

APPENDIX C

TABULATED GROWTH DATA USED IN LIFE STAGE DURATION STUDIES

Lot #6		Temperature 24°C		
Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
34	1	4.79 4.88 (5) 4.96 5.04 5.12	4.920	0.100
44	1	4.71 (2) 4.88 (2) 4.96 (2) 5.04 (3)	4.911	0.129
48	2	4.88 (2) 4.96 (2) 5.04 (2) 5.12	5.449	0.338
52	2	5.04 5.20 5.36 5.44 (3) 5.53	5.350	0.1715
56	2	5.53 5.44 5.69 (3) 5.85 (2)	5.675	0.152
60	2	5.36 5.44 5.53 (2) 5.61 5.69 (3) 5.77	5.587	0.133

*Number in parenthesis is the number that length in the sample.

Lot #6, Temp. 24°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
64	2	5.85 5.93 6.01	5.673	0.195
68	2	5.20 5.44 (2) 5.53 (2) 5.61 (2) 5.69 (4) 5.85 (2) 5.93 6.01	5.649	0.210
76	3	5.36 (2) 5.53 5.61 5.69 (2) 5.77 5.85	5.721	0.210
84	3	5.53 5.85 5.93 6.01 6.18	5.898	0.241
92	3	5.53 5.69 6.26	5.822	0.383
100	4	5.69 5.77 5.85 (2)	5.789	0.078
108	4	5.69 (2) 5.85	5.741	0.094
116	4	5.20 5.36 (2) 5.69 6.01 (2)	5.606	0.352
124	5	4.79 4.88 4.96 5.04 (2) 5.20 5.36 (2) 6.18 (3)	5.377	0.543

Lot #6, Temp. 24°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
132	5	4.88		
		5.20		
		5.53	5.492	0.465
		5.85		
		6.01		
	7	4.88		
		5.36	5.647	0.694
		5.85		
		6.50		
	8	5.20 (2)		
		5.36	5.922	0.713
		5.69		
		5.85 (2)		
		6.01		
		6.99		
		7.15		
	9	5.53		
		6.34	6.337	0.813
		7.15		
	10	5.36		
		5.53 (2)		
		5.85	6.546	1.406
		6.50		
		8.45		
		8.61		
	11	5.36		
		8.29	7.690	2.094
		9.42		
	12	6.66		
		7.15	7.961	1.278
		8.61		
		9.42		
	14	8.45		
		9.42	9.359	0.625
		10.08		
		9.75		
		9.10		
	17	9.10		
		9.59	9.035	0.741
		9.91		

Lot #6, Temp. 24°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	25	12.40 14.00 14.40	13.600	0.106
	30	21.20 18.20 18.40	19.267	1.677
	54	30.30 29.65 26.65 26.80 26.90	28.060	1.765

Lot #6		Temperature 18°C		
H†	0	4.39 (4) 4.46 (2) 4.55 (2) 4.63	4.468	0.091
4	1	4.23 4.39 4.55 (6)	4.489	0.121
8	1	4.39 4.47 (2) 4.55 (10) 4.63 (4) 4.71 (2)	4.567	0.079
12	1	4.39 4.55 4.71 4.79 (3) 4.88 (4) 4.96	4.771	0.167
16	1	4.79 4.88 (11) 4.96 (5) 5.04 (3)	4.915	0.067

†Sample near end of hatching time.

Lot #6, Temp. 18°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
20	1	4.88 5.20	4.915	
24	1	4.88 (2) 4.96 5.04 (4) 5.12 5.20 (3)	5.052	0.120
28	2	4.88 (2) 4.96 (2) 5.04 (2) 5.12 (2) 5.20	5.019	0.113
32	2	5.20 (2) 5.28 (3) 5.36 (2)	5.281	0.066
40	2	5.04 (2) 5.12 5.20 5.36	5.151	0.136
48	2	5.20 (2) 5.36 (2) 5.44	5.313	0.108
66	3	5.53 (3)		
74	3	5.20 5.77	5.482	
82	3	5.69		
90	4	5.36 5.53 5.69 (2)	5.565	0.156
98	4	5.53 5.69 5.85	5.687	0.163
	9	5.69 5.85 (2) 6.01	5.850	0.133
	10	5.53 5.69 5.85 (3) 6.01 (2)	5.827	0.174

Lot #6, Temp. 18°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	11	5.53 5.69 6.01 (2)	5.809	0.244
	16	6.01 (2) 6.18 (2) 7.31	6.337	0.551
	54	14.80 12.30 17.10	14.733	2.401

Lot #7		Temperature 21°C		
H†	0	3.25 3.33 (3) 3.41 (4)	3.361	0.060
4	0	3.49 3.58 (2)	3.547	0.048
8	0	3.41 3.58 (3) 3.66 (3) 3.82 3.74 (7)	3.672	0.103
12	1	3.58 3.66 3.74 (3) 3.82 (2) 3.90 (4) 4.06	3.930	0.179
16	1	3.98 4.06 (6) 4.23 (2)	4.089	0.082
24	1	4.06 4.41 4.23 4.38 (3)	4.310	0.139

†Sample near end of hatching time.

Lot #7, Temp. 21°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
32	1	4.55 (2) 4.63 (2) 4.59	4.590	0.040
40	2	4.88 (2) 4.96 5.04 (3)	4.969	0.080
48	2	4.88 (2)		
56	2	4.71 4.88 (2) 5.04 5.20 (3) 5.28	5.047	0.206
64	3	4.88 (4) 4.96 5.04 (3) 5.12 (2) 5.20 (3)	5.031	0.130
72	3	4.71 (3) 4.88 (7) 5.04 (8) 5.12 5.20 (3) 5.28 5.36 4.96 (3)	4.992	0.166
	5	5.04-5.53		
	7	5.36 5.53 (3) 5.69	5.525	0.115
	8	5.04 5.20 5.69 6.01 6.18	5.622	0.496
	9	6.01 6.18 6.34 6.66	6.297	0.277

Lot #7, Temp. 21°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	10	5.36		
		6.01		
		6.18	6.202	0.498
		6.34		
		6.50		
		6.83		
	12	6.01 (2)		
		6.34 (2)		
		6.50	6.384	0.307
		6.66		
		6.83		
	15	5.85		
		6.18	6.337	0.344
		6.34		
		6.66 (2)		
	19	6.83		
		7.31	7.312	0.488
		7.80		
	23	9.30		
		10.80		
		13.65	13.150	3.075
		15.30		
		16.70		
	28	11.90		
		19.40	15.237	
	35	13.80		
		24.00	18.900	
	53	26.60		
		25.55		
		24.25	24.100	2.068
		22.45		
		21.65		

Lot #7		Temperature 18°C		
H†	0	3.25 (2)		
		3.41 (8)		
		3.49 (2)	3.448	0.111
		3.58 (3)		
		3.66		

†Sample near end of hatching time.

Lot #7, Temp. 18°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
4	0	3.41		
		3.49		
		3.58	3.469	0.121
		3.74		
8	0	3.74 (3)		
		3.90		
		3.82		
		3.66	3.926	0.260
		4.14		
		4.23		
		4.39		
16	0	4.71		
24	1	4.23 (2)		
		4.31	4.319	0.080
		4.39 (3)		
32	1	4.39		
		4.55	4.467	
40	1	4.55		
		4.63	4.631	0.081
		4.71		
48	2	4.55 (2)		
		4.63 (2)		
		4.67	4.707	0.129
		4.79 (2)		
		4.88 (2)		
56	2	4.71		
		4.88 (3)	4.936	0.121
		5.04 (4)		
92	4	5.53 (6)		
128	5	5.04		
		5.36 (4)	5.427	0.175
		5.53 (4)		
		5.69		
152	6	5.20		
		5.36		
		5.53	5.557	0.291
		5.85 (2)		
	8	5.20		
		5.53		
		5.69 (3)	5.537	0.212

Lot #7, Temp. 18°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	9	5.36 (3)		
		5.53		
		5.69	5.594	0.263
		5.85		
		6.01		
	11	5.53		
		5.69 (2)		
		5.85	5.931	0.395
		6.34		
		6.50		
	14	5.36		
		6.01		
		6.34 (2)	6.142	0.493
		6.66		
	16	5.53		
		5.85 (2)		
		6.01		
		6.18 (3)	6.160	0.352
		6.34 (2)		
		6.50		
		6.83		
	18	6.01 (2)		
		6.18		
		6.34	6.207	0.212
		6.50		
	22	5.36 (2)		
		6.01		
		8.45	7.107	2.214
		10.35		
	27	6.66		
		7.64		
		7.80	8.850	2.294
		9.70		
		12.45		
	34	16.90		
		17.80		
		13.40	14.320	2.882
		12.20		
		11.30		
	41	12.60		
		15.00	16.000	3.995
		20.40		

Lot #7, Temp. 18°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	52	26.50		
		21.50		
		21.20		
		20.90	20.275	3.199
		19.30		
		19.80		
		17.00		
		16.00		

Lot #7		Temperature 15°C		
8	0	3.25	3.330	
		3.41		
16	0	3.41	3.450	
		3.49		
24	1	3.58		
		3.66 (2)	3.688	0.092
		3.74		
		3.82		
32	1	4.06 (4)	4.095	0.073
		4.23		
40	2	3.90		
		4.06 (4)		
		3.98	4.072	0.110
		4.23 (2)		
48	2	4.23		
		4.39		
		4.55	4.351	0.227
		4.71		
84	4	4.55		
		5.04 (2)	4.875	0.281
120	5	4.88		
		5.04		
		5.20	5.314	0.217
		5.36 (4)		
		5.53 (3)		

Lot #7, Temp. 15°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
169	7	4.71		
		5.04		
		5.20		
		5.36	5.443	0.361
		5.26		
		5.69 (4)		
		5.85		
	9	5.36 (2)		
		5.53 (2)	5.579	0.222
		5.85 (2)		
	11	5.20 (2)		
		5.69 (5)	5.548	0.238
	14	5.53		
		5.69 (3)	5.687	0.115
		5.85		
	18	5.20		
		5.36		
		5.53	5.850	0.558
		5.69 (4)		
		5.85 (2)		
		6.83		
		6.99		
	22	6.18		
		6.66 (2)	6.622	0.335
		6.99		
	27	6.99		
		7.15	7.540	0.636
		7.48 (2)		
		8.61		
	34	7.64 (2)		
		8.13		
		10.50	8.980	1.638
		11.00		
	41	9.60		
		9.30		
		12.00	11.260	1.797
		13.60		
		11.80		

Lot #7, Temp. 15°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	52	14.70		
		14.80		
		12.70		
		12.30		
		11.80	12.300	1.720
		10.10		
		11.20		
		10.80		
	69	18.90		
		16.30		
		15.30	14.780	3.124
		11.20		
		12.20		
	83	18.50		

Lot #8		Temperature 24°C		
	0	3.25		
		3.33		
		3.41		
		3.49 (8)	3.557	0.084
		3.52		
		3.58 (25)		
		3.66 (6)		
		3.74		
	1	4.71		
		4.79 (2)		
		4.71	4.868	0.102
		4.88 (6)		
		4.96		
		5.04 (2)		
	4	5.04		
		5.36	5.308	0.248
		5.53		
	5	5.04 (5)		
		5.20 (3)	5.098	0.084
	6	5.36		
		5.53 (2)	5.471	0.094

Lot #8, Temp. 24°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	7	4.88 (2)		
		5.36		
		5.53	5.502	0.491
		5.85		
		6.01 (2)		
	8	6.18		
		6.50	6.744	0.488
		7.15 (2)		
	9	6.18		
		6.50		
		7.15	6.784	0.537
		7.31		
	11	6.99		
		7.48	7.540	0.337
		7.64		
		7.80 (2)		
	14	6.50		
		6.99		
		7.15	7.150	0.445
		7.48		
		7.64		
	16	7.75		
		7.50		
		7.95	7.690	0.233
		7.40		
		7.85		
	22	8.75		
		9.70		
		9.50	10.540	2.525
		9.75		
		15.00		
	27	14.50		
		11.00	15.267	4.697
		20.30		
	41	15.50		
		17.75	16.625	1.591
	52	26.60		
		23.65		
		27.80		
		29.55		
		26.00	25.979	2.283
		25.25		
		23.00		

Lot #8		Temperature 21°C		
Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	0	3.25		
		3.33		
		3.41		
		3.49 (8)	3.557	0.084
		3.52		
		3.58 (25)		
		3.66 (6)		
		3.74		
	1	4.71 (7)		
		4.79 (2)		
		4.63	4.784	0.086
		4.88 (7)		
	4	5.53 (3)		
	5	5.53		
		5.69 (5)	5.748	0.172
		6.01 (2)		
	6	5.69		
		6.01 (2)	5.904	0.188
	7	5.20 (2)		
		5.69 (3)		
		5.85 (3)	5.669	0.287
		6.01		
	8	5.69		
		5.85	5.890	0.156
		6.01 (2)		
	9	5.53		
		5.69 (3)	5.817	0.388
		6.50		
	11	5.53		
		5.69 (2)		
		6.18	6.045	0.664
		7.15		
	14	5.53 (2)		
		5.69 (3)	5.622	0.089
	16	6.01		
		7.15	7.096	1.058
		8.13		

Lot #8, Temp. 21°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	18	6.01		
		6.66		
		6.99	7.682	1.587
		9.50		
		9.25		
	22	10.80		
		14.40	12.140	2.256
		14.00		
		12.50		
		9.00		
	27	20.10		
		17.50		
		12.30	15.475	3.985
		12.00		
	34	14.60	18.800	
		23.00		
	41	22.25	17.800	
		13.35		
	52	29.45		
		27.30	26.920	2.745
		24.00		

Lot #8		Temperature 18°C		
	0	3.25		
		3.33		
		3.41		
		3.49 (8)	3.557	0.084
		3.52		
		3.58 (25)		
		3.66 (6)		
		3.74		
	1	4.55 (2)		
		4.63 (2)		
		4.71 (6)	4.693	0.082
		4.79 (3)		
	4	5.36		
		5.53 (3)	5.571	0.123
		4.69 (3)		

Lot #8, Temp. 18°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	5	5.53 5.69 (6) 5.85 (5) 6.01	5.762	0.126
	6	5.69 5.85 (2) 6.01	5.850	0.133
	7	5.69 5.85 (2) 6.01 (2)	5.882	0.136
	9	5.85 (2) 6.01 (2) 6.18 (2)	6.012	0.145
	18	5.69 (2) 5.85 6.01	5.809	0.156
	34	11.40 10.00 14.00 10.30 16.80 8.65	11.858	3.013
	41	11.85 20.25	16.050	
	52	23.70 15.40 24.35 22.40 23.60	21.890	3.696
	69	26.15 24.60 21.45 22.10	23.575	2.189

Lot #8		Temperature 15°C		
Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	0	3.25 3.33 3.41 3.49 (8) 3.52 3.58 (25) 3.66 (6) 3.74	3.557	0.084
	1	4.39 (3) 4.47 (2) 4.55 (10) 4.63	4.510	0.073
	4	5.04 5.20 (3)	5.160	0.082
	5	4.88 5.04 5.20 (2) 5.36 5.53	5.120	0.230
	7	5.36 5.53 (3) 5.69	5.525	
	9	5.53 (3) 5.69	5.566	0.081
	11	5.53 (4) 5.69 (3)	5.594	0.087
	14	5.53 (2) 5.69 (2)	5.606	0.093
	18	5.04 5.53 (4) 5.69 5.85 6.18 (2) 6.50	5.752	0.428
	22	5.36 5.53 6.50 6.99	6.094	0.779

Lot #8, Temp. 15°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	27	5.85		
		5.69		
		6.34	6.506	0.823
		6.50		
		6.66		
		8.00		
	34	6.50		
		6.99	8.087	1.537
		9.80		
		7.50		
		9.65		
	41	6.34		
		6.01		
		8.60		
		8.70	8.557	1.890
		9.35		
		9.40		
		11.50		
	52	8.50		
		10.70		
		10.50	10.967	1.715
		10.80		
		11.50		
		13.80		
	69	18.00		
		14.10		
		12.05		
		15.70	15.736	2.131
		18.10		
		16.10		
		16.00		
	83	19.65		

Lot #8	Temperature 12°C		
0	3.25		
	3.33		
	3.41		
	3.49 (8)	3.557	0.084
	3.52		
	3.58 (25)		
	3.66 (6)		
	3.74		

Lot #8, Temp. 12°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	1	4.23 (2) 4.31 4.39 (4) 4.47 (2) 4.55 (3)	4.407	0.116
	4	4.88 5.04 (2)	4.983	0.094
	5	5.20 (3) 5.36 (2)	5.265	0.089
	7	5.36 5.53 (2) 5.69	5.525	0.133
	9	5.36 5.53 (4) 5.69 (2)	5.548	0.112
	11	5.36 (2) 5.53 5.69 (3)	5.552	0.160
	14	5.20 5.53 (4)	5.460	0.145
	22	5.36 5.53 (4)	5.492	0.073
	67	5.36 5.69	5.525	0.230

Lot #9		Temperature 24°C		
	0	3.74 (3) 3.90 4.06	3.835	0.145
	1	4.55 (3) 4.71 (3) 4.88	4.666	0.123
	2	5.04 5.20 (4) 5.36	5.200	0.103

Lot #9, Temp. 24°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	3	4.88 (3) 5.04 (2)	4.940	0.089
	4	5.04 5.20 (2) 5.36 5.53 5.69	5.335	0.239
	5	4.88 5.04 (5)	5.010	0.066
	7	5.04 5.36 (2) 5.53 5.76	5.410	0.265
	10	5.20 5.69 5.85 6.01 (2)	5.752	0.337
	12	5.36 5.69 (3) 5.85	5.655	0.178
	14	5.36 5.85 6.01 6.18 6.34 6.50	6.039	0.404
	18	6.18 6.34 (2) 7.15 13.75	7.950	3.265
	23	11.00 15.50 21.50	16.000	5.268

Lot #9	Temperature 21°C		
0	3.74 (3) 3.90 4.06	3.835	0.145

Lot #9, Temp. 21°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	1	4.55 (5)		
	2	4.88		
		5.04 (3)	4.997	0.081
	3	4.39 (3)		
		5.04	4.712	0.460
		5.36		
	4	4.88		
		5.04 (5)	5.010	0.066
	5	5.04 (2)		
		5.20 (2)	5.223	0.146
		5.36 (3)		
	7	5.20 (4)		
		5.36		
		5.53	5.480	0.253
		5.69 (4)		
		5.85		
	10	5.36		
		5.69	5.395	0.371
		5.85		
	12	5.69		
		6.01 (2)		
		6.34	6.142	0.371
		6.66		
	14	5.20		
		5.36 (2)		
		5.53	5.757	0.521
		6.01		
		6.34		
		6.50		
	18	6.01		
		6.34	6.987	1.028
		7.31		
		8.29		
	23	6.01		
		7.48		
		7.80	9.807	3.998
		12.00		
		15.75		
	30	14.00		
		18.00	16.000	

Lot #9		Temperature 18°C		
Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	0	3.74 (3) 3.90 4.06	3.835	0.145
	1	4.39 (2) 4.55 (3)	4.485	0.089
	2	5.04 (5)		
	3	5.04 (4) 5.20	5.070	0.073
	4	5.04 (2) 5.20 5.36	5.159	0.156
	5	5.04 (2) 5.20 (2) 5.36	5.167	0.136
	7	5.04 5.20 5.53 (2) 5.69	5.395	0.267
	10	5.20 (4) 6.01	5.362	0.363
	12	5.36 (2) 5.85 6.18	5.687	0.398
	14	5.36 (2) 5.53 (3)	5.460	0.089
	18	5.53 5.69 5.85 6.50 (2)	6.012	0.460
	23	6.18 6.01 6.83 7.48 9.25	7.147	1.310

Lot #9, Temp. 18°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	30	7.05		
		8.00		
		12.25	9.150	1.977
		8.85		
		9.60		
	37	16.90		
		15.75		
		16.65	14.680	2.801
		14.00		
		10.10		
	48	20.60		
		20.50		
		18.05		
		16.65		
		21.25	18.869	3.245
		23.50		
		17.25		
		13.15		
	65	23.85		
		20.55		
		19.70		
		19.30		
		20.10	21.468	1.790
		23.60		
		21.99		
		22.65		

Lot #9	Temperature 15°C		
0	3.74 (3)		
	3.90	3.835	0.145
	4.06		
1	4.39 (5)		
3	5.04 (3)		
	4.88	5.037	0.115
	5.20		
5	5.04		
	5.20 (5)	5.200	0.094
	5.36		

Lot #9, Temp. 15°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	7	5.04 (2) 5.20 (3)	5.135	0.089
	10	5.04 5.20 (3) 5.53	5.232	0.178
	12	5.04 (2) 5.20 5.36 (2)	5.200	0.163
	14	5.04 5.20 (3) 5.53	5.232	0.178
	18	5.04 5.53 5.85 (2)	5.566	0.384
	23	5.36 5.69 6.18	5.741	0.409
	30	5.04 6.66 6.50 (2) 6.99	6.337	0.754
	37	6.34 (2) 6.66 6.99 7.31	6.727	0.424
	48	6.83 7.31 (3) 7.96 8.13 11.75	8.085	1.675
	65	8.94 8.13 8.61 9.70 16.75 13.50 14.00	11.375	3.348

Lot #9, Temp. 15°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
	79	16.25 14.25 16.40 15.73 13.00	15.126	1.461

Lot #9		Temperature 12°C		
	0	3.74 (3) 3.90 4.06	3.835	0.145
	1	4.39 (2) 4.55 (3)	4.485	0.089
	3	4.71 5.04 (4)	4.972	0.145
	5	5.20 (4) 5.36	5.232	0.072
	7	5.20 (2) 5.28 5.36 (2)	5.281	0.081
	10	5.04 5.20 (2) 5.36	5.200	0.133
	12	5.04 (2) 5.36 (2)	5.200	0.188
	14	5.04 (2) 5.20 (2) 5.36	5.167	0.136
	18	5.20 (2) 5.36 (3)	5.297	0.089

Lot #5		Temperature 15°C		
1	0	3.58 (2) 3.66 (5) 3.74 (13) 3.82 (3) 3.90 (3)	3.737	0.086

Lot #5, Temp. 15°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
6	0	3.74 (2) 3.90 (5) 3.98 4.06 (2)	3.908	0.111
10	0	4.06 (5) 4.14 (2) 4.23 (6)	4.150	0.078
14	0	3.90 4.06 4.14 (2) 4.23 (7) 4.31 4.39	4.193	0.117
18	0	4.06 4.23 (4)	4.192	0.073
36	1	4.55 (2) 4.71 (3)	4.647	0.089
40	2	4.79 5.20 5.04	5.010	0.210
48	2	5.04 (3)		
64	3	5.36 (4) 5.53 (2)	5.281	0.237
100	5	5.36 (4) 5.53 (2) 5.69	5.455	0.128
108	6	5.53 (4) 5.69 5.61	5.565	0.068

Lot #7		Temperature 24°C		
4	0	3.58 (4) 3.66 (3) 3.74	3.625	0.060

Lot #7, Temp. 24°C, continued

Hours After Hatching	Days After Hatching	Total Length* (mm)	Mean Length	Standard Deviation
8	0	3.41 3.58 (5) 3.66 3.74	3.585	0.091
12	0	3.74 (2) 3.82 3.90 (2)	3.818	0.082
16	0	3.82 3.90 (2) 3.98 (2) 4.06 (7) 3.94	3.996	0.084
20	1	4.06 (4) 4.14 4.23 (5) 4.39	4.173	0.105
24	1	3.58 4.23 4.31 4.39 (7)	4.281	0.254
32	1	4.55 (3)		
40	1	4.71 (3)		
48	2	4.63 4.88	4.753	
56	2	4.71 4.88 5.04	4.875	0.163
64	2	4.79 5.53	5.159	0.518
72	3	4.88 4.96 5.04 (3) 5.12	5.010	0.084
80	3	4.88 5.04 (2) 5.36 5.53	5.167	0.267

TABULATED MORTALITY DATA USED IN

LIFE STAGE DURATION STUDIES

Lot #6, Temperature 24°C — Hatched 5/24/75, 890 Stocked

Days After Hatching	Number in Live Sample	Number of Dead Removed
1	39	17
2	51	
3	17	
4	14	43
5	21	600
6	4	
7	9	
8	3	8
9	8	10
10	3	
11	5	
13	5	
16	5	
24	3	
29	3	
31		3
32		10
33		2
40		1
43		1
54	5	

Lot #6, Temperature 18°C — Hatched 5/25/75, 1178 Stocked

0	26	173
1	75	
2	27	
3	9	183
4	8	476
9	5	80
10	8	74
11	4	
16	5	20
47		2
54	3	

Lot #7, Temperature 21°C — Hatched 5/26/75, 1585 Stocked

Days After Hatching	Number in Live Sample	Number of Dead Removed
0	40	
1	35	
2	17	88
3	47	
4		403
5	200	
6		178
7	5	192
8	11	20
9	4	
10	6	
12	7	59
13		44
15	7	123
17		67
19	3	
21		11
23	5	
28	5	
35	2	
40	1	
55	5	

Lot #7, Temperature 18°C — Hatched 5/27/75, 538 Stocked

0	43	
1	15	6
2	18	
4	6	
5	20	95
6	6	39
7		54
8	5	
9	7	54
11	6	25
14	5	44
16	11	30
18	5	14
22	5	6
27	5	
30	5	
34		1
37	3	

Lot #7, Temp. 18°C, continued

Days After Hatching	Number in Live Sample	Number of Dead Removed
43		1
44		1
45		1
48	8	

Lot #7, Temperature 15°C — Hatched 5/27/75, 683 Stocked

0	6	
1	14	20
2	13	
4	4	
5	15	
6		14
7	18	76
8		28
9	6	96
11	7	105
14	5	11
16		13
18	11	
20		60
22	5	83
27	5	16
30	5	
34		7
37	5	9
48	8	
63		1
64	5	
66		1
68		2
69		5
70		3
78	1	

Lot #8, Temperature 24°C — Hatched 5/27/75, 921 Stocked

0		
1	15	
4	3	778
5	11	29
6	3	
7	7	
8	4	

Lot #8, Temp. 24°C, continued

Days After Hatching	Number in Live Sample	Number of Dead Removed
9	4	
11	5	
12		10
14	5	
16	5	17
18		8
22	5	
27	3	
41	2	
52	7	

Lot #8, Temperature 21°C — Hatched 5/27/75, 326 Stocked

0		
1	18	
4	3	
5	14	185
6	4	
7	11	
8	4	
9	5	
11	5	
14	5	14
16	5	16
18	5	
20		1
22	5	2
27	4	
34	2	
36		1
38		3
39		2
41	2	2
43		1
45		1
47		1
48		1
52	3	

Lot #8, Temperature 18°C — Hatched 5/27/75, 697 Stocked

0		
1	17	
4	8	
5	30	25

Lot #8, Temp. 18°C, continued

Days After Hatching	Number in Live Sample	Number of Dead Removed
6	5	23
7	5	105
8		127
9	7	179
10		16
11		26
12		19
14		15
16		10
18	5	
20		8
22		46
34	6	
38		1
41	2	
52	5	
65		1
66		1
69	4	1

Lot #8, Temperature 15°C — Hatched 5/27/75, 1139 Stocked

0		
1	16	
4	4	
5	14	
7	20	144
8		138
9	7	261
11	8	84
12		36
14	5	5
16		98
18	16	
20		27
22	4	15
27	6	
34	5	
36		30
38		58
39		49
40		17
41	7	14
44		5
46		2
52	6	2

Lot #8, Temp. 15°C, continued

Days After Hatching	Number in Live Sample	Number of Dead Removed
62		2
69	7	
80		1
81		8
82		6
83	1	7

Lot #8, Temperature 12°C — Hatched 5/27/75, 508 Stocked

0		
1	12	
4	3	
5	13	
6		20
7	14	70
8		57
9	7	158
10		49
11	6	
12		70
14	5	
18		17
22	5	
27	2	

Lot #9, Temperature 24°C — Hatched 5/31/75, 551 Stocked

0		
1	15	
2	6	26
3	9	277
4	6	
5	6	59
7	8	17
8		17
10	5	3
12	10	60
14	10	
16		5
18	5	
23	3	
37		4

Lot #9, Temperature 21°C — Hatched 5/31/75, 1238 Stocked

Days After Hatching	Number in Live Sample	Number of Dead Removed
0		
1	16	
2	6	
3	54	205
4	6	260
5	7	200
7	20	142
8		24
10	5	170
12	11	47
14	7	
16		20
18	5	5
23	5	
29		8
30	2	8
32		5

Lot #9, Temperature 18°C — Hatched 5/31/75, 504 Stocked

0		
1	8	
2	5	
3	9	
4	4	
5	6	10
6		141
7	13	50
8		27
10	6	44
12	14	15
14	9	
16		64
18	5	17
23	5	
30	5	
34		2
37	5	3
40		5
41		1
42		3
44		3
46		1
48	8	

Lot #9, Temp. 18°C, continued

Days After Hatching	Number in Live Sample	Number of Dead Removed
60		2
61		2
63		1
64		1
65	8	3

Lot #9, Temperature 15°C — Hatched 5/31/75, 430 Stocked

0		
1	11	
3	14	
5	7	
7	15	
10	5	
12	10	
14	11	
16		14
18	5	
23	5	80
27		43
30	5	
32		32
34		7
37	5	28
41		3
44		11
46		28
48	7	13
50		3
56		3
60		3
64		4
65	7	
67		1
70		10
71		13
73		9
76		9
79	6	3

Lot #9, Temperature 12°C — Hatched 5/31/75, 1517 Stocked

Days After Hatching	Number in Live Sample	Number of Dead Removed
0		
1	10	
3	10	
5	7	
7	8	150
8		12
10	4	43
12	11	100
13		74
14		83
16		250
18	5	110
23		10
26		172
27		258
28		200