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Potential Effects of Maternal Contribution on Egg and Larva Population Dynamics of Striped Bass: Integrated Individual-Based Model and Directed Field Sampling

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ABSTRACT

We have used a bioenergetically-driven, individual-based model (IBM) of striped bass as a framework for synthesizing available information on population biology and quantifying, in a relative sense, factors that potentially affect year class success. The IBM has been configured to simulate environmental conditions experienced by several striped bass populations; i.e., in the Potomac River, MD; in Hudson River, NY; in the Santee-Cooper River System, SC, and; in the San Joaquin-Sacramento River System, CA. These sites represent extremes in the geographic distribution and thus, environmental variability of striped bass spawning. At each location, data describing the physio-chemical and biological characteristics of the spawning population and nursery area are being collected and synthesized by means of a prioritized, directed field sampling program that is organized by the individual-based recruitment model. Here, we employ the striped bass IBM configured for the Potomac River, MD from spawning into the larval period to evaluate the potential for maternal contribution to affect larva survival and growth. Model simulations in which the size distribution and spawning day of females are altered indicate that larva survival is enhanced (3.3-fold increase) when a high fraction of females in the spawning population are large. Larva stage duration also is less ($\bar{X}$ = 18.4 d and 22.2 d) when large and small females, respectively, are mothers in simulations. Although inconclusive, these preliminary results for Potomac River striped bass suggest that the effects of female size, timing of spawning and maternal contribution on recruitment dynamics potentially are important and illustrate our approach to the study of recruitment in striped bass. We hope to use the model, field collections and management alternatives that vary from site to site, in an iterative manner for some time to come.

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INTRODUCTION

Recruitment success of populations of anadromous striped bass Morone saxatilis varies widely throughout its range and much attention has been focused on early life dynamics (Setzler-Hamilton et al. 1981; Boreman and Austin 1985; Goodyear 1985; Bulak et al. 1985; Houde et al. 1988; Stevens 1988; Secor 1990; Rose and Cowan, submitted; Cowan et al., submitted). The role of maternal contribution in recruitment potentially is significant because large females spawn greater numbers of heavier eggs (Rogers and Westin 1981; Zastrow et al. 1989; Monteleone and Houde 1990). Egg weight and embryo size also are correlated (Eldridge et al. 1982; Zastrow et al. 1989; Monteleone and Houde 1990) suggesting that the maternal contribution to egg size may influence survival of embryos and larvae through increased energy and nutrient stores (Secor 1990).

Recent studies of maternal influences on striped bass eggs and larvae and possible effects on recruitment produced contradictory results. In Chesapeake Bay, MD, Monteleone and Houde (1990) showed that small (<4 kg) females produced smaller larvae (20% by weight) than large (>15 kg) females. The small larvae grew slower in length at 19 ± 0.5°C and remained small (~20% by weight) to 25 days post hatch. Monteleone and Houde concluded that maternal influences on egg quality may be a factor that affects recruitment potential because slow growth prior to metamorphosis subjects larvae to high mortality during pre-recruitment. In Santee-Cooper, SC, Secor (1990) reported egg size variability but no significant relationship between striped bass female size and egg weight for >3 to 12.2 kg females. Large eggs used stores faster but produced larger larvae (16% by weight) than broods of small eggs. Initial egg weight advantages persisted for less than one week in feeding larvae reared at ~20.0°C, although larvae from large egg broods were somewhat less vulnerable to starvation. Secor concluded that variation in egg size could be adaptive to variable feeding situations but cautioned against the assumption that egg investment always is positively related to larval fitness and increased recruitment.

Germane to this apparent contradiction is the anecdotal belief that large female striped bass in some populations spawn at cooler temperatures, earlier in the spawning season than do smaller females (Hollis 1967). Neither of the studies described above considered the energetic consequences of egg and larva size at different temperatures nor was there good agreement in female size (Secor 1990, 3.2 to 12.2 kg; Monteleone and Houde 1990, <4 and >15 kg) between experiments. Moreover, Houde et al. (1989) showed that early spawned (early April) egg cohorts in the Potomac River, MD, episodically are killed by cold weather events causing temperatures to drop below 11°C.

The size distribution of striped bass female spawners in the Potomac River and upper Chesapeake Bay has changed dramatically over the past ten years, showing a substantial decrease in modal length from 1982 until 1985. Modal lengths have increased since 1985, presumably due to a moratorium on striped bass fishing in Chesapeake Bay. Modal lengths of females on the spawning grounds were ~1000 mm standard length (SL) in 1982, ~425 mm in 1985 and ~750 mm in 1990 (Maryland Department of Natural Resources (MD DNR), Tidewater Administration).

To evaluate the potential for maternal contribution to affect striped bass larva survival and growth, we use an individual-based population model (IBM) of striped bass as a framework for synthesizing available information and quantifying, in a relative sense, their interactive effects on population dynamics. Here, we employ an IBM of striped bass in the Potomac River subestuary of Chesapeake Bay from spawning into the larval period (~135 days) to describe some aspects of the model. The IBM also has been configured to simulate environmental conditions experienced by other striped bass populations; i.e., in Hudson River, NY; in the Santee-Cooper River System, SC; and, in the San Joaquin-Sacramento River System, CA. These sites represent extremes in the geographic distribution and thus, environmental variability of striped bass spawning.

At each location, data describing the size distribution of female spawners in the spawning grounds are being collected for model input by a directed field sampling program sponsored by the Electric Power Research Institute's long-term study of compensatory mechanisms in fish populations (COMPMECH). Sampling is performed in cooperation with John Young and the Consolidated Edison Co., New York, Don Stevens and the California Department of Fish and Game, Bay-Delta Fishery Project, and Jim Bulak and the South Carolina Wildlife and Marine Resources Department. Evaluation of the implications on young-of-the-year dynamics of changes in female size distributions (e.g., due to alternative fisheries management strategies), as well as other factors that potentially influence striped bass recruitment, is a long-term goal of this integrated modeling and field project.

In addition to directed field sampling for spawning-related information, we also are re-examining historical data and, in some cases, initiating new field studies designed to provide data for model corroboration and testing. Corroborative data from each site are being collected and cataloged by life stages, cohorts within life stages, years classes and other appropriate units. Parameters of interest are tied directly to clearly defined life cycle units in the IBM and include:

(1) Abundance estimates of striped bass entering and leaving a particular life stage, cohort, or population unit.

(2) Size- and age-frequency distributions at the beginning and end of each cohort or life stage. New field sampling that focuses on time-varying size distributions of female spawners on the spawning grounds at each site has been initiated (1990).

Items (1) and (2) permit estimation of age/size and cohort-specific growth and mortality rates.

(3) Sex ratios and maturation schedules.

(4) Measurements of time-varying physio-chemical and biological parameters (prey levels) in spawning and nursery areas.

(5) Egg size distributions and appropriate measures of egg quality. (Field sampling initiated in 1990).

These data, where appropriate, will be used for either model input for hypothesis testing or for corroboration of model output to field observations.

Hypotheses about factors that potentially affect striped bass recruitment are location-specific. Besides experiencing wide environmental variability, striped bass populations at the directed sampling locations also vary widely in the level of exploitation and potential, or perhaps need, for management. Some of the factors that have been identified for development of recruitment hypotheses include:

1) Overfishing, changes in numbers and size distributions of spawning females (MD and SC),

2) Changes in spawning and nursery habitat including water temperature and flow regimes and productivity of food for larvae and juveniles (MD, SC, CA, NY),

3) Toxics and pollution, environmental degradation and low dissolved oxygen (MD, SC, CA, NY),

4) Water management and diversion from critical habitat (CA), and

5) Introduction of exotics (CA).

METHODS

Model Description

The striped bass IBM is described in detail in Rose and Cowan (submitted) and will be summarized here only briefly. The model begins with the spawning of individual females and simulates the growth and mortality of young striped bass as they develop through the egg, yolk-sac larva (YSL), feeding larva (LAR) and (JUV) early juvenile stages. The model represents these dynamics in a daily time step in a single, well mixed 1000m x 1000m x 4m compartment.

Each female's spawn of eggs is followed as an individual entity (i.e., female brood) through hatching and the yolk-sac stage. Then a random subsample of individual feeding larvae is followed through the remainder of the simulation. Length (L, mm), weight (W, mg dw), age (days), and lifestage are chronicled for each individual. The environmental conditions in the mixed compartment consist of daily water temperature (°C), fraction of the day there is daylight, and density (no. m^{-3} or m^{-2}) of zooplankton prey types.

Whenever possible, environmental and biological conditions in the model for this example have been specified using information derived from sampling in the Potomac River. This ensures that the site-specific environmental and biological conditions, that can co-vary in time and space in the River, are simulated in a realistic manner. For edification, a detailed description of female spawning and maternal effects on egg size is given (from Rose and Cowan, submitted). The remainder of the model description will be narrative except where more detail is critical to the readers' understanding of this study. Place markers of topics where specific data relevant to this study are lacking are denoted in the text.

Daily Temperature and Daylight: Daily temperatures from the striped bass spawning grounds on the Potomac River were used to fit the regression equation of long-term average temperature (T°C):

$$(1)\quad T = 14.79 - 12.02 * \cos (0.0172 * \text{day}) - 6.60 * \sin (0.172 * \text{day})$$

Stochastic realizations of daily temperatures around equation (1) were simulated by: 1) randomly determining with probability 0.5 whether a positive (above average) or negative (below average) run of temperature occurs; 2) randomly determining the magnitude (greatest absolute deviation from the long-term average) of the run from a gamma probability distribution; 3) specifying the duration (number of days) of the run from the magnitude (duration = 1.33 magnitude$^{1.41}$); 4) linearly interpolating temperatures between the beginning and end of the run such that the magnitude (peak) occurs at the midpoint of the run; and, 5) determining whether a neutral (no deviation from long-term average temperatures) or positive (if previous run was negative) or negative (if previous run was positive) occurs. These five steps are then repeated until an annual temperature series is generated. The fraction of the 24-hr day that is daylight (DL) is:

(2) $DL = 0.51 + 0.11 * \cos(0.0172 * (day-173))$ (Dalton 1987)

<u>Spawning of Females</u>: The model simulation begins with the spawning of 50 females (~0.05; 1000 m^{-2}); all are assumed to spawn (i.e., no mortality of females before spawning). We use a size distribution of spawners similar to the 1987-1988 period in the Potomac River as baseline (Figure 1). Thus, lengths of baseline spawners ranged from 503.3 to 979.5 mm SL, with a modal of 650.9. Large female spawners resembled the 1982 Potomac River spawning population ranging in length from 511.1 to 1284.6 mm SL, with a mode of 1037.8. Spawning temperature for each female, ranging from ~14 to 23°C (Setzler-Hamilton et al. 1980), is generated by a random deviate from a triangular distribution with:

(3)
$T°C\ minimum = 15.5 - 0.00305 * L_f$
$T°C\ mode = 20.0 - 0.0045 * L_f$
$T°C\ maximum = 24.0 - 0.0053 * L_f$ (MD DNR)

The temperature endpoints of the distribution, when related to female length (L_f, mm SL), result in larger females tending to spawn at lower temperatures (earlier in the spawning season) than smaller females, while smaller females show high variability in temperature at spawning (Figure 2).

Spawning of a female takes place on the first day: (1) temperature (T) exceeds the assigned temperature of spawning; and (2) there are three successive days of increasing temperature. Females not spawning on the first day T exceeds the assigned spawning temperature, spawn on the next available day that is the third of three consecutive days of increasing temperature.

Female weight (W_f, Kg wet weight (ww)) is derived from:

(4) $W_f = 2.27 * 10^{-8} * L_f^{2.94}$ (Westin and Rogers 1978)

The number (N_e) and averaged weight (W_e, mg dw) of eggs per female are determined from female weight (kg ww) by:

(5) $N_e = 218000 * W_f - 11700$ (Setzler-Hamilton et al. 1980), and

(6) $W_e - 0.00883 * W_f + 0.215$ (Zastrow et al. 1989).

<u>Development of Eggs and Yolk-Sac Larvae</u>: Each female's spawn of eggs is followed as a cohort through the YSL stage until the initiation of first feeding; development proceeds as a function of daily temperature (Boreman 1983). Upon initiation of first feeding, initial weights of LAR are determined from egg weights of each female cohort (Zastrow et al. 1989). Development rate of eggs and YSL are not related to egg weight-temperature combinations due to a lack of specific data. We here denote place marker 1 as a topic for needed research.

Mortality of Eggs and Yolk-Sac Larvae: The number of eggs, then YSL in each female's egg cohort is reduced daily by a fraction dying. Egg mortality is temperature-dependent and is based on a parabolic relationship between hatching success and temperature (URI 1976; Setzler-Hamilton et al. 1980; Morgan et al. 1981). When the temperature-dependent mortality rates fall below field estimates of egg and YSL mortality (Dahlberg 1979; Olney et al., in press), we simply add constant mortality terms to reconcile the field data and the model in lieu of specific information on size-dependent predation and other sources of egg and YSL mortality. We here denote place marker 2.

Initial Numbers and Sizes of First Feeding Larvae: A sub-sample of individual first-feeding striped bass larvae are taken from each female egg/YSL cohort and followed in daily time steps through growth and/or mortality. Larvae from each cohort are sub-sampled in proportion to the number surviving in the cohort compared to the total number of all survivors. For model simulations presented here, we follow 20,000 first-feeding larvae (LAR). Initial lengths and weights of LAR vary for female egg-cohorts as a function of female size; LAR sub-sampled from a given female egg cohort are identical.

Growth of Feeding Larvae: Daily growth of individual larva beginning with first feeding is represented with a difference form of a bioenergetics equation:

$$W_t = W_{t-1} + P * C_{max} * A - R_{tot} \quad (7)$$

where W_t = weight (mg dw) at time t in days,
C_{max} = maximum consumption rate (mg dw d^{-1}),
A = assimilation efficiency, and
R_{tot} = total metabolic rate (mg dw d^{-1}).

The proportion of C_{max} realized by a larva on a given day is:

$$P = \frac{C_r}{C_{max}} \quad \text{and} \quad (8)$$

$$C_r = \sum_{i=1}^{n} B_i * PW_i \quad (9)$$

where C_r = biomass (mg dw) of prey consumed,
B_i = number of prey type i eaten, and
PW_i = weight (mg dw) per individual of prey type i.

C_{max} is a function of weight and temperature. P is bounded by 0 and 1 because C_r is ≥ 0 and not allowed to exceed C_{max}. The summation over i prey types in computing C_r is performed via optimal foraging theory (Krebs 1978; Hughes 1980). Determination of the number of each prey type consumed (B_i) encompasses most of the computations of the model and is highly dependent on larva size and capabilities. Values for C_{max} (Cox and Coutant 1981; Moore 1988; Tuncer 1988; Chesney 1989; Houde 1989; Zastrow and Houde 1989), A (Ware 1975; Govoni et al. 1986; Tuncer 1988; Moore 1988; Zastrow and Houde 1989; Houde 1989; MacKenzie et al. 1990), and R_{tot} (Eldridge et al. 1982; Moore 1988; Zastrow and Houde 1989) are from the literature, adjusted for temperature effects following Hewitt and Johnson (1987).

Computation of p: p is computed based on encounters of a feeding larva with four zooplankton prey types. B_i is generated for each prey type and larva using a binomial distribution, dependent on the number of encounters and the capture probability.

Larvae are assumed to encounter patchy prey during the day. Mean number of encounters is calculated as the product of search volume (or area for JUV) and prey density, search volume (S_i) for LAR is the volume of a cylinder with radius equal to the larva's reactive distance (RD_i) and height equal to distance swam during daylight hours.

$$(10) \qquad S_i = \pi \cdot RD_i^2 * [\text{Distance}] * \frac{10^{-6}\ \text{liters}}{\text{mm}^3} \qquad \text{for LAR}$$

Distance swam, RD_i and, thus, encounters with prey items are related to larva length. Larger larvae swim faster and have a larger RD_i (lower angle of acuity) for a given prey size (Breck and Gitter 1983). We use a swimming speed of 0.63 body length's (BL) s^{-1} for LAR based on observations of free-swimming 8 mm striped bass larvae with food present at 20.0°C (Bowles et al. 1976).

RD is calculated based on the angle of acuity (α), formed between sides of a triangle from the larva's eye to the prey item, with each side of the triangle being RD_i and the base of the triangle opposite the eye being the height of the prey item. α is the minimum angle detectable by a larva and decreases with larva length (Guma 1982). Reactive distances specific to striped bass larvae, and the effect of turbidity on striped bass RD_i have not been determined. We here denote place marker 3.

Prey Capture: We use a single "capture probability" term (susceptibility, Bailey and Houde 1989) to encompass all of the events between encounter and ingestion. Capture probabilities are specified for each prey type, and are dependent on either larva age or length. We make capture success of small prey eaten just after first feeding (rotifers and copepod nauplii) a function of age to resemble a learning process; regardless of larva size, capture success increases with age. Capture success of larger zooplankton (adult copepods and cladocerans) eaten during the later portion of the LAR stage is a function of larva length to resemble physical development and ability; larger larvae have a greater capture success than smaller larvae regardless of age.

Temporal Dynamics of Prey: Densities or abundance of each prey type (number liter^{-1} for zooplankton, are updated daily based on: (1) number of prey consumed by fish larvae (in this case striped bass and white perch Morone americana): (2) how close prey densities are to equilibrium densities; and, (3) turnover rate. Seasonal equilibrium densities of zooplankton were determined from cumulative distribution functions based on Potomac River field data (Setzler-Hamilton et al. 1981; Houde et al. 1988). Turnover rates are estimated from temperature and prey biomass using a general regression relationship (Plante and Downing 1989) corrected for temperatures in the Potomac River.

Prey Consumption by Larvae: Zooplankton are consumed by striped bass as well as by white perch (Morone americana). Effects of white perch consuming prey are explicitly represented in the model because: (1) striped bass and white perch larvae are ecologically similar and share spawning and nursery areas (Setzler-Hamilton et al. 1981; Hjorth 1988); (2) white perch larvae generally outnumber striped bass (Setzler-Hamilton et al. 1980; Houde et al. 1990); and, (3) adequate information for model configuration with white perch in the Potomac River is available (Houde et al. 1990). White perch are treated as 10 size-cohorts (3-12 mm by 1 mm size intervals) whose bioenergetics are assumed to be similar to larval striped bass.

Mortality of Feeding Larvae: Mortality of individual LAR and JUV is a function of larva weight and length. Our representation of weight-dependent mortality is based on laboratory data at low food levels without predators (Rogers and Westin 1979, 1981; Eldridge et al. 1981, 1982; Chesney 1989) and therefore can be viewed as starvation related mortality. Length-dependent mortality is estimated from field data (Logan 1985) and represents predation or other losses such as transport and gear avoidance. In the model, a larva dies if its weight (mg dw) becomes less than some minimum weight at length at time t in days, which is a barrier at 0.65 of the weight predicted for the larva's length. Larvae are not allowed to lose length.

Length-based mortality is evaluated daily for each individual daily by:

$$M_L = \frac{1.25}{L} \qquad \text{(11)} \qquad \text{(Logan 1985)}$$

If a generated number from a uniform distribution between 0 and 1 is less than the probability of the larva dying, the larva is assumed to die. No explicit information is available on the sources of striped bass mortality and its size-dependence in the Potomac River. We here denote place marker 4.

Model Simulations

Four model simulations were performed to evaluate the relative effects of maternal contribution on recruitment variability of striped bass in the Potomac River. We compare combinations of baseline and large female spawners with day of spawning temperature-related or random. Egg production, larva mortality rates and size distributions of survivors on day 135 are compared between simulations. Day 135 is the earliest day of metamorphosis of larvae. We focus on spawning throuigh the larval period under the premise that recruitment success is established during that time (Houde et al. 1988; Uphoff 1989).

RESULTS AND DISCUSSION

The timing of female spawning, when related to female size and water temperature (i.e., when temperature rule is "on"), was similar in pattern for baseline and large model females (Figure 3). The temperature rule produced three spawning days by baseline females, with a peak occurring on day 112 (April 22) when 60% of the females spawned. Large females also spawned on three days but most spawning (64%) occurred on day 100 (April 10), approximately two weeks earlier than by the baseline females. When the temperature rule was toggled "off", model females spawned at random with no more than 16% of the females spawning on any one day in the simulation between day 100 and 121 (April 10 - May 1).

Discrete peaks in spawning and egg production by striped bass are typical of wild populations, Frequently, one to three sharp egg production peaks occur during a spawning season and account for a significant portion of total eggs produced (Johnson and Koo 1975; Combs 1979; Bulak et al., in press).

Egg production in the simulations varied as an increasing function of female size. Baseline females produced a total of 49,571,000 eggs compared to 159,680,000 produced by the large model females (Table 1), giving a 3.2-fold increase in egg production when the 50-fish spawning population contained a higher fraction of larger females.

Length-frequency distributions of surviving striped bass larvae (Figure 4) and numbers of survivors (Table 1) also differed between model simulations. In general, simulation results suggest that progeny from populations containing large females may grow faster on average, resulting in a higher survival rate (Table 1). A snapshot of the length-frequencies of larvae alive on day 135 (May 15) in each simulation (Figure 4) shows that larvae produced by large females were larger on that day. Mean stage duration, i.e., the time in days from first-feeding to 20 mm SL (metamorphosis) also was shorter for larvae spawned by large females (18.4 d) compared to 22.2 d for larvae from baseline mothers. Because the larvae from large females were larger and growing faster, the model predicts lower mortality ($\bar{X}$ = 0.167 d^{-1}) for these small striped bass as well (Table 1, compared to 0.194 d^{-1} for baseline).

The simulations further suggest that the interactive effects on spawning day and subsequent larva survival, of female size and water temperature (i.e., when the rule is toggled "on") are complex. Larvae surviving on day 135 from baseline mothers who spawned at random were larger than those produced by baseline mothers spawning by the temperature rule (Figure 4), despite a small difference in mean spawn date between simulations. The opposite is true for large females, however, as larvae were larger on day 135 in the simulation when female spawning day was determined by the temperature rule. These large larvae also were older as mean spawn day in simulations with large females differed by 5 days due to the temperature rule (Table 1). Survivorship increased slightly when females spawned at random in both cases (Table 1), but mortality rates in simulations with large females were similar.

Model simulations also indicate that the increased survivorship when more large females are present is not merely a function of increased egg production. The ratio of numbers of larva survivors to metamorphosis from large and baseline females, respectively, was 3.5:1, which is higher than the 3.2-fold increase in egg production obtained in the model runs. When large and baseline females spawned by the temperature rule, the ratio of survivors to metamorphosis was 3.6:1, further illustrating the complex interaction between female size, spawning temperature and larva survivorship.

Wherever they occur, striped bass populations are year-class dominated, and depend on a strong recruitment every 5-10 years to maintain spawning stock and spawning potentials (Van Winkle et al. 1979; Goodyear 1989). Density-independent, environmental factors have most often been implied to cause high mortalities of striped bass eggs and influence growth and survival of larvae (Ulanowicz and Polgar 1980; Rogers and Westin 1981; Chesney 1989; Uphoff 1989. Logan (1985) and Houde (1987, 1989) also have examined data on striped bass growth and have discussed the implication of variable larva growth rate on recruitment success. Results from these studies suggest that variability in larva stage duration may be important and that significant error in mortality estimates may be generated if constant stage duration is assumed.

Although these preliminary results for Potomac River striped bass are inconclusive, they show that the effects of female size, timing of spawning and maternal contribution on recruitment dynamics potentially are important and warrant further research.

Plans for the Future

We have used this Potomac River example to illustrate our approach to the striped bass recruitment problem. Available process-oriented information, mostly from the published literature, has first been organized in the form of an individual-based population model of striped bass. Major gaps in data are recognized. We are now acting to fill in gaps through a prioritized, directed field sampling program at several locations that is organized by the individual-based model. It is too early to measure the success of these efforts but the outlook appears promising. Field collection sites span the striped bass' range of environmental variability, as well as variability in levels of exploitation and potential for management. We hope to use the model, field-collections and management alternatives in an iterative manner for several years to come to increase the understanding of factors affecting recruitment of striped bass.

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TABLE 1. Summary of results of individual-based model simulations of striped bass spawning and larva growth and mortality in the Potomac River, MD. Baseline spawners have a modal length of 650 mm compared to 1000 mm SL for large females.

Simulation	Mean Day of Spawn	No. of Eggs Produced	Fraction of Larvae Surviving to Metamorphosis	Mean Stage Duration	Mortality Rate (d^{-1})
Baseline and Temperature Rule	109.72	4.96×10^7	0.0115	22.5	0.198
Large and Temperature Rule	104.60	1.60×10^8	0.0418	18.8	0.169
Baseline and Random	109.48	4.96×10^7	0.0159	21.9	0.189
Large and Random	109.48	1.60×10^8	0.0530	17.9	0.164

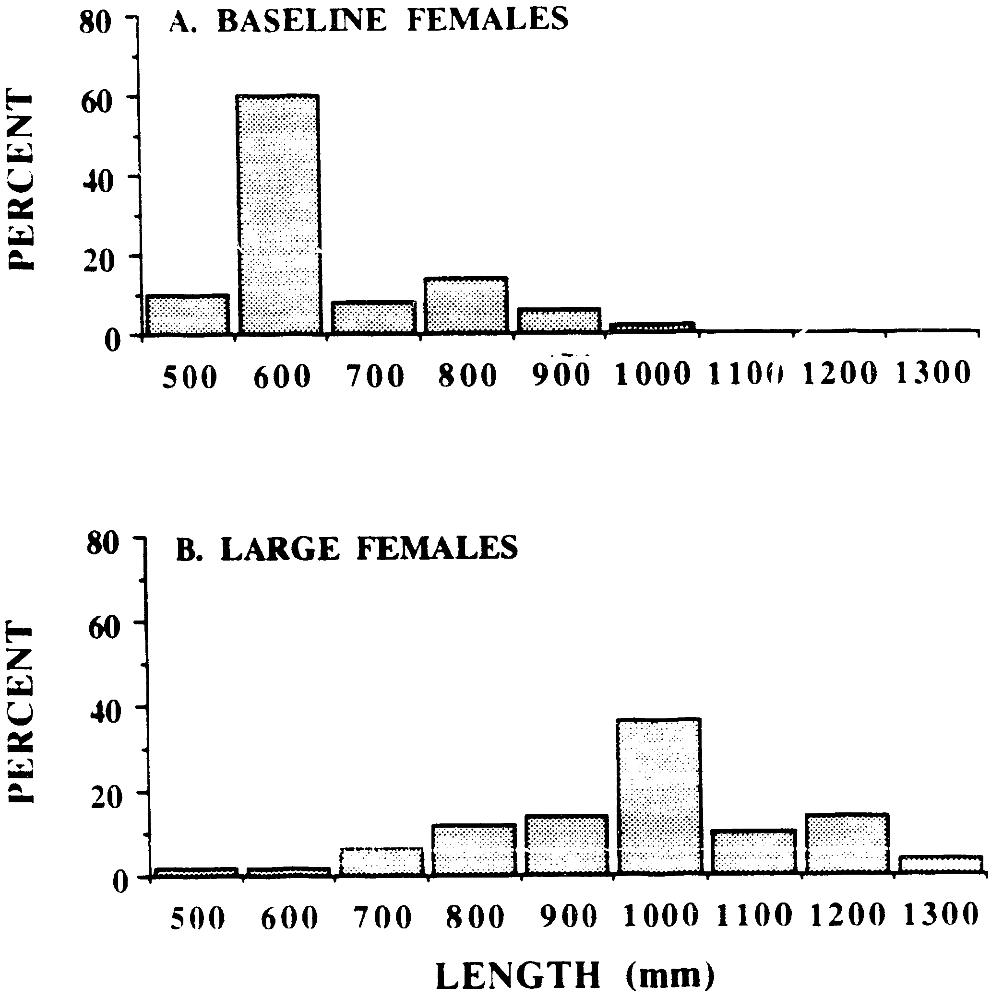

Figure 1. Length-frequency distributions of female spawners used in individual-based model simulations to evaluate the effect of maternal contribution on recruitment dynamics of striped bass. Modal length of baseline females was 600 mm SL compared to 1000 mm SL for large spawners.

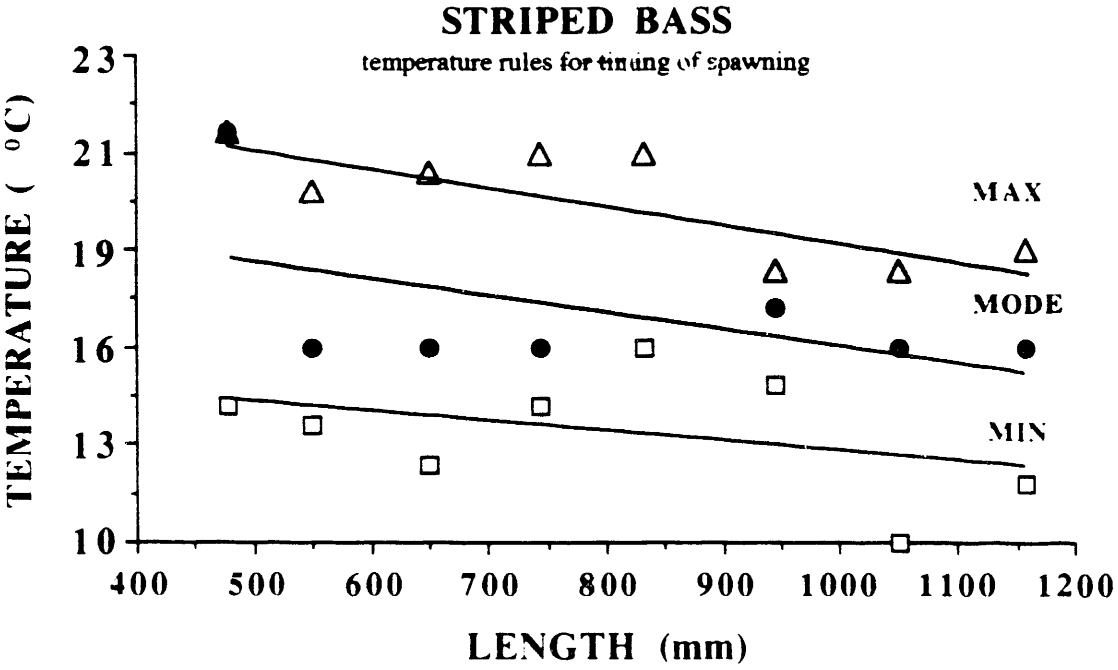

Figure 2. Summary of Potomac River, MD data used to generate the rule relating size of female spawners to temperature in simulations employing an individual-based model of striped bass life history.

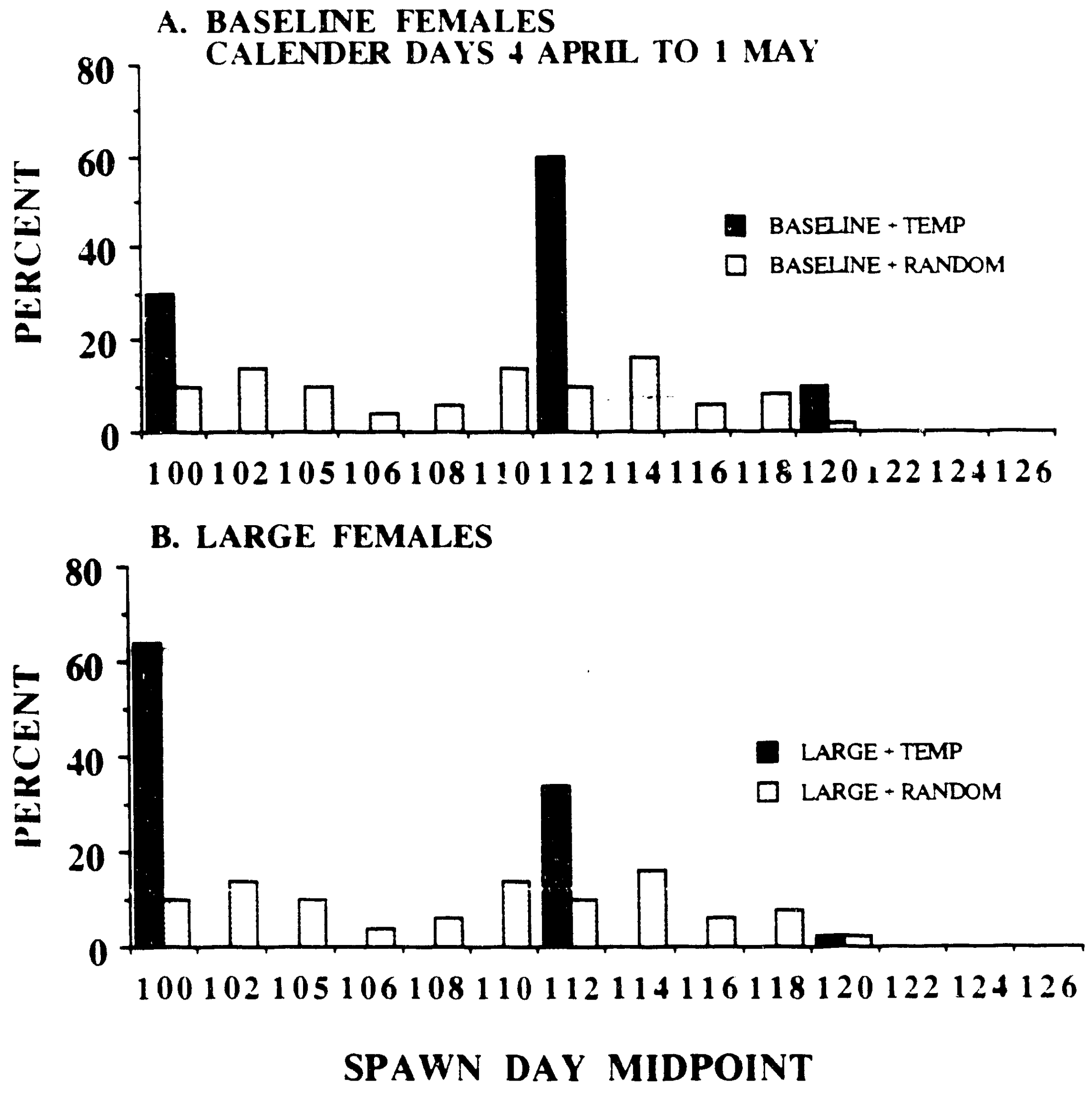

Figure 3. Spawn day-frequency of baseline and large striped bass females in individual-based model simulations with and without a temperature rule relating female size to day of spawning.

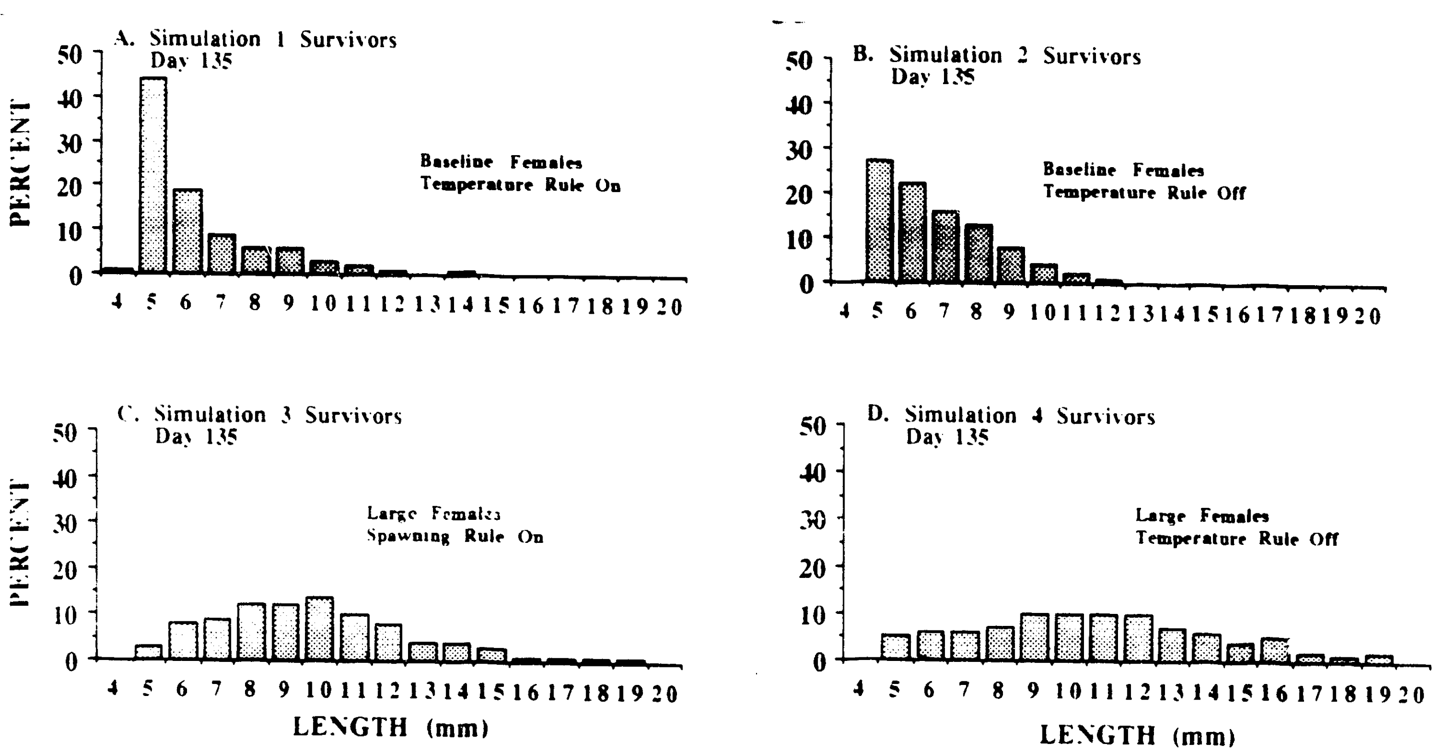

Figure 4. Length-frequency distributions of larvae alive on day 135 in individual-based model simulations of striped bass in the Potomac River, MD. Size of female spawners (baseline and large) and spawn day were altered in the simulations.

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