

Recruitment Models For Colorado Squawfish:  
Tools For Evaluating Relative Importance Of Natural And Managed Processes.

Final Report

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## Introduction

Endangered Colorado squawfish *Ptychocheilus lucius*, is a piscivorous cyprinid endemic to the Colorado River Basin. Colorado squawfish have been negatively affected by human-induced changes in their physical and biological environment. Physical changes are largely due to regulation of rivers which has reduced magnitudes of discharge, water temperature, and seasonal hydrograph variation, but has increased daily hydrograph variation, and restricted movements of Colorado squawfish (Vanicek and Kramer 1969; Holden 1979; Tyus and Karp 1989; Tyus 1991). Some biological changes can be attributed to indirect effects of modifying the physical environment, but many are directly related to introduction of over 40 non-native fishes into the Basin (Carlson and Muth 1989). Many of these fishes are potential competitors or predators of different life stages of Colorado squawfish. As a result of these physical and biological changes, natural populations of Colorado squawfish have declined and are currently restricted to the San Juan and Colorado River basins upstream of Lake Powell (Platania et al. 1991; Tyus 1991). Within the Colorado River Basin, populations in the Green River system are thought to be relatively large and stable. Recruitment of age-0 Colorado squawfish in fall to these populations has been documented annually since 1979, but is variable (Nesler et al. 1988; Tyus and Haines 1991; Tyus 1991).

Establishing causal relationships between putative environmental factors and recruitment patterns has been the goal of the *Recovery Implementation Program for Endangered Fish Species in the Upper Colorado River Basin* since its inception (Wydoski and Hamill 1991). Well established causal relationships could be used to guide management actions aimed at ensuring

survival and recovery of Colorado squawfish. Data describing aspects of the ecology of Colorado squawfish life stages have been collected for over 15 years, but causal mechanisms that affect recruitment have not been identified and efforts to synthesize individual studies have been limited by lack of integrative approaches. A primary goal of this research was to quantitatively integrate existing knowledge of biotic and abiotic factors that influence recruitment of Colorado squawfish early life stages. This was accomplished by constructing a conceptual life-history model, and a mechanistic computer simulation model that estimates relative survival and growth of age-0 Colorado squawfish during their first summer. The mechanistic model presented in this report estimates the response of age-0 Colorado squawfish to a variety of environmental conditions including (a) interactions with a potentially predacious and abundant nonnative species, the red shiner *Cyprinella lutrensis*, (b) temperature regime, (c) water clarity, and (d) availability of alternate prey for red shiner. To illustrate how the mechanistic model can be used to evaluate the relative effects of environmental factors and potential management actions on Colorado squawfish populations, we implemented the model using different water-temperature regimes, larval growth rates, predator densities, and date of colonization of nursery habitat. The effect of each environmental factor was assessed by analyzing survival and growth of Colorado squawfish during each simulation.

### **The Conceptual Life History Model**

#### *Model Development*

We constructed a conceptual life history model for Colorado squawfish that links recruitment to successive developmental stages with important biotic and abiotic controlling

factors (Figure 1). Some life stages were combined because (a) they have similar habitat requirements and limiting factors (e.g., juveniles and adults), (b) their life history requirements and controlling factors are poorly understood (e.g., age-0, age-1 fish in winter habitat), or (c) they are hypothesized to have weak effects on recruitment dynamics (e.g., juveniles).

### *Model Results*

The life-history model illustrates how recruitment and outcomes of management actions are potentially affected by multiple and interacting biotic and abiotic processes at different temporal scales. For example, number of age-0 Colorado squawfish that survive to fall may be a function of the number of larvae produced, their growth rates, predator density, and quantity and quality of backwaters available that summer. Predation, habitat selection, and stochastic events are factors that affect survival and growth on a daily basis. The model also conveys an annual temporal structure that begins with deposition of embryos in the substrate. Recognition of various temporal scales is important because it emphasizes that recruitment to a life stage is a function of numerous processes occurring at different times and that in order to explain characteristics of a population it might be necessary to study events that occurred days, months, years, or even decades ago. Similarly, this temporal aspect of Colorado squawfish life history should be considered when management actions are implemented, because detectable changes in population structure may not occur until well into the future.

Four of five compartments in the life-history model refer to age-0 fish. This structure was not intended to imply that early life stages are more important than juveniles or adults; rather, it is due to the dramatic changes in physical ability and environmental requirements that

age-0 fish undergo. In addition, because of their small size and limited energetic reserves, early life stages are susceptible to a greater variety of harsh conditions and controlling factors compared to juvenile and adult fish.

The life-history model was based on recent literature, ongoing research, and our personal experiences. Researchers who are familiar with Colorado squawfish will find some parts of the life-history model useful, but may disagree with the importance of other components. We encourage critical review of the model because other researchers will undoubtedly have different knowledge and perspectives regarding factors that influence Colorado squawfish recruitment. We advocate that the life-history model be used as a foundation for future investigations and hope that it will serve as a useful tool for developing and testing hypotheses related to factors that control recruitment of Colorado squawfish. Over time, the life-history model should be revised as gaps in life history knowledge are identified and studied, and alternative hypotheses are supported or refuted. For example, age-0 and age-1 fish in winter habitat may be divided into separate model components if future studies suggest a basis for doing so. This evolution of the life-history model is consistent with the scientific basis of endangered fish research in the Colorado River Basin, and adaptive management of Colorado squawfish populations. Despite the reality that uncertainty exists in our understanding of Colorado squawfish recruitment processes, the life-history model provides an efficient means for organizing and presenting the current state of knowledge. We are encouraged that the utility of the life-history model has already been realized by another group of researchers who have used it as a template to organize life history information for endangered humpback chub *Gila cypha* (L. Lentsch, Utah Division of Wildlife Resources, pers. comm.).

## Structure and Components of The Mechanistic Simulation Model

The conceptual life-history model illustrates the larger framework within which the mechanistic simulation model was used to evaluate the effects of environmental factors on survival and growth of age-0 Colorado squawfish during their first summer. Age-0 fish were chosen as the subject of study for the simulation model for several reasons. First, recruitment from early life stages has been shown to be an important factor in determining year-class strength in other fishes (Houde 1987). Second, early life stages of Colorado squawfish have been the subject of numerous field and laboratory studies. Third, we intended to collect empirical data for construction of the model by conducting pertinent experiments, and hatchery-reared age-0 Colorado squawfish were readily available. During model construction, results of these experiments were integrated with field observations; thus the model has a foundation grounded in empirical data which increases the likelihood that its predictions are ecologically relevant.

An individual-based model (IBM) structure was selected as the fundamental basis for the simulation model because we suspected that *individual differences* in size and growth of larvae may affect recruitment patterns as much or more than average differences of populations (Rice et al. 1993; DeAngelis and Rose 1992). The IBM that was initially proposed had components that (a) linked river discharge to prey availability for larvae, (b) incorporated starvation effects on larvae, (c) allowed multiple species to prey on larval Colorado squawfish, and (d) simulated the influence of temperature regime on growth of larvae (Figure 2). Every effort was made to identify pre-existing data that could be used to derive quantitative relationships relevant to each component of the IBM. However, during early stages of IBM development, it became evident

that although some of these components had obvious conceptual importance, data were not available to support their inclusion in a mechanistic model.

Virtually no data were available on the relationship between water discharge and availability of prey for larvae, so this component was excluded from the final model. The starvation component was also omitted despite its important role in recruitment of other fishes (Houde 1987). Vulnerability to starvation is primarily a function of body size of fish larvae (Miller et al. 1988). Although Colorado squawfish larvae are not extremely large, they have demonstrated considerable starvation resistance. Bestgen (1996) starved laboratory-reared larvae for 17.5 d and reported that 57% recovered and survived when offered food. Thus, we concluded that direct starvation mortality was probably not a major factor in recruitment dynamics of age-0 Colorado squawfish.

Lastly, we reduced the number of potential predator species in the model from three to one: red shiner. Green sunfish *Lepomis cyanellus* and channel catfish *Ictalurus punctatus* were omitted because they are relatively rare in Colorado squawfish nursery habitats compared to red shiner (Haines and Tyus 1990). Although red shiner is not typically perceived to be an important predator of other fish, recent studies have suggested that they may consume significant numbers of fish larvae. Ruppert et al. (1993) reported that 15% of red shiners collected in backwaters near the confluence of the Yampa and Green rivers contained 1 to 9 fish larvae in their gut. Because fish larvae are rapidly digested and remain recognizable in the gut of predators for only 1-2 hours (Rice et al. 1987), results of Ruppert et al. (1993) suggest that predation rates on larvae by red shiner were high. Colorado squawfish larvae do not commonly occur at the localities sampled by Ruppert et al. (1993) and none were identified in gut contents, but during the same collection

period other researchers found abundant Colorado squawfish larvae co-occurring with red shiners in backwaters of the Green River (Haines and Tyus 1990, Tyus and Haines 1991). Red shiners were often the most abundant species collected in those backwaters and regularly attained densities greater than 5 individuals/m<sup>2</sup> of backwater (Haines and Tyus 1990). At these densities even relatively low predation rates can have a substantial impact on survival and recruitment of Colorado squawfish larvae. Thus, red shiner was considered to be the most important predator for inclusion in the IBM.

The mechanistic model focused primarily on the interacting effects of temperature-dependent Colorado squawfish growth and size-dependent red shiner predation (Figure 3). Temperature directly influences growth of fish and as a consequence, indirectly influences developmental changes in swimming speed, foraging ability, predator avoidance, and the length of time larvae are susceptible to predation (Weatherly and Gill 1987; Miller et al. 1988). Bestgen (1996) showed that water temperatures ranging from 18 to 30°C strongly affected growth rates of Colorado squawfish. Thermal regimes in the regulated Green River vary substantially with discharge patterns and weather conditions (Bestgen 1997). Therefore water temperature may be an important factor regulating recruitment processes of Colorado squawfish.

#### *Red Shiner Size Distributions and Density*

The potential for predation by red shiners on Colorado squawfish larvae depends on red shiner size and density throughout the season. Estimates of red shiner densities and size distributions were based on field collections from the Green River, Utah (Haines and Tyus 1990; K. Bestgen, unpublished data). In early June the red shiner population was dominated by age-1



and age-2 adults, and the mean and variance for total length were relatively large (Figure 4). From mid-June to mid-July, total length of red shiners declined due to mortality of adults. Subsequently, average size increased from late July until water temperatures declined and red shiner growth rates slowed in fall (Figure 4).

During a simulation, daily red shiner size distributions were estimated by linear interpolation between data-based distributions. Each time a larva encountered a red shiner, the predator's total length was randomly drawn from the size distribution for that day. Adult red shiners regularly attain densities greater than five individuals/m<sup>2</sup> in Green River backwaters (Haines and Tyus 1990). Unless otherwise noted, we used a relatively conservative density of three red shiners/m<sup>2</sup> in simulations.

#### *Temperature-Dependent Growth*

Bestgen (1996) conducted experiments to describe the affects of ration and temperature on growth rate of Colorado squawfish larvae. Results of this study were used to parameterize the model for the effect of temperature on larval growth, and to estimate the degree of variation in growth rate among individuals. At the beginning of a simulation each larva was assigned a baseline growth rate drawn at random from a normal distribution with a specified mean and a

coefficient of variation (14.1%). During a simulation, daily growth rate was calculated using a temperature-dependent growth equation:

$$\text{Daily growth rate} = \text{baseline growth rate} \cdot \frac{(-0.279 + 0.0387 \cdot \text{temp} - 0.000637 \cdot \text{temp}^2)}{0.283} \quad (1)$$

where *temp* is daily water temperature, *baseline growth rate* is the growth rate assigned to the larva at the beginning of the simulation, and 0.283 is the solution to Bestgen's (1996) temperature- and ration-dependent growth equation at 24°C and high ration.

Simulations were conducted using two different temperature regimes based on data from the U.S. Geological Survey hydrologic gauge on the Green River near Jensen, Utah: a relatively warm thermal regime observed during summer 1994, and a substantially cooler regime observed in 1983, when temperatures were 6-10°C cooler for much of the season (Figure 5).

Because water temperatures change substantially throughout the season, temperatures and predator size distributions experienced by Colorado squawfish larvae will be affected by the timing of spawning and subsequent larval arrival in backwater nursery areas. The arrival of larvae in backwaters varies among years from as early as 1 June to as late as 1 August. To examine the effect of time of arrival on squawfish growth and survival we conducted simulations using arrival times of 1 June, 1 July, and 1 August.

#### *Probability of Capture*

The likelihood of a larva being eaten is the product of at least three probabilities: the probability of being encountered by a predator, the probability of being attacked if encountered,

and the probability of being captured if attacked (Gerritsen and Strickler 1977). Unfortunately, no data were available to estimate the probability that a larval Colorado squawfish would be attacked and eaten by a red shiner, so we conducted laboratory and outdoor mesocosm experiments in order to obtain the necessary information.

Laboratory experiments were conducted using 38-L aquaria to estimate the probability that a larval Colorado squawfish would be captured by a red shiner when an attack occurred. In each trial, five larvae were added to an aquarium containing three similar-sized red shiners from one of six different size groups (mean TL = 38, 47, 53, 61, 63 and 69 mm). Larvae in trials had mean TL of 9.8, 11.1, 13.6, 15.3, 17.2, and 18.7 mm. Each of three predators was watched by a different observer, and the number of attacks and successful captures during two consecutive 10-min intervals were recorded. If three or more larvae were eaten during a trial, an additional five larvae were added to the aquarium. A total of 39 trials were conducted. Predators were assumed to be acting independently because red shiners rarely interacted when capturing Colorado squawfish larvae. The mean number of attacks per trial by an individual was 21; total number of attacks by an individual ranged from 0 to 72.

Logistic regression analysis was used to estimate the probability of capture of a larva as a function of predator length, prey length, and their squared and interaction terms. A global general linear model was fit using the method of maximum likelihood, and a model selection tool called Akaike's Information Criterion (AIC) was used to sequentially eliminate predictors that were unimportant for explaining variation in the dependent variable. Model selection suggested that the best predictors of probability of capture ( $P(\text{capture})$ ) were ( $\text{prey TL}$ )<sup>2</sup> and the

*predator TL · prey TL* interaction term. The form of the size-dependent capture equation was:

$$\text{logit of } P(\text{capture}) = -2.2621 - 0.0136(\text{prey TL})^2 + 0.0036(\text{predator TL} \cdot \text{prey TL}) \quad (2)$$

and can be transformed to probability of capture using the formula:

$$P(\text{capture}) = e^{\text{logit of } P(\text{capture})} \cdot (1 + e^{\text{logit of } P(\text{capture})})^{-1}. \quad (3)$$

This analysis demonstrated that red shiners were moderately successful and persistent predators on Colorado squawfish larvae. Probability of capture peaked at about 0.25 for large shiners attacking small larvae, and declined to near zero for small shiners attacking large larvae (Figure 6). Each time a larva was attacked by a red shiner in a simulation, these equations were used to calculate the probability of capture based on size of prey and predator.

#### *Attack Rate*

Direct estimation of the rate of encounter and the rate of attack given an encounter requires extensive data about the behavior and physical abilities of the species of interest (Gerritsen and Strickler 1977; Bailey and Batty 1983; Fuiman and Gamble 1989). As an alternative, we used a methodology that combined the probabilities of encounter and attack into a single parameter that predicted the daily number of attacks on individual larvae (hereafter called attack rate) as a function of larval size and environmental conditions. Data for estimating this quantity were obtained from studies conducted in outdoor mesocosms.

Mesocosms were intended to mimic characteristics of shoreline habitats typically occupied by Colorado squawfish larvae. This was accomplished by positioning 1.5-m-diameter plastic wading pools on a sloping surface so that when filled with water, each pool had water depths ranging from 0 to 25 cm. Each pool was filled with well water, and the bottom was covered with 1 to 2 cm of washed sand. Mesocosms had a surface area of 1.48 m<sup>2</sup> and contained about 225 L of water.

Standard trials were conducted under daylight conditions for 6 h using clear water and no alternative prey; these conditions were intended to maximize successful predation by red shiners. Additional trials were conducted using environmental conditions that might reduce predation by red shiners: presence of alternative prey (chironomid larvae), and turbid water. Mesocosm turbidity was manipulated by adding a suspension of naturally-occurring material obtained from a mixture of unwashed sand and water. The turbidity suspension was added until a Secchi depth of about 5 cm was achieved. Water temperatures during trials ranged from 15-31°C but were generally > 25°C; pools were shaded during all trials to prevent water temperatures from exceeding 31°C.

Most mesocosm trials were conducted using the same predator-prey size combinations and predator groups (N = 3 per group) as those used in the probability-of-capture studies except that the 38-mm-TL predator group was not used. A few early trials with 9.8 and 11.1-mm-TL Colorado squawfish had five or 10 predators in a mesocosm. Predators were acclimated to mesocosm conditions overnight. Larvae were acclimated to mesocosm temperatures for approximately 30 minutes, then were released immediately before the start of the 6-hour trials. Total mass of prey in all trials was maintained at 90% of red shiner maximum consumption for a

6-hour period. This quantity was estimated by conducting laboratory studies in which red shiners were offered a surplus of chironomid larvae prey. Mean maximum consumption of Colorado squawfish larvae in a 6-hour period was approximately 10% of red shiner body mass. The number of larvae used in each trial varied from 15 for the largest larvae to 227 for the smallest. In alternative prey trials, an equal mass of Colorado squawfish larvae and chironomid larvae were used such that the total mass of prey did not exceed 90% of red shiner maximum ration. Generally, 25 to 100 chironomid larvae (0.005 to 0.01 g each) were added. At the conclusion of a trial, predators were captured and remaining larvae and alternative prey were recovered from pools by washing sediment and straining pool contents through fine-mesh nets. Recovered fish larvae were counted, and chironomid larvae were weighed to determine red shiner consumption. Preliminary trials showed that in 5 of 5 cases, the removal protocol recovered all 25 10-mm fish larvae and chironomids released into mesocosms.

The response variable measured for each mesocosm trial was number of larvae eaten. To estimate the number of attacks that occurred in a trial, this quantity was divided by its respective size-dependent capture probability from equations 2 and 3. For example, if ten larvae were eaten and probability of capture was 0.25, then  $10 \cdot (0.25)^{-1} = 40$  attacks must have occurred. The estimated total number of attacks in each trial was then scaled to  $(\text{number of attacks} \cdot \text{m}^2) \cdot (\text{larva} \cdot \text{red shiner} \cdot \text{day})^{-1}$  where day was defined as being 14-hours long which approximates the daylight period during summer in the Colorado River Basin.

Data from 69 pool trials was analyzed with a general linear model that assumed a Poisson distribution of the responses because most observations were at or near zero with relatively few large values. The data were used to estimate a statistical model that predicted  $\log_e(\text{attack rate})$  as

a function of the independent variables: *predator TL*, *prey TL*, (*predator TL*)<sup>2</sup>, (*prey TL*)<sup>2</sup>, *predator feeding strategy*, *water clarity*, *alternative prey*, and second-order interactions.

*Predator feeding strategy* was included as a predictor variable because each of the five groups of red shiners exhibited different levels of predation that were not related to their size. We assumed these different behaviors represented the range of feeding strategies that were employed by groups of red shiners in the natural environment. A global model was fit using the method of maximum likelihood, and model selection was by AIC. Model selection suggested that the best predictors of attack rate were *prey TL*, *predator feeding strategy*, *water clarity*, and *alternative prey*. Attack rate increased with larval size and was independent of red shiner size. Larger larvae may be attacked more often than small ones because they are more active and visible to predators and because they are energetically more profitable (Litvak and Leggett 1992, Bertram 1996). Clear water and the absence of alternative prey each increased attack rate 2-3-fold relative to conditions with turbid water or alternative prey present. The attack-rate equation had the form:

$$y = -4.75 + 0.147 \cdot x_1 + 0.909 \cdot x_2 + 1.157 \cdot x_3 - 0.439 \cdot fs_1 + 0.1036 \cdot fs_2 - 4.45 \cdot fs_3 - 1.88 \cdot fs_4 \quad (4)$$

where:  $y = \log_e ((\text{number of attacks} \cdot \text{m}^2) \cdot (\text{larva} \cdot \text{red shiner} \cdot 6 \text{ hour})^{-1})$

$x_1 = \text{prey TL}$ ,

$x_2 = 1$  if water is clear; 0 if water is turbid,

$x_3 = 1$  if alternative prey is absent; 0 if present,

$fs_1 = 1$  if simulating the feeding strategy of predator group 1; else = 0,

$fs_2 = 1$  if simulating the feeding strategy of predator group 2; else = 0,

$fs_3 = 1$  if simulating the feeding strategy of predator group 3; else = 0,

$fs_4 = 1$  if simulating the feeding strategy of predator group 4; else = 0.

Note that when all  $fs$  coefficients = 0, the model simulates the feeding strategy of predator group 5.

Standard errors for coefficients are: intercept = 0.557,  $x_1 = 0.0294$ ,  $x_2 = 0.266$ ,  $x_3 = 0.331$ ,  $fs_1 = 0.272$ ,  $fs_2 = 0.239$ ,  $fs_3 = 1.224$ , and  $fs_4 = 0.360$ .

A goodness-of-fit test did not detect significant lack of fit ( $p = 0.25$ ) and suggested that the model fit the data reasonably well. Model fit was further assessed by plotting deviance and chi-square residuals as functions of predictor variables and predicted values. No trends in residuals were observed.

The attack-rate equation was used in model simulations in the following way to determine the daily number of predator attacks on each larva. For each larva on each day, equation 4 was solved using the size of the larva, conditions of water clarity and alternate prey, and one of the five feeding strategies selected at random. This daily attack rate was then multiplied by predator density (number/m<sup>2</sup>) to estimate *mean total attacks*:

$$\text{Mean total attacks} = \text{predator density} \cdot \text{daily attack rate} \quad (5)$$

The actual number of attacks on the larva for that day was determined by randomly drawing a value from a Poisson distribution with a mean equal to *mean total attacks*.



### *IBM Simulation Steps*

Each simulation started with a cohort of 10,000 dispersing larvae arriving in, or "colonizing" nursery habitat. Colonization occurred on either 1 June, 1 July, or 1 August. Initially all larvae were 9.0 mm TL which is the typical size of Colorado squawfish larvae entering backwaters, but were assigned different baseline growth rates (mm/day) randomly drawn from a normal distribution with a mean specified for each simulation and a coefficient of variation of 14.1% (Bestgen 1996). For each larva each day, the number of attacks was determined using equations 4 and 5. For each attack, a predator size was drawn at random from that day's predator size distribution, and  $P(\text{capture})$  was determined using equation 2. The probability that a larva would survive all attacks on a given day ( $P(\text{survival})$ ) was determined by multiplying together the individual probabilities of surviving each attack (i.e.,  $1 - P(\text{capture})$ ) on that day. Whether or not the larva survived the day was determined by randomly drawing a number from a uniform distribution between 0 and 1; if the random number was less than or equal to the larva's probability of survival for the day, then it survived. Probability of survival was set to 1 for larvae  $> 25$  mm because the capture equation and other observations showed that larvae of this size were no longer vulnerable to red shiner predation. At the end of a day, length of each surviving larva was increased based on the larva's initial baseline growth rate and that day's temperature using equation 1.

This process was repeated for each larva each day, then the time step was incremented and surviving larvae were exposed to predation on the next day. Fish that survived to 25 mm or 1 October were considered to have recruited to the age-0 population in winter habitat. At the end

of a simulation, data that described the numbers, size distribution, and growth rate distributions of survivors and mortalities were output for further analysis.

### **Simulation Results**

We implemented the IBM under several different sets of conditions to evaluate the relative effects of red shiner predation on survival and TL of squawfish cohorts at the end of the growing season, as a function of thermal regime, arrival time, larval growth rate, and predator density. For most simulations we assumed conditions of turbid water with alternate prey present, because we expected these conditions to be fairly typical for backwater nursery habitats. Unless specified otherwise, we used a moderate mean baseline growth rate of 0.3 mm/d for the larvae, and a moderate red shiner density of 3 predators/m<sup>2</sup>. Results reported below each represent the mean of three replicate simulations started with different random number seeds.

An additional simulation was added in the final stages of report preparation at the request of a funding sponsor (E. Wick). This simulation compared survival and growth of a cohort of Colorado squawfish in the middle and lower Green River where water temperatures, arrival date of Colorado squawfish larvae, and timing of availability of alternative prey may differ. These results are reported in Appendix I.

#### *Effects of Thermal Regime and Colonization Date*

To examine the effects of thermal regime and the timing of backwater colonization (arrival) by larvae, we simulated six scenarios using warm and cool temperatures with early,

middle, and late arrival dates. Results from these simulations suggested that red shiner predation was a significant source of mortality for young squawfish: squawfish survival to the end of the growing season ranged from 8 to 25% (Figure 7). Survival was about one third lower with the cool thermal regime than with warmer temperatures, because the larvae grew more slowly at cooler temperatures and they remained vulnerable to predation longer. In all cases the number of surviving larvae declined rapidly, with only 20-30% of larvae surviving more than a month (Figure 8).

Survival was relatively low for cohorts arriving in the backwaters early or late in the season, and was highest for those with intermediate arrival dates (Figure 7). Larvae arriving early experienced rapid growth because temperatures were warm and increasing (Figure 5), but the shiners were large during this time, so survival was still relatively low. Larvae that arrived in mid-season encountered the best conditions for survival; predators were relatively small and the larvae experienced a full month of relatively warm water temperatures which allowed rapid growth to sizes that were not vulnerable to predation. By the time late-spawned cohorts arrived, temperatures were beginning to decline and predators had grown to relatively large size again, so these late-arriving larvae experienced high mortality rates. Their survival was about equal to early-arriving cohorts, even though they were exposed to predation for half as much time.

Squawfish size at the end of the growing season was strongly affected by arrival time (Figure 9). Survivors from cohorts that arrived early were almost twice the size of those from late-arriving cohorts, because they had much more time to grow. Larvae that arrived in June became invulnerable to red shiner predation half-way through the season, while survivors from

cohorts that arrived in August were still small enough for large red shiners to eat at the end of the season.

Date of arrival in backwaters by Colorado squawfish may influence survival beyond the first summer. Our simulations suggest that larvae with early colonization dates consistently attain larger size. Over-winter survival of age-0 Colorado squawfish has been hypothesized to be influenced by size. Other studies have demonstrated that larger size confers an energetic advantage (Cargnelli and Gross 1997). Thus, the effects of date of colonization may continue to act on a fish for months or even years and may be a significant factor affecting cohort strength.

#### *Effect of Predator Density*

The density of red shiners used in previous simulations ( $3/m^2$ ) is conservative compared to densities observed in the field which may exceed twice this level (Haines and Tyus 1990). To examine the effect of predator density we ran a series of simulations using 1 to 6 shiners/ $m^2$ . Predator density had a strong effect on number of larvae attacked and captured; survival declined from  $>50\%$  at 1 red shiner/ $m^2$  to 3-7% at 6 shiners/ $m^2$  (Figure 10). This nonlinear effect is due to the exponential change in the number of attacks and capture rates of larvae as predator density increases. These results suggest that any management action that decreases the abundance of predators will result in a proportionately larger increase in the number of larvae that escape predation.

### *Effect of Larval Growth Rate*

Analysis of growth rates in wild fish showed that natural growth rates range from 0.15 to 0.65-mm TL/d (Bestgen 1997). A variety of factors besides temperature may affect growth rates. For example, longevity of backwaters may be related to production of food for larval fish and consequently, growth rates. To examine the effect of mean growth rate on survival, we conducted a series of simulations with baseline growth rates ranging from 0.2 to 0.6 mm/d.

Mean growth rate of larval Colorado squawfish had a major effect on cohort survival (Figure 11). Survival declined from 40-50% at the highest mean growth rate to <10% at the lowest mean growth rate. Results of this scenario suggest that management actions that increase larval growth rates may enhance recruitment of Colorado squawfish.

### *Selection for Fast Growers*

In all our simulations, growth rate varied with individual as it does in natural populations. Although all the larvae in our simulations started at the same size, these growth rate differences generated variation in size among individuals over time. Because size-selective predation by red shiners tended to remove relatively small individuals within a cohort, the distribution of growth rates of squawfish that survived to the end of the growing season was shifted noticeably higher than the initial growth rate distribution (Figure 12). This same pattern was noted in field studies in the Green River, Utah, where size-selective mortality of age-0 Colorado squawfish was presumed due to predation by non-native fishes (Bestgen 1997).

## Conclusions and Recommendations for Future Research

Our level of knowledge about factors that affect recruitment patterns of Colorado squawfish has been greatly expanded over the last 18 years. The conceptual life-history model represents a summary of this knowledge in a holistic format (Figure 1). It encourages a process-oriented view of Colorado squawfish recruitment and of potential controlling environmental factors. Unfortunately, our ability to conceptualize and hypothesize about recruitment of Colorado squawfish far exceeds our ability to quantitatively describe this process.

The IBM presented here represents an attempt at quantitative synthesis of biotic and abiotic factors that influence growth and survival of age-0 Colorado squawfish. The model and its output are intended to be used as a tool to evaluate the *relative* changes in recruitment that might be observed under different environmental conditions. Emphasis should be placed on the direction of the predicted change and the prediction should be viewed as a hypothesis to be tested during the course of future research. For example, red shiner predation was the only source of mortality in our model; mortality from other sources can be expected to act in addition to red shiner predation. Therefore, emphasis should not be placed on the absolute values of model predictions because the model is a simplification of the natural world and it is unlikely that it will exactly correspond to events that occur there.

The model simulations suggest that predation by red shiners may be a major source of mortality for larval Colorado squawfish. Our simulations generally assumed relatively benign conditions with low red shiner densities and an environment that greatly reduced the efficiency of red shiner predation (turbid water, alternate prey present). Simulations that used conditions of clear water or no alternate prey showed that red shiner predation reduced squawfish survival

another order of magnitude. Predation with both clear water and no alternate prey reduced survival three orders of magnitude. It is unlikely that these conditions would prevail all season in the field, but these simulations suggest that when periods of clear water or low food availability occur, mortality from red shiner predation is increased.

The scope of the IBM was restricted by a lack of data amenable to inclusion in a mechanistic model. For example, existing data for modeling the relationship between discharge and availability of prey for larval Colorado squawfish in backwaters were not available. This component was originally proposed because it has an intuitive link to ecosystem management: manage discharge to provide warm, persistent backwaters that provide food-rich habitat for larval Colorado squawfish. Despite omission from the IBM, this component has great conceptual importance and quantitative field studies should be conducted so that the indirect relationship between discharge and growth of Colorado squawfish is better understood. When information on this relationship and other relevant factors (e.g., role of other predator species) becomes available, it can be incorporated into the modeling approach presented here.

Water temperature regime is correlated with discharge. Thus, water temperature can be used as a surrogate for discharge. The IBM is well-equipped for evaluating the influence of water temperature because the temperature-dependent growth equation is incorporated in the model and any temperature regime can be simulated. U.S. Geological Survey hydrologic data could be used to describe relationships between discharge and water temperature, and effects of discharge manipulations could be explored.

Other suggestions for research that would aid this modeling effort include:

1. Conduct a sensitivity analysis of the IBM so that the model components can be ranked with regard to their influence on the outcome of a simulation. This analysis will identify which components are most important so that an evaluation can be conducted to determine if additional information may improve the predictive capability of the IBM.
2. Validate IBM model predictions with data collected in the field. For example, predator removal experiments could be used to evaluate if reductions in predator density enhance recruitment of age-0 Colorado squawfish as predicted by the IBM.
3. Experimentally determine probability of capture and attack rates by other potentially important non-native predator fishes on Colorado squawfish. These species might include channel catfish and a representative centrarchid species.
4. Conduct laboratory and field studies to describe relationships of discharge, water temperature, habitat availability, and abundance of alternate prey with survival, growth, reproduction, and size-structure of native and non-native fishes in the Colorado River Basin.



Suggestions for research that would aid modeling efforts for razorback sucker *Xyrauchen texanus* include:

1. Experimentally determine probability of capture and attack rates by red shiners and other predators on early life stages of razorback sucker so that the IBM model can be adapted for this species.
2. Develop relationships that describe effects of water temperature and food density on growth of razorback sucker. Effects of water temperature (range 16-25°C) on growth of early life stages of razorback sucker under high food rations have already been investigated in laboratory experiments (K. Bestgen, unpublished data).
3. Conduct laboratory and field studies to describe relationships of discharge, water temperature, habitat availability, and abundance of alternate prey with abundance, growth, survival, and size-structure of razorback sucker and important non-native fishes in the Colorado River Basin.

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Figure 1. Conceptual life-history model of Colorado squawfish recruitment to developmental stages (boxes), and important biotic and abiotic controlling factors affecting them (biotic controlling factors summarized on the left, and abiotic factors on the right). "Remarks" refer to characteristics of fish that recruit to the next developmental category.

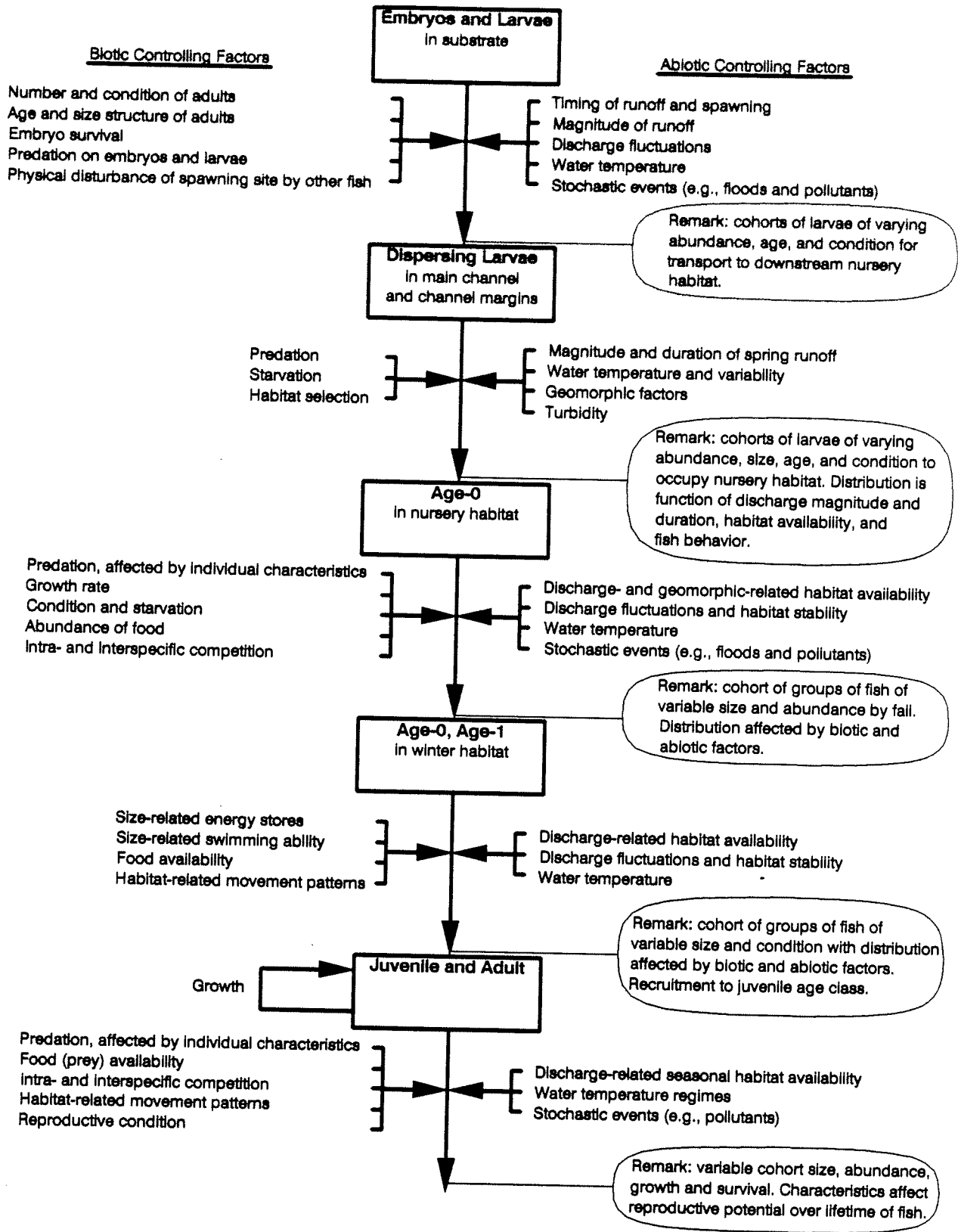


Figure 2. Preliminary flow diagram for individual-based model of Colorado squawfish recruitment in the Colorado River Basin.



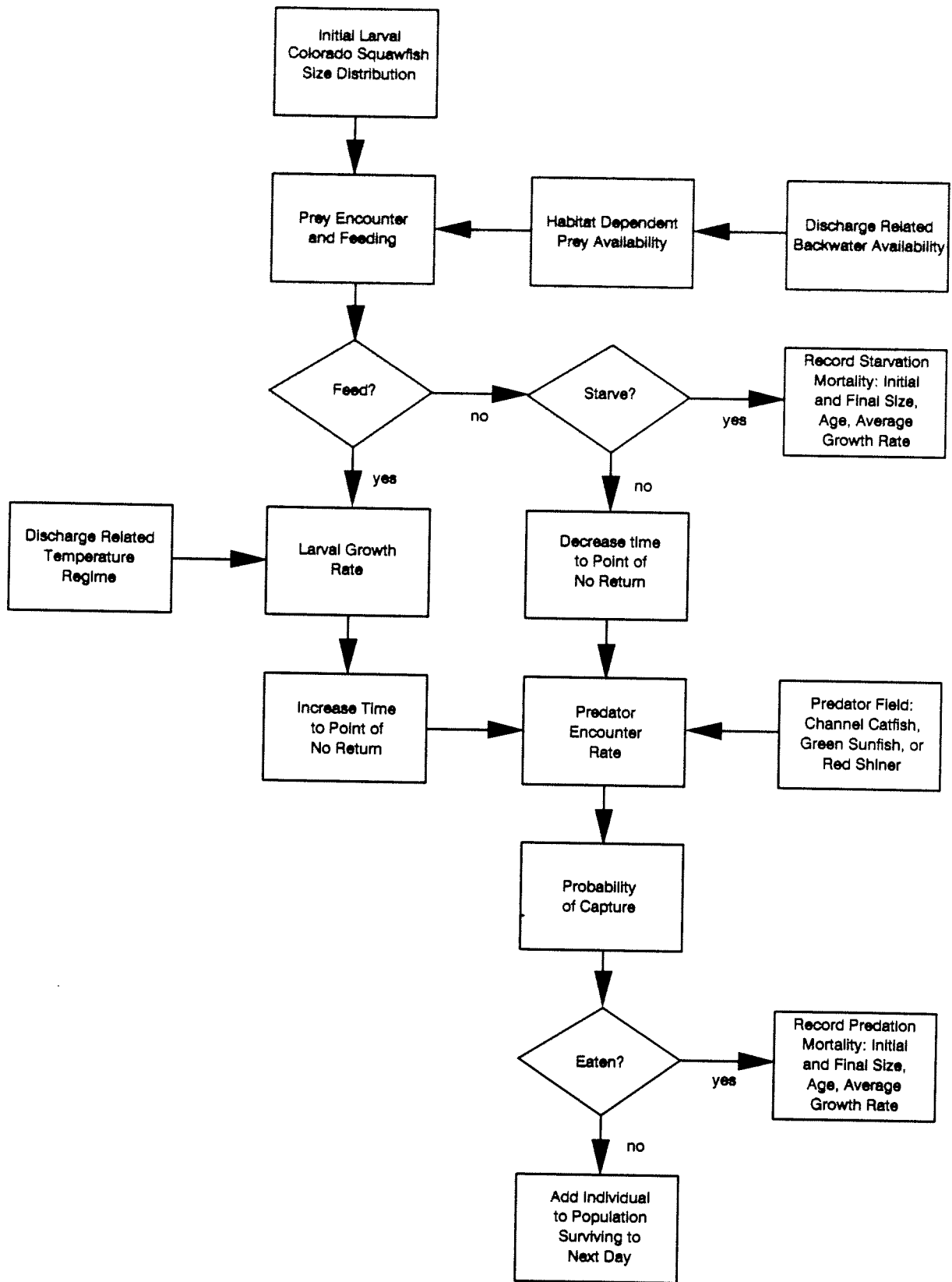


Figure 3. Flow diagram for individual-based model of Colorado squawfish recruitment in the Colorado River Basin.

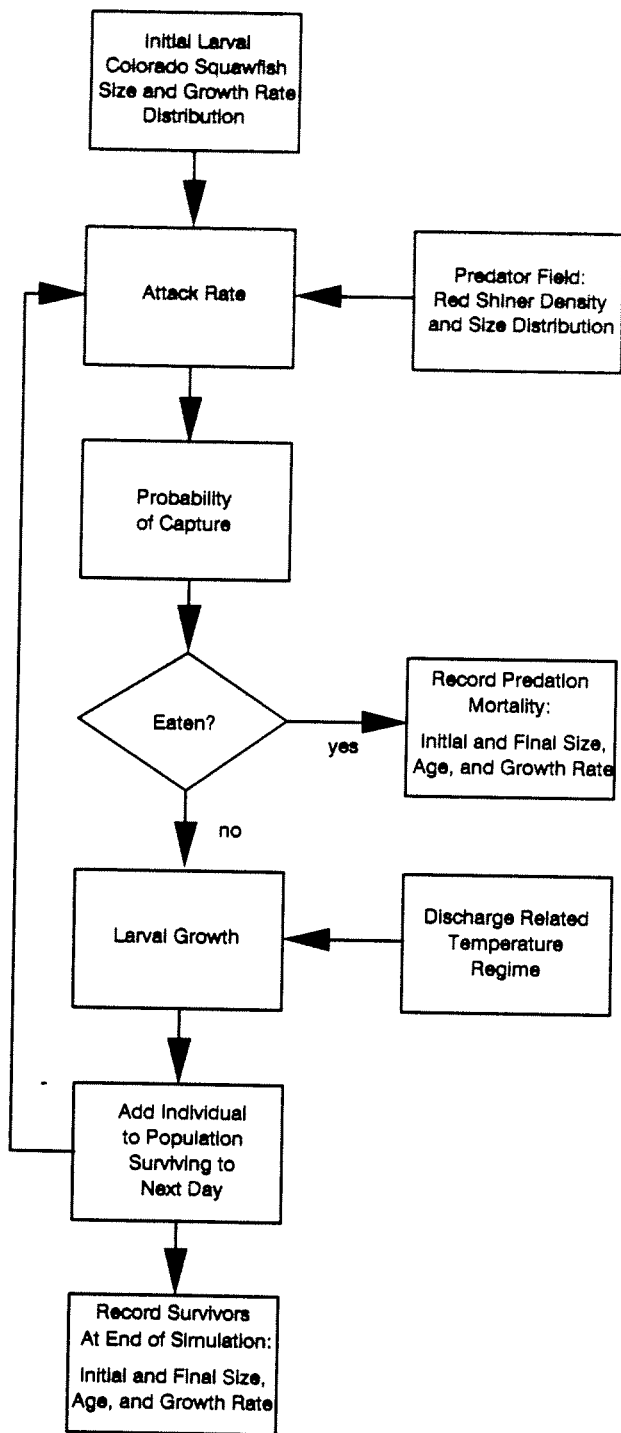


Figure 4. Red shiner length-frequency distributions used in the individual-based model. Daily distributions were estimated by linear interpolation.

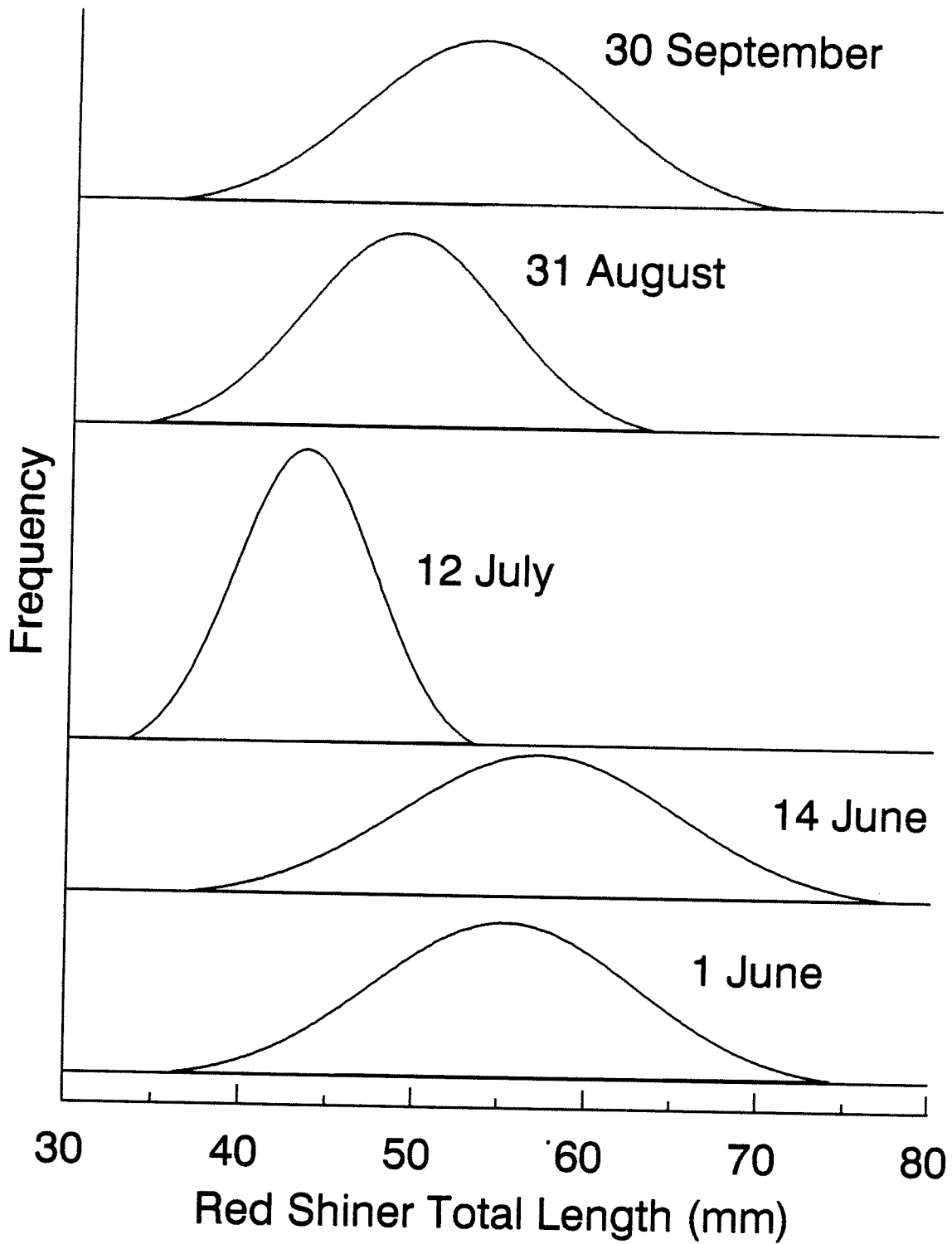


Figure 5. Thermal regimes used in simulations. Arrows on X-axis indicate the two colonization dates used in simulations.

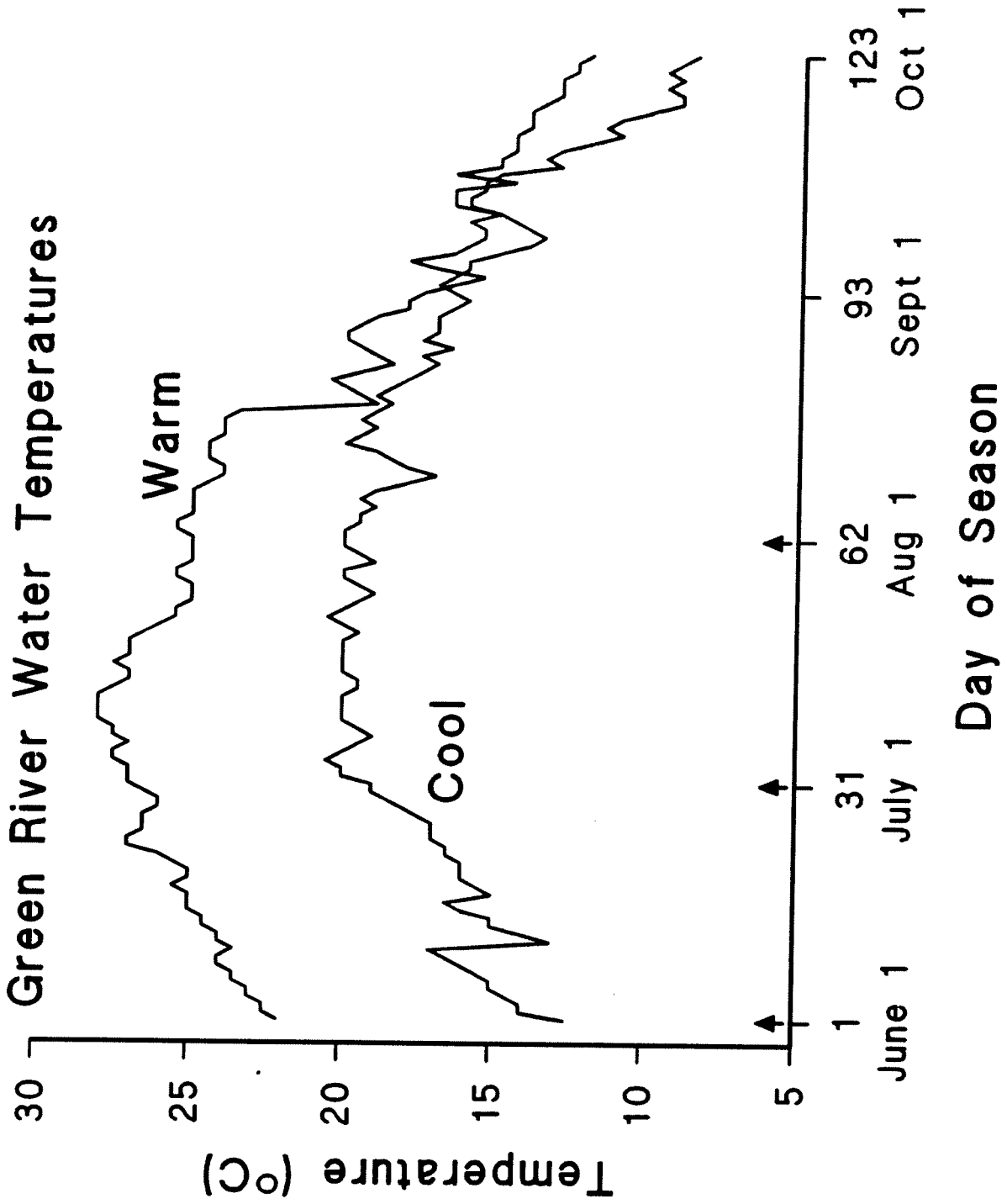


Figure 6. Probability of capture of Colorado squawfish by red shiner as a function of total length.



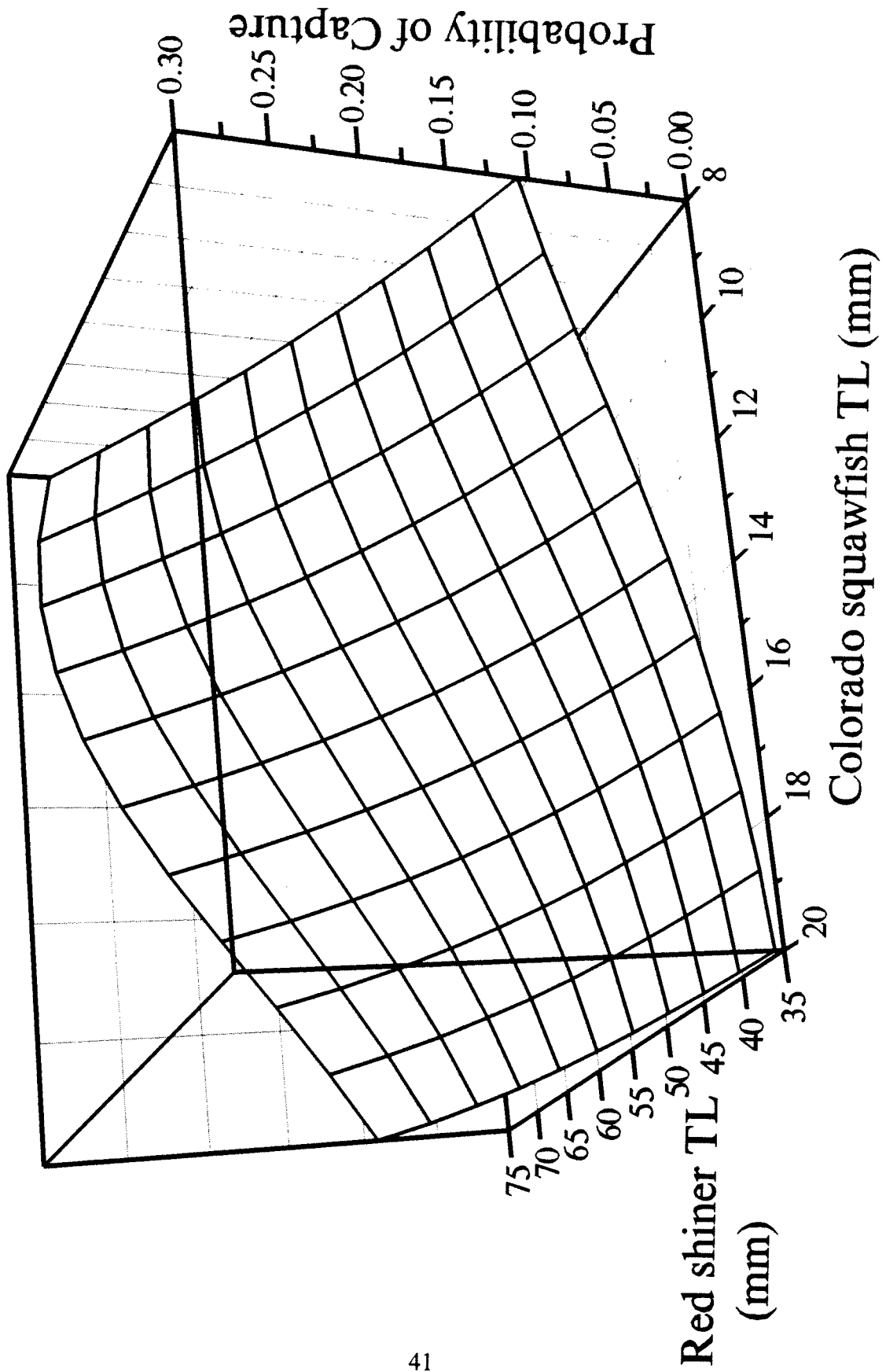


Figure 7. Larval cohort survival from simulations using warm and cool thermal regimes with larvae arriving in backwaters on 1 June, 1 July, and 1 August.

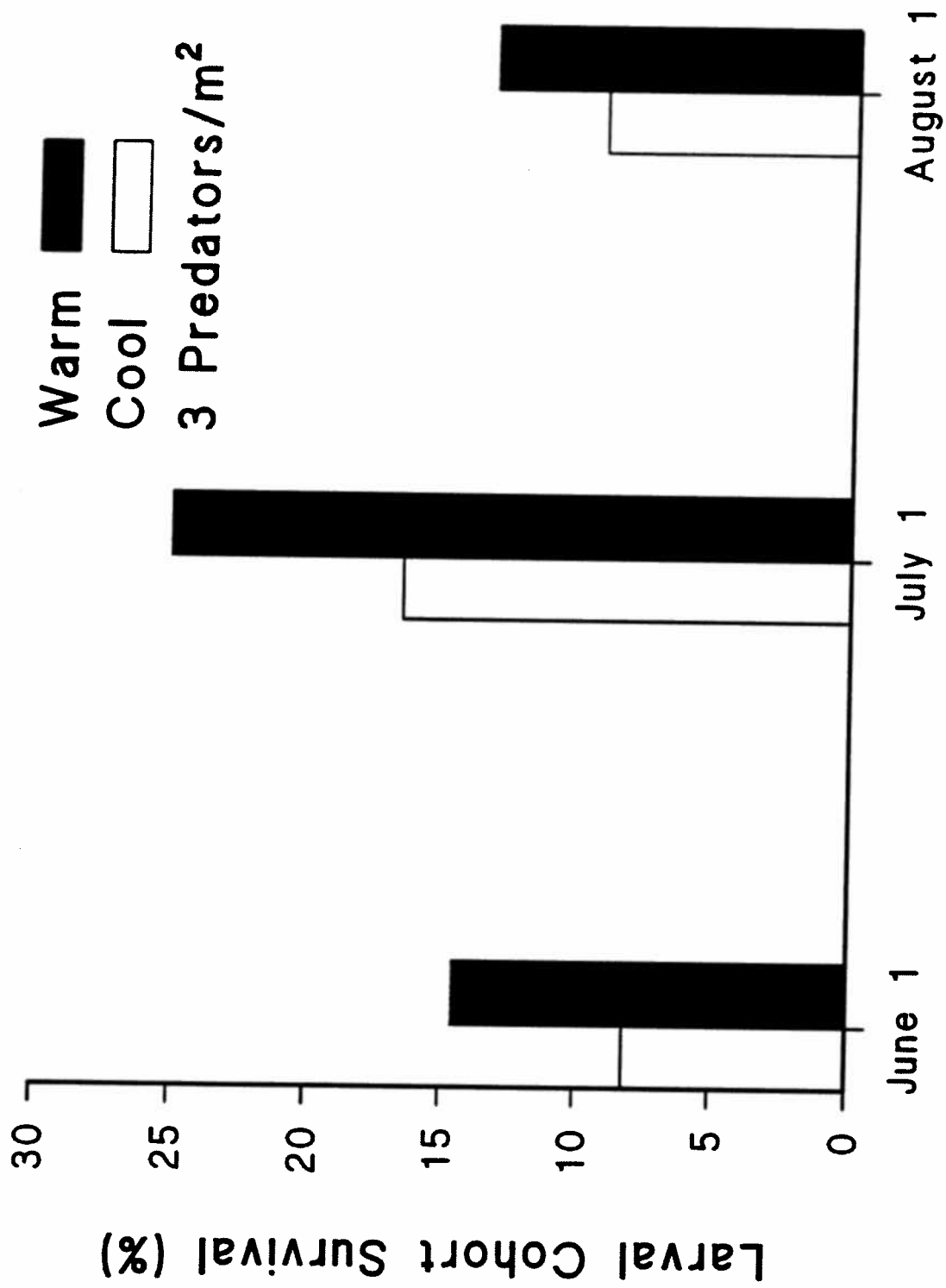


Figure 8. Decline in larval cohort survival over time from simulations using warm and cool thermal regimes with larvae arriving in backwaters on 1 June.

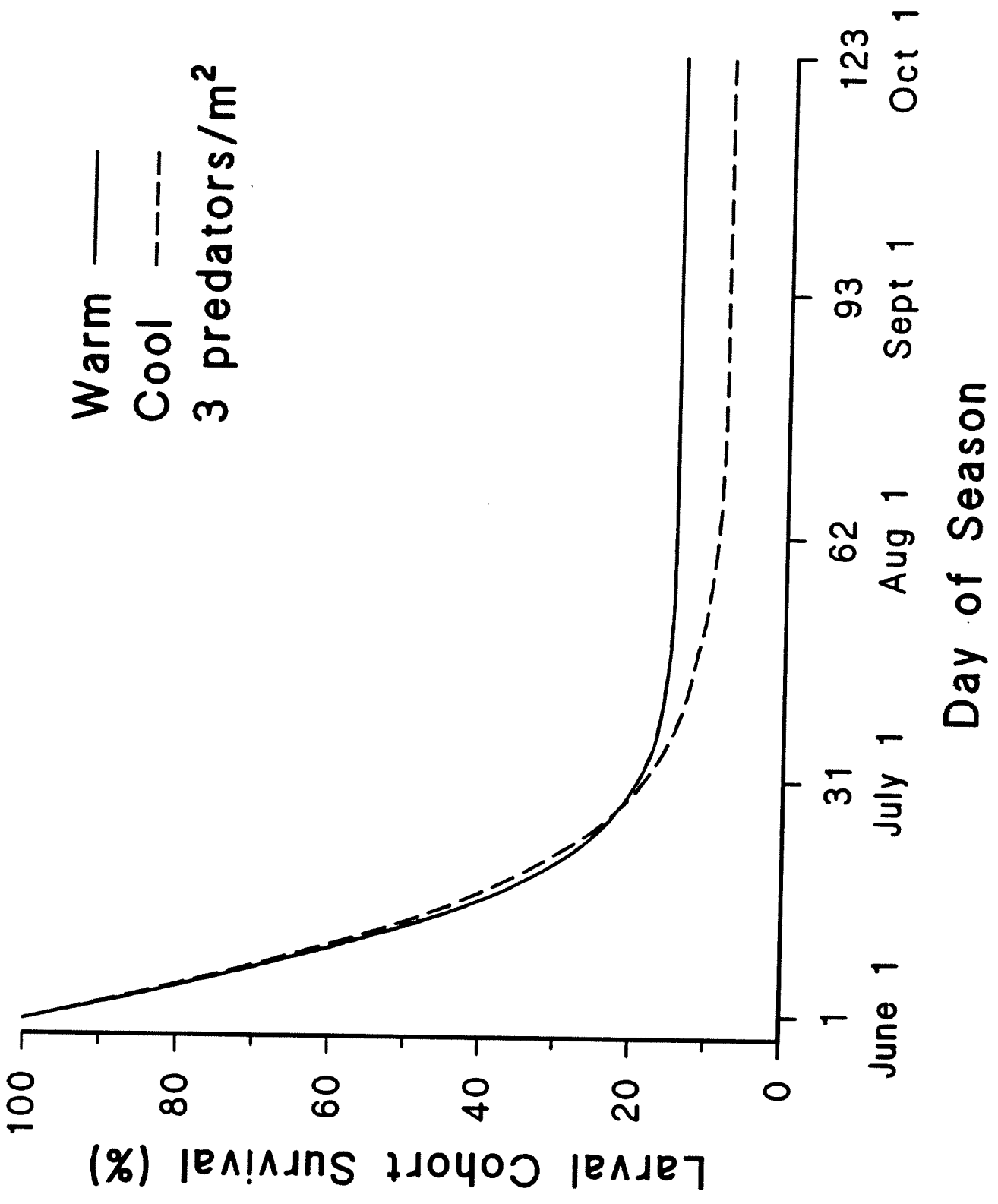


Figure 9. Mean Colorado squawfish lengths at the end of the growing season from simulations using warm and cool thermal regimes with larvae arriving in backwaters on 1 June, 1 July, and 1 August.

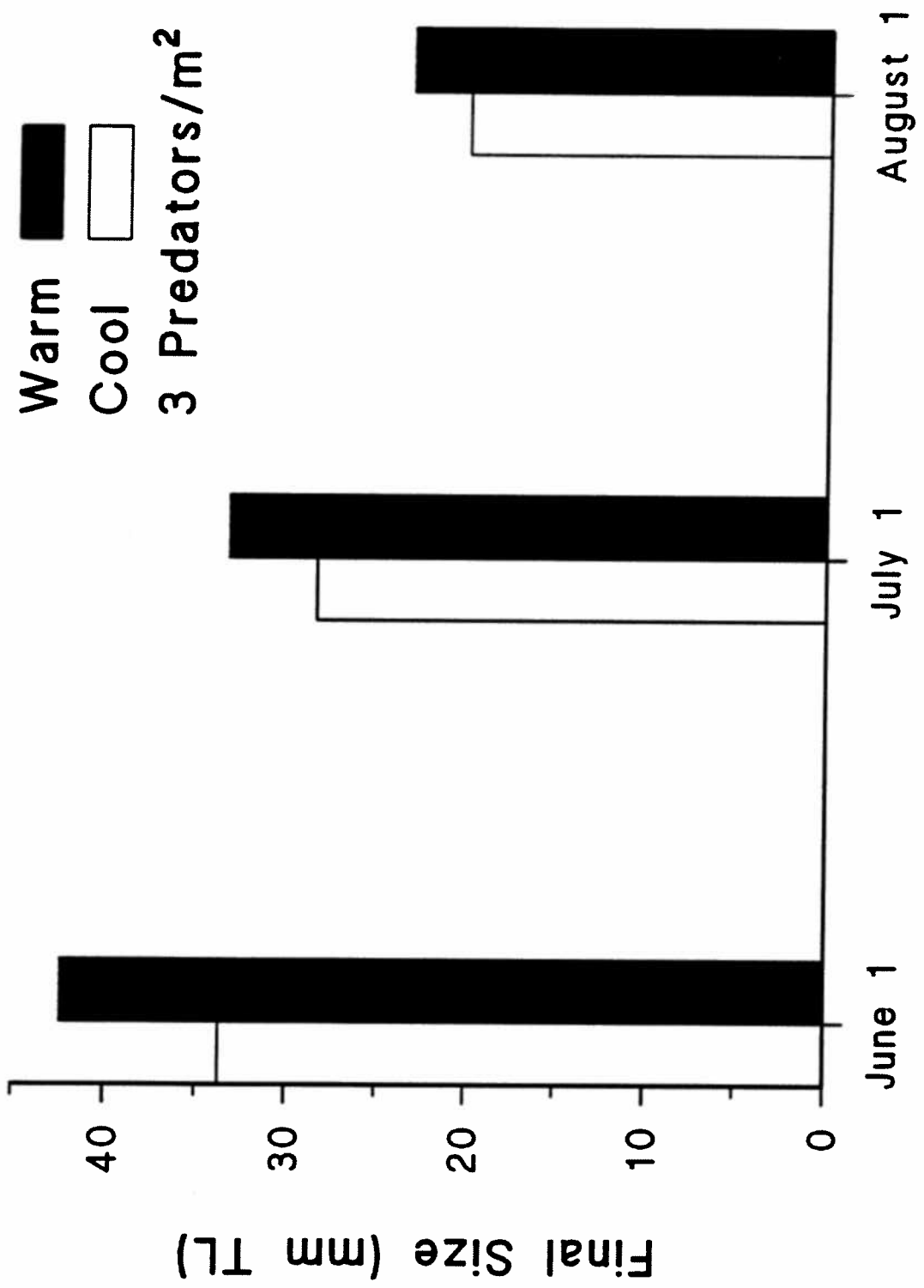


Figure 10. Decline in larval cohort survival with increasing red shiner density, from simulations using warm and cool thermal regimes.



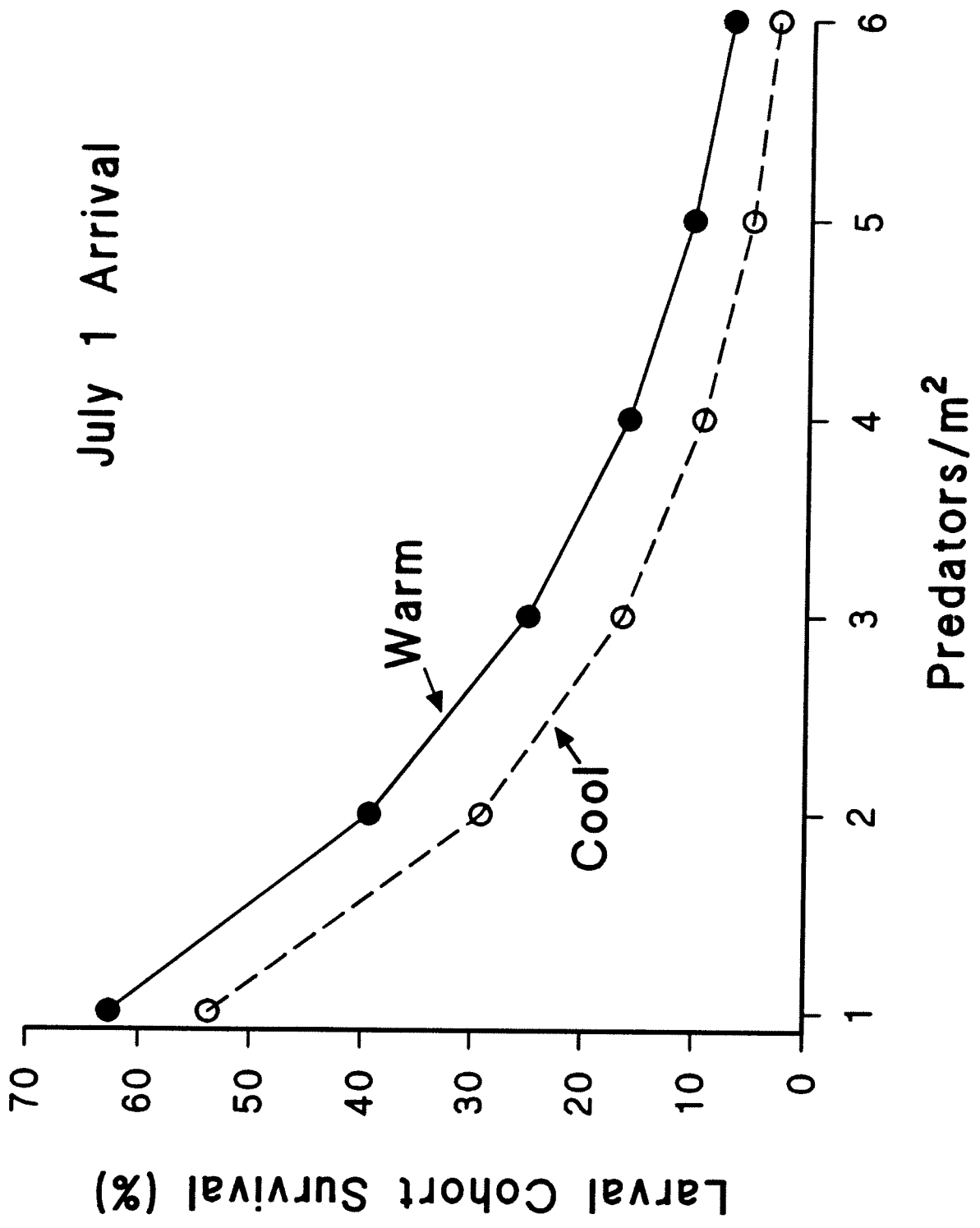


Figure 11. Increase in larval cohort survival with increasing mean baseline growth rate, from simulations using warm and cool thermal regimes.

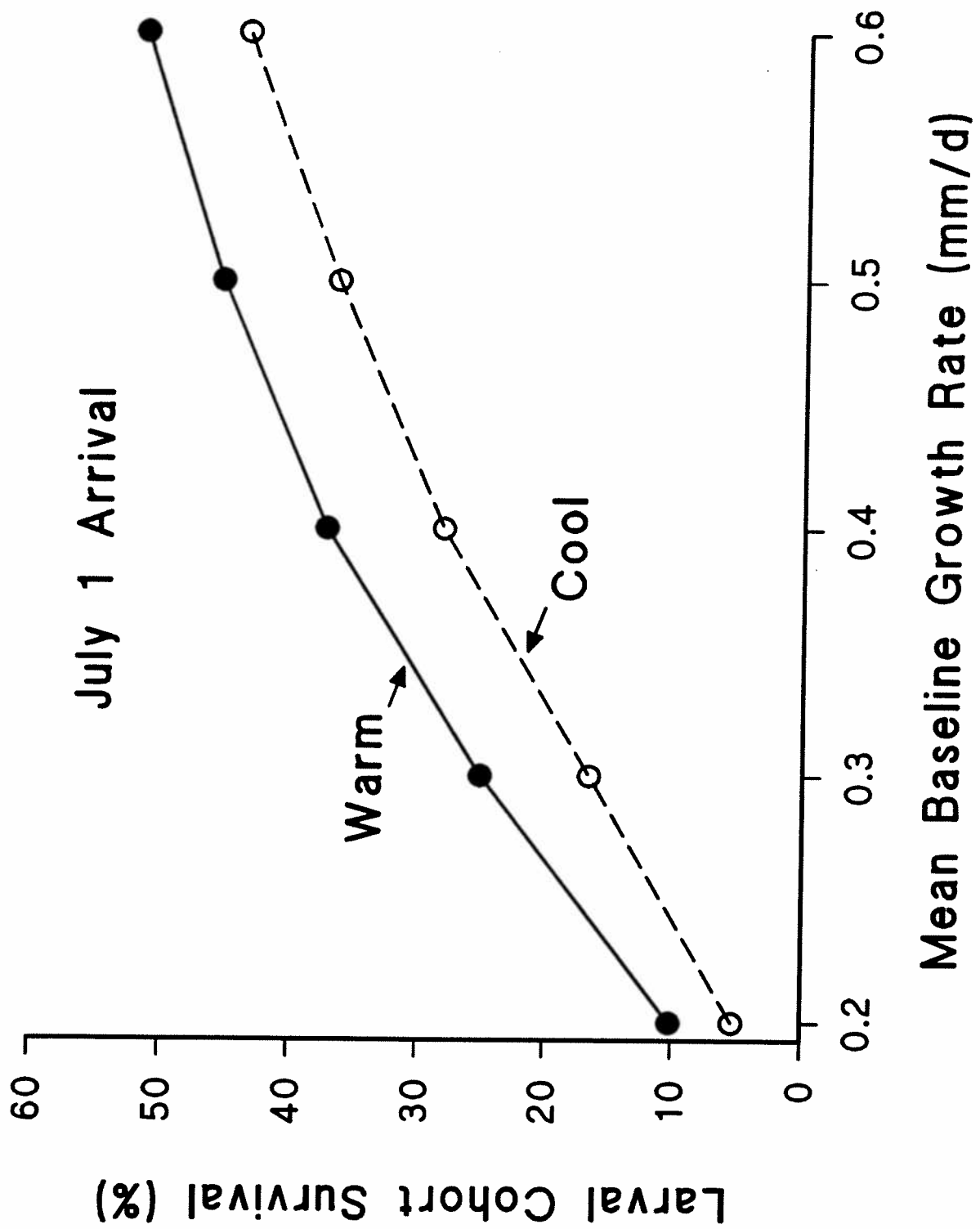
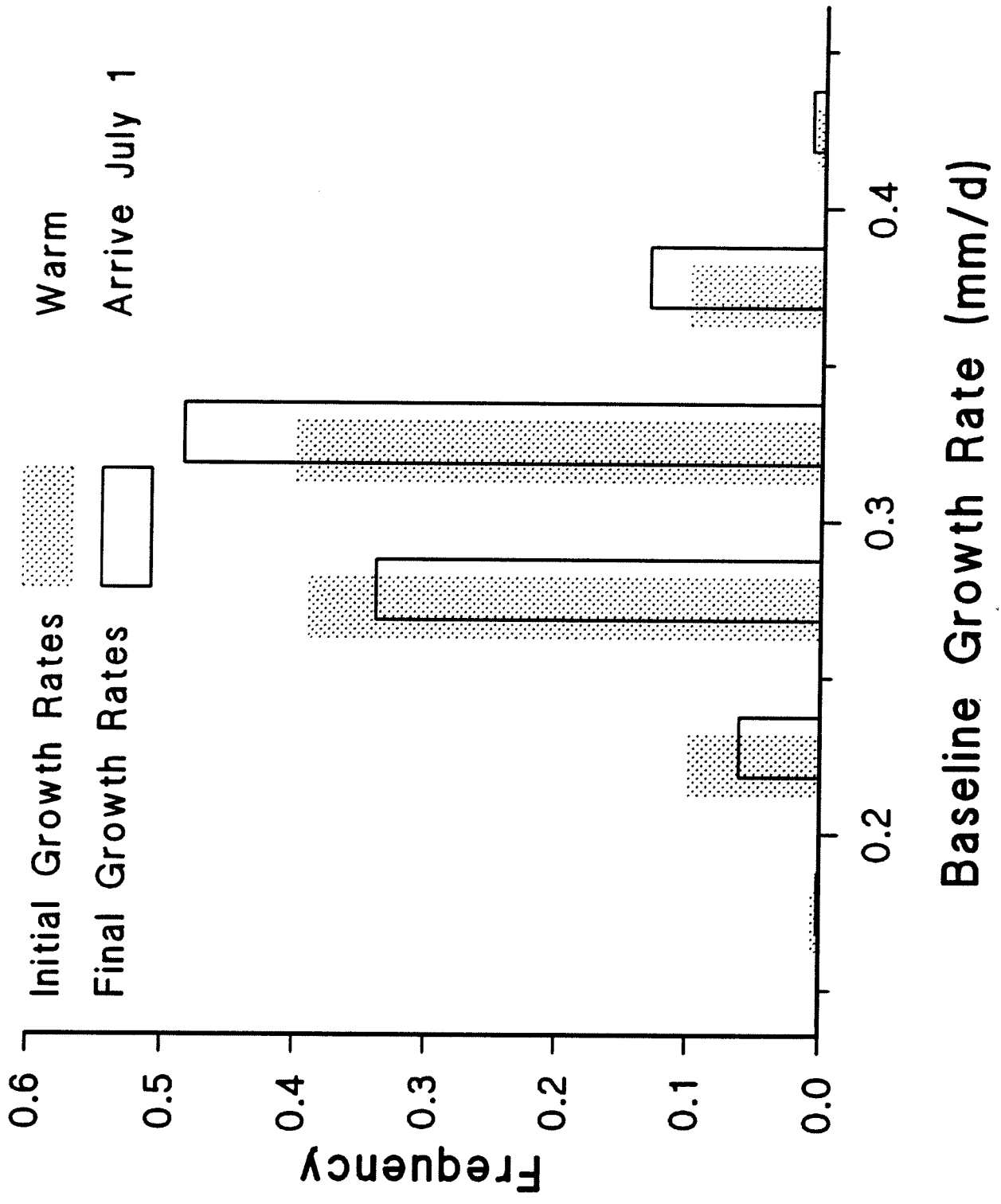


Figure 12. Distribution of initial and final (survivor) baseline growth rates from a simulation using an arrival date of 1 July and a warm thermal regime.



## Appendix I.

The special simulation results presented here compare growth and survival of cohorts of larvae in the middle and lower Green River where water temperatures, colonization dates of Colorado squawfish larvae, and timing of availability of alternative prey (cyprinid larvae) were estimated from field data. Data were available for 1993, 1994, and 1995. Discharge was unusually high in 1995 and unusually low in 1994, so 1993 was selected for the simulation. Date of colonization in simulations was 12 July in the middle Green River and 6 July in the lower Green River based on first appearance of Colorado squawfish larvae in 1993 drift net samples. Temperature regimes for middle and lower Green River reaches were taken from thermograph data collected at the Jensen, Utah, and Green River, Utah, U. S. Geological Survey gauges, respectively. In these simulations, the effect of the presence of alternate prey in the form of non-native cyprinid larvae was studied. Presence of these larvae may release Colorado squawfish larvae from predation by red shiner adults and timing of the appearance of this alternative prey may be different in each of the reaches relative to appearance of Colorado squawfish larvae (pers. comm. E. J. Wick). In the simulations, alternative prey were made available on dates that corresponded to the first appearance of non-native cyprinid larvae in drift net samples. The timing of changes in the size structure of red shiner predators was adjusted so that Colorado squawfish larvae in each reach would be subjected to an identical predator field after colonization. Predator density was  $3/m^2$  and baseline growth rate was 0.283 mm TL/d.

Survival of cohorts of Colorado squawfish in the middle and lower Green River were nearly equivalent (11%) because appearance of alternative prey followed the appearance of

Colorado squawfish by nine days in each reach in 1993. The slightly larger size of Colorado squawfish survivors in the lower Green River (mean TL = 33.4 mm) compared to the middle Green River (31.2 mm TL) resulted from earlier colonization by the former and the subsequent longer growing season. Mean water temperatures were slightly warmer in the middle Green River than in the lower Green River in 1993, (22.4 and 22.0°C, respectively) suggesting that this variable was not responsible for differences in simulated growth.