

A model of survival and growth of striped bass larvae *Morone saxatilis* in the Potomac River, 1987

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ABSTRACT: A Stella™ model based on laboratory-derived growth data was developed to simulate abundances, cohort survival and growth rates of striped bass eggs and larvae. The goal was to compare the simulations to 1987 field survey results from the Potomac River (Chesapeake Bay, USA). Key factors in the model were striped bass egg production, water temperature, surface light and penetration, turbidity and zooplankton concentration. Growth and survival were simulated from the predicted effects of turbidity, light at depth, and zooplankton concentration. Predation terms simulated survival under different predation pressures. The model estimated daily instantaneous growth rates ranging from -0.07 to 0.19 d^{-1} . The model predicted poor survival and growth of cohorts produced early in the spawning season when water temperatures and zooplankton concentration were low. Mortality of eggs was predicted to be 54% by simulation with most of the mortality attributable to low temperatures early in the spawning season. Simulated growth rates ranged widely and were highest in the down river sections of the Potomac. Predicted growth was in close agreement with field estimates during the second half of the spawning season. Early in the season, field growth rates were higher than those modeled, possibly because survival was more growth-rate dependent at that time than later when temperature, light and food levels were nearer to optimum. Trends in simulated larval abundances resembled Potomac River estimates but there were differences in simulated peak abundances. Mortality was partitioned and attributed to causes other than that caused by low temperature anomalies and growth-dependent factors. The difference between modeled and field observed larval abundances estimated a rate of mortality for 'other' causes at $13.7\% \text{ d}^{-1}$, a rate that can readily be attributed to predation.

INTRODUCTION

During the 1970's and 1980's populations of striped bass and other anadromous species that spawn in Chesapeake Bay (USA) tributaries declined. Seining surveys for juvenile striped bass by the Maryland Department of Natural Resources indicated that declines probably are the result of poor survival during the first 60 d of life (Boone 1980). Many potential causes for population declines of Chesapeake striped bass have been proposed and studied, including overfishing (Goodyear 1985), disease, pollution (Hall et al. 1985, Westin et al. 1985, Hall 1991), acid precipitation, starvation (Martin et al. 1985), predation (McGovern & Olney 1988) and habitat loss, alteration or deterioration (Coutant 1985, Price et al. 1985, Coutant & Benson 1990). Some hypotheses have been

tested and discounted as major causes of the declines while others are difficult to test directly. A moratorium was imposed on fishing of striped bass in the Maryland portion of Chesapeake Bay in 1985. These restrictions brought about a resurgence of stock within Chesapeake Bay suggesting that fishing pressure may have played a significant role in the declines. A thorough understanding of how survival and growth are influenced by natural environmental variables (i.e. food resource, temperature, light, predation) would help to interpret observed mortality patterns of larval stages in the spawning tributaries of the Chesapeake as well as in other river systems and tributaries where striped bass have experienced poor recruitment in recent years.

A model utilizing laboratory and field-derived data was undertaken to address the question of how natural

environmental factors might affect growth and survival of striped bass larvae. One of the primary goals of this study was to determine if laboratory-derived survival and growth data could be used to simulate or predict growth and/or survival rates that were observed in a 1987 field survey in the Potomac River (Houde et al. 1988a, b, Rutherford & Houde 1992). If predicted growth rates resembled those of larval cohorts in the field, it might be possible to determine the relative importance of water temperature declines, food concentration and other mortality factors that are known to influence the survival of striped bass early life stages. The model focused on 2 principal questions: (1) What are the simulated attrition rates of striped bass due only to temperature-related and growth-related (i.e. food-dependent) mortality? (2) What rates of mortality must be attributed to other potential factors, such as predation or toxicants, that could account for the total mortality and patterns of abundance observed in the Potomac River during the 1987 spawning season?

THE MODEL

A modeling software called StellaTM was used to develop the model. The model has 3 basic subunits which functioned to simulate growth and survival of striped bass larvae: (1) an egg production, egg mortality and hatching subunit; (2) a larval growth subunit; and (3) a larval development and mortality subunit.

Egg production subunit

The egg production subunit utilized the daily egg production estimates (Houde et al. 1988a) for a given river segment and hatches eggs based upon the ambient temperature on the day they were spawned. On any given day an egg may hatch, die or continue to incubate. Once hatched, eggs were allocated to cohorts. The importance of low temperature anomalies to striped bass egg survival has been described based on field observations (Dey 1981) and has been modeled (Boreman 1983). Temperature or predation can cause mortality of eggs in the field. Laboratory studies demonstrated that some mortality of striped bass eggs and larvae can occur at temperatures below 14 °C and that near-total mortality occurs below 12 °C (Morgan et al. 1981). In this model, mortality from low temperature was set at 25 % d⁻¹ at 12 to 13 °C and at 100 % d⁻¹ below 12 °C. An egg mortality term due to predation was incorporated into the egg production subunit that could be varied as desired.

Larval growth subunit

The larval growth subunit was replicated 38 times in the model to follow growth of the first 38 daily cohorts. This corresponded to the period when 99 % of the egg production occurred in 1987. Whatever eggs were available to hatch on a given day in a particular river segment were allocated to a single cohort. Growth was assumed to begin at 6 d posthatch when a striped bass larva normally begins to feed. Growth rate was dictated by the ambient conditions of food, turbidity and light in a given river segment on a particular day. The model assumed that all larvae within a given river section were subjected to the same mean environmental conditions on a given day.

Larval development and mortality subunit

Survival of a cohort was followed in each of 8 river segments over time. Stations and river segments that they represent are given in Fig. 1. Mortality terms were included (as in the egg production unit) which 'kills' larvae due to low temperature anomalies and predation. A third factor applied to account for larval mortality was a growth-dependent mortality term that was not designated to be density-dependent. The reason for including the growth rate-dependent mortality term was that, while growth variability was significant in laboratory studies among striped bass larvae exposed to essentially identical conditions (see Fig. 7 in Chesney 1989), mortality and growth rates were inversely correlated in laboratory experiments (Chesney 1989). A regression of the mortality rates from all experimental treatments against daily instantaneous growth rates provided estimates of growth-rate-dependent mortality which was allowed to reach a maximum value of 0.06 d⁻¹, the maximum rate observed in starvation experiments in the laboratory (Fig. 2).

Model assumptions and data inputs

The following data inputs, simplifying assumptions and equations were used to construct the model:

(1) River temperature was based on mean riverwide temperatures during each ichthyoplankton survey and from daily measurements made by Occoquan Associates near river segment 7. In the model river temperature was assumed to be uniform over the entire spawning and larval nursery area on a given day. The river temperatures are included in Houde et al. (1988a) as their Fig. 4 and their Appendix Table 8A.

(2) Zooplankton concentrations (no. l^{-1}) and turbidities (NTU's) were input from the 1987 Potomac River sampling program (Houde et al. 1988a). Values were estimated at approximately weekly intervals at each station at the surface, mid-depth and bottom. In the model, values were averaged for the 3 depth intervals and assumed to change linearly from one sampling date to the next. Fig. 3a, b shows the temporal and spatial trends in the mean concentration of nauplii, cladocerans and copepodite and adult copepods. Zooplankton data were input as the mean concentration of all zooplankters, minus rotifers, in the lower two-thirds of the water column. Turbidity was input as the mean of surface, mid-depth and bottom values at each station. Zooplankton data are summarized in Houde et al. (1988a) as their Figs. 19 to 24. Turbidities are summarized in Houde et al. (1988a) as their Appendix Table 11A.

(3) Weekly sampling provided estimates of striped bass egg densities (number per m^3) in the river over time. The densities were used to estimate daily egg production in 4 subsections of the river (Houde et al. 1988a). For the model, daily egg production estimates were input for each sampling station in the river in 2 different ways: as flat distributions allocated evenly between sampling periods and as normally distributed values with peaks on sampling dates. This was done because the egg production method originally applied to these data allocates egg production evenly over the days between sampling dates. Actual spawning events are likely to produce sharp peaks of activity in response to warming trends, which can be more readily approximated by a normal distribution.

Hatching times of striped bass eggs are a function of water temperature (Rogers et al. 1977, Morgan et al. 1981). Hatching times were estimated using the equation of Rogers et al. (1977)

$$D = 10.77 e^{-0.0934T}$$

where D = development time (d); T = water temperature ($^{\circ}C$).

(4) Depth-stratified sampling in the Potomac River in 1987 provided information on abundance and depth distributions of striped bass larvae (Tables 19 & 20A and Fig. 18 in Houde et al. 1988a). Samples were

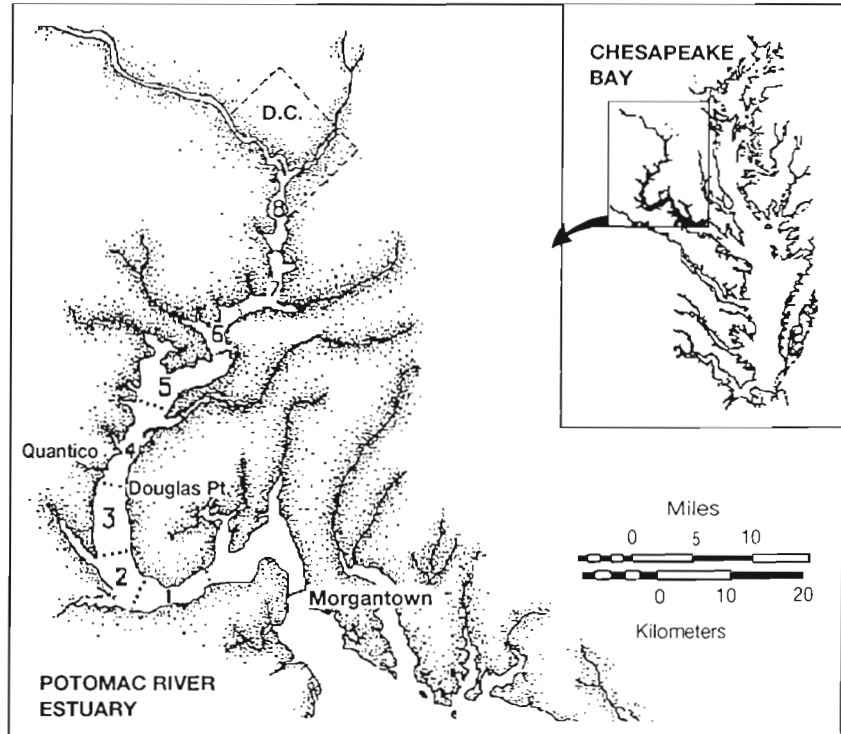


Fig. 1. Eight River segments of the Potomac River that were sampled in 1987 and simulated in this study

collected at the surface, mid-depth and near-bottom with an opening-closing net. In the field survey, almost all of the striped bass larvae were collected in the lower two-thirds of the water column. Thus, for purposes of the model all striped bass larvae were assumed to have been in the lower two-thirds of the water column throughout their growout period. Because little is known about the specific behavior of a larva with respect to its vertical distribution over time or how it might change with age, simulated depth or

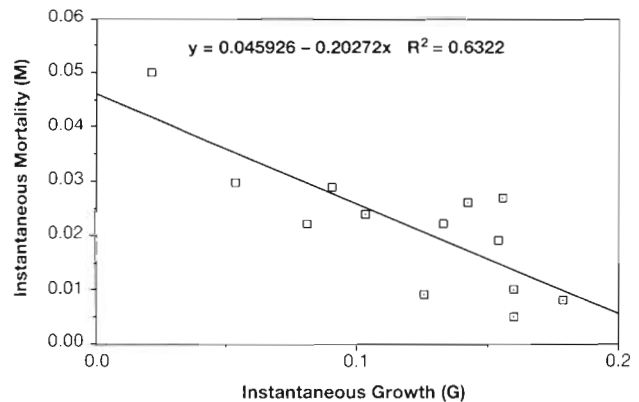


Fig. 2. Regression of daily instantaneous mortality (M) versus daily instantaneous growth (G) for striped bass larvae. Data are from laboratory growth experiments (Chesney 1989)

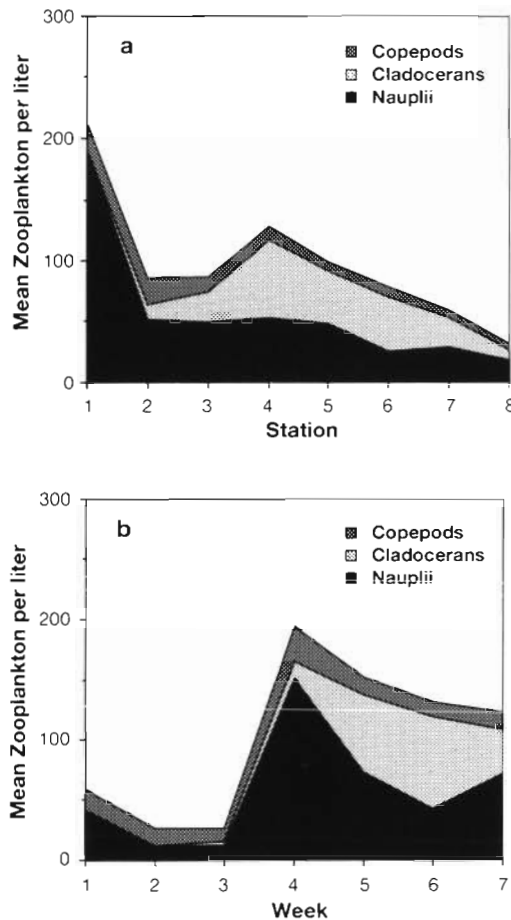


Fig. 3. Mean concentration of nauplii, cladocerans and copepodites and adult copepods in the Potomac River during the 1987 striped bass spawning season. Values are reported as number per liter (a) for all dates by station and (b) river-wide over time

location of individuals within a cohort was input in 2 ways. In the first simulation, depth was input as the mean depth of each river segment and assumed to be constant. In subsequent runs, depth was input as a standard normal deviate, which allowed the average depth of the larval cohort to vary randomly from day to day within the lower two-thirds of the water column.

(5) The availability of light for feeding is known to be a critical factor affecting feeding, growth and survival of fish larvae (Blaxter 1966, 1986, Kiyuno & Hirano 1981, Dabrowski 1982, Bagarinao & Hunter 1983), including striped bass (Chesney 1989). In the field, light attenuation is affected by the ambient light field, turbidity in the water column, the amount of cloud cover and depth of the water column. These variables were incorporated into the model to obtain an estimate of the mean daily light available for prey perception by a cohort of feeding larvae, assuming that the average larvae resided at some mean depth within

the lower two-thirds of the water column. This was implemented in the model by deriving 2 empirical relationships.

First, mean daily light levels (Einsteins d^{-1}) were input from data collected with a Licor radiometer located at the Benedict Estuarine Research Laboratory (J. Sanders pers. comm.). Because we had no records of incident solar radiation for each day of the spring 1987 spawning season and because it would be useful if the model were general enough to be used in years when no light measurements were taken, it was necessary to derive a relationship to predict surface light levels on any day based on a readily available index.

NOAA weather data at National Airport, adjacent to the Potomac River, provided estimates of percent cloud cover derived from minutes of sun per day (cloudless daylight). These were regressed against total daily radiation in Einsteins $m^{-2} d^{-1}$ to predict surface illumination for any given day (Fig. 4). This regression equation estimated the mean surface irradiance (Einsteins $m^{-2} d^{-1}$) given the reported cloud conditions on a given day of the spawning season.

The second factor to be considered before light at depth could be predicted was attenuation due to ambient conditions within the water column. Light extinction in the Potomac River is primarily a function of depth and turbidity. Extinction coefficients estimated from field measurements of light penetration were regressed against turbidities (Fig. 5) to provide an estimate of light at depth for any station and depth on a given day.

(6) Two empirical equations were derived to estimate daily instantaneous growth-in-weight rates. These empirical relationships were developed based on laboratory growth studies (Chesney 1989). These studies were used because they were conducted with Chesapeake Bay striped bass, they addressed most of the variables relevant to the model and they were the only studies of growth conducted to date at food densities typical of the Potomac River and with a natural prey species of striped bass larvae (e.g. the copepod *Eurytemora affinis*). Growth rate of a striped bass larva can be strongly influenced by light, turbidity and food concentration (i.e. zooplankton) at a station for a particular day and depth. Data from laboratory studies of growth were used to set the limits for the interaction of light and zooplankton concentration. Below light levels of approximately $2.5 \mu E m^{-2} d^{-1}$, the influence of light on growth rate of striped bass larvae is dramatic (Chesney 1989). In the model it was assumed that at light levels $> 2.5 \mu E m^{-2} d^{-1}$ and zooplankton densities $> 50 l^{-1}$, growth was dependent upon food concentration alone. Below light levels of $2.5 \mu E m^{-2} d^{-1}$ growth was assumed to be dependent upon both light and food, and a term was added to the light equation to

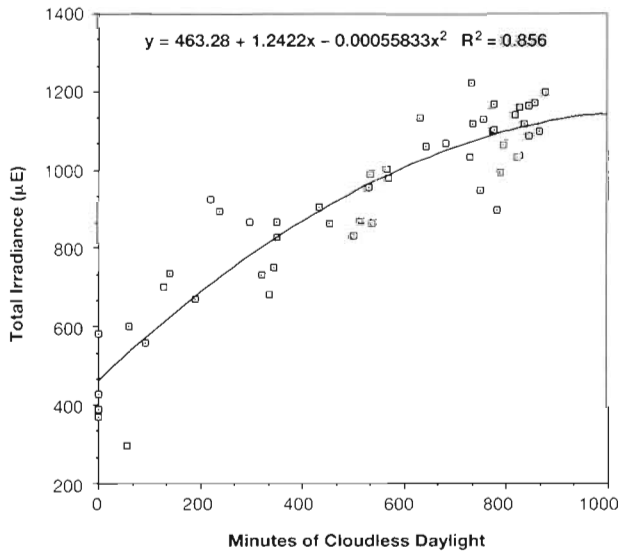


Fig. 4. Minutes of cloudless daylight plotted against total daily irradiance ($\mu\text{E m}^{-2} \text{d}^{-1}$) for May 1987. (Data courtesy of NOAA weather and J. Sanders, Benedict Estuarine Laboratory)

correct for food concentration effects. The model assumed that food concentration effects had a proportional influence on growth that was the same regardless of the amount of light available. It was also assumed that weight loss could be no greater than the maximum observed in laboratory starvation experiments (i.e. $-7.0\% \text{d}^{-1}$) (Chesney 1989). In the laboratory experiments where light intensity was manipulated (Chesney 1989), no food concentrations below 50 l^{-1} or above 250 l^{-1} were tested. Effects of food concentrations between 0 and 50 l^{-1} on growth rate were assumed to be linear. Based upon the approximate upper limit observed for laboratory and field observations of larval striped bass growth (Houde & Lubbers 1986, Houde et al. 1988b, Chesney 1989), an upper limit of 0.19 d^{-1} was placed on the daily instantaneous weight-specific growth coefficient.

The mean length of larvae in a cohort was estimated from the larval weights projected in the model. A length-wet weight regression derived from laboratory-cultured striped bass was used to convert weight to length where:

$$\text{Length (mm SL)} = 5.942 \text{ Weight}^{0.2387}; R^2 = 0.98, N = 50$$

Runs of the model were integrated on a daily basis over a period of 60 d. This allowed an evaluation of striped bass growth and survival during the period encompassed by the 1987 sampling program (April 12 to June 10, 1987). The model simulated the number of larvae remaining in a cohort over time, the estimated and mean wet weights (mg) and corresponding lengths (mm). Each station was represented by a single configuration of the model with the unique input data

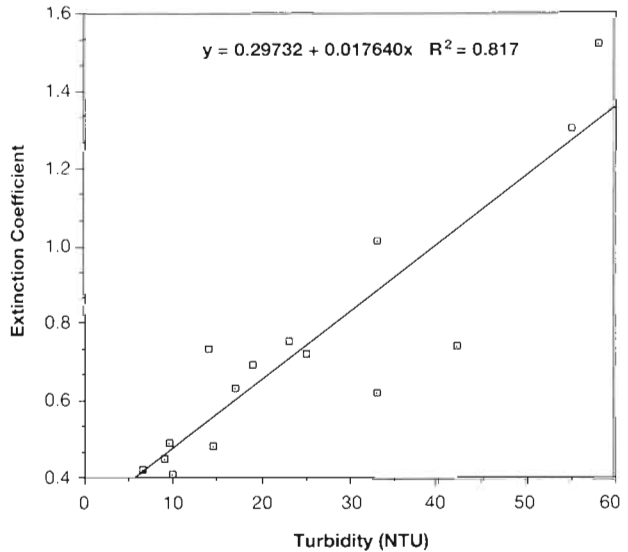


Fig. 5. Regression of extinction coefficients of light versus turbidity. Data are from the 1987 survey of the Potomac River (Houde et al. 1988a)

for that river segment. Data from 8 runs of the model were compiled to evaluate riverwide trends in abundance and growth over time. In the initial runs instantaneous predation loss rates (Z) were set at 0.0513 d^{-1} for eggs and 0.0253 d^{-1} for larvae (5 and 2.5% d^{-1} , respectively). Higher rates of Z were assigned for subsequent runs to evaluate potential predation effects.

RESULTS

The projected instantaneous growth rates of striped bass larvae in the 8 river segments of the Potomac River for the entire spawning season indicated significant differences among sections, particularly early in the season (Fig. 5). In the model, growth rates were projected for all sections of the river system based upon known environmental conditions and regardless of whether larvae were actually present or not. The initial run assumed that larvae resided at the mean depth in each river segment. The second run assumed that larvae randomly varied their location about the mean depth in the lower two-thirds of the water column. The assumptions were reasonable because sampling effort was concentrated in the channel of the Potomac River, which is considerably deeper than the mean depth in each river segment and almost all larvae collected in 1987 were in the lower two-thirds of the water column at those stations (Houde et al. 1988a). Growth rates (G) were similar under the 2 assumed depth distributions. Differences in the station mean G under these 2 assumptions ranged from 0.0013 to 0.016 d^{-1} . Overall mean growth rate was 0.0041 d^{-1} lower when larval

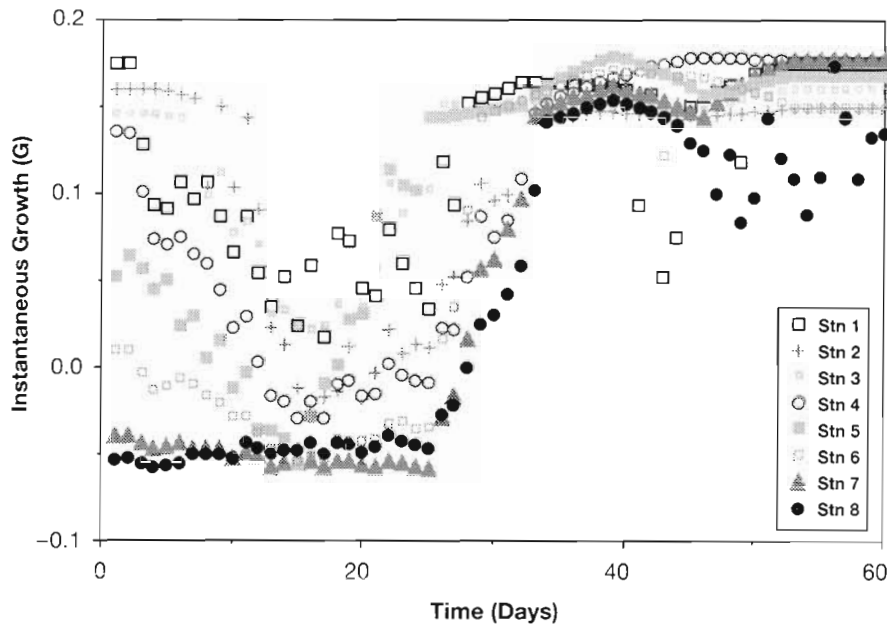


Fig. 6. *Morone saxatilis*. Simulated weight-specific daily instantaneous growth rates (G) for cohorts of striped bass larvae in the Potomac River, 1987. Depths of larvae were input as a standard normal deviate of the mean depth in the lower two-thirds of the water column of each of the 8 river segments

depth was input as a random normal deviate. Therefore only the results from the randomly varied run are shown (Fig. 6).

The simulations generated daily growth rates (G) that covered the entire range of the model from -0.07 to 0.19 d^{-1} . The instantaneous growth-in-weight rates clearly indicated that growth conditions were most favorable in the second half of the spawning season during 1987. In the first half of the spawning season, growth conditions generally were more favorable in the downstream section (Stns 1, 2 & 3) and highly unfavorable in the upstream section of the river (Fig. 6).

Simulated cohort-specific growth rates varied both temporally and spatially. Cohorts produced earliest in the season generally had lower growth rates than those produced later. The slowest average growth rates were predicted for early cohorts in the river segments represented by Stns 2, 6, 7 & 8. Cohorts produced later were predicted to grow faster, with only minor differences among river segments. The peak growth rates were predicted for cohorts produced near the middle of the spawning season and were uniformly high at all the stations (Figs. 6 & 7).

Riverwide 3-day cohorts were reconstructed with growth data generated by the model and predicted cohort lengths at 30 d posthatch were compared to the estimates from 1987 field sampling (Houde et al. 1988b). These estimates were expressed as mm d^{-1} and converted to 3-day cohorts so they could be compared directly to the field estimates that were grouped and expressed in length. Cohorts produced early in the spawning season (Cohorts A to E) did not survive in sufficient numbers in the field to be compared to the model estimates of growth.

The field estimates of length at 30 d after hatch, which were derived from otolith-aging (Houde et al. 1988b), showed a similar trend for both the model results and the field, however specific cohorts did not always follow the pattern predicted by the model (Fig. 7). During the middle of the spawning season (Cohorts F, G & H) field growth estimates were highly variable and generally

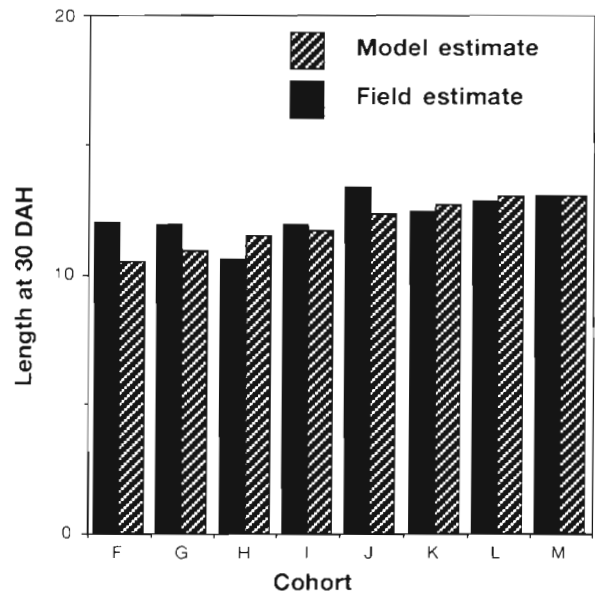


Fig. 7. *Morone saxatilis*. Riverwide comparison from field studies and model simulated growth in length at 30 d after hatch (DAH) of striped bass larval cohorts for the Potomac River, 1987. Cohort F was hatched on 25 April and Cohort M on 16 May 1987. Larvae were simulated to randomly vary about the mean depth of the river segment

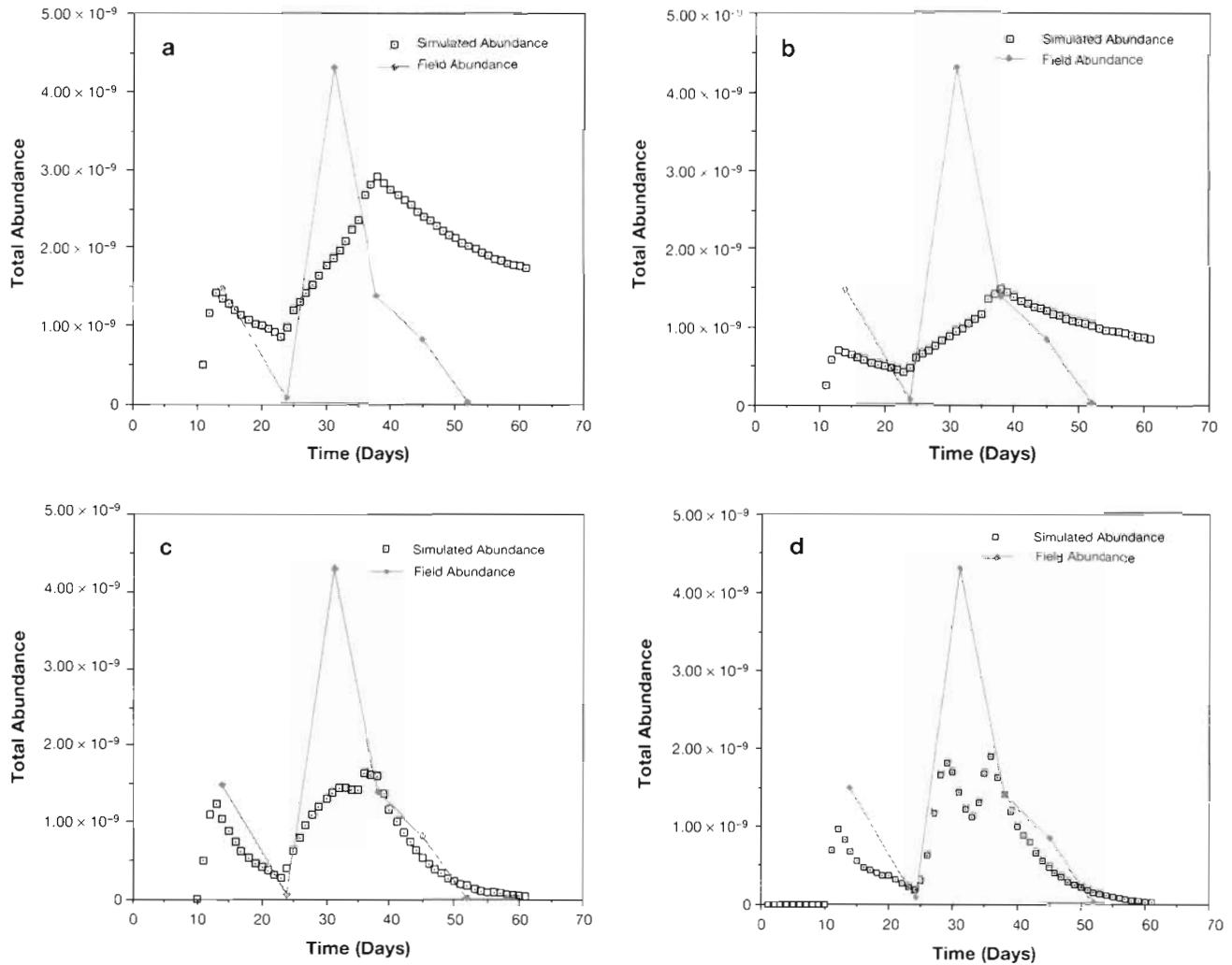


Fig. 8. *Morone saxatilis*. Simulated (squares) and estimated abundances (line) of striped bass larvae in the Potomac River during the 1987 spawning season. (a, b) Simulations comparing a 100 % (a) and 50 % (b) hatchability of eggs. Both simulations were assigned an egg predation rate of 5 % d^{-1} and a larval predation rate of 2.5 % d^{-1} . (c, d) Simulations assuming a 100 % hatchability of eggs. Both simulations were assigned an egg predation rate of 5 % d^{-1} and a larval predation rate of 13.7 % d^{-1} . Simulation in (d) was as (c), but with egg production estimates input as normal distributions. In all simulations larval depth was input as a standard normal deviate about the mean of the lower two-thirds of the water column

exceeded the model estimates (Fig. 7). For the later spawned cohorts growth generally showed excellent agreement between the model and field estimates (Cohorts I, K, L & M) (Fig. 7). The modeled and field estimates of growth for Cohort J, which was spawned near the middle of the season, differed considerably. Field estimates of early season growth rates tended to be higher than those projected in the model. The modeled lengths of cohorts at 30 d post-hatch increased consistently as the season progressed. The field estimates also tended to increase for cohorts hatched later in the season, but results were variable (Fig. 7).

The estimated abundances of striped bass larvae during the sampling season in the Potomac River (from Table 16A in Houde et al. 1988a) were compared with

those simulated in the model under 3 sets of model conditions. First, abundances were projected assuming 100 % viability of eggs that were not killed by predation or low temperatures and assigning modest predation rates (5.0 % d^{-1} for eggs and 2.5 % d^{-1} for larvae) (Fig. 8a). Second, simulated results assumed the same predation rates but a 50 % egg viability (Fig. 8b). Third, abundances were simulated assuming 100 % egg viability but a higher predation rate (13.7 % d^{-1}) in the larval mortality subunit (Fig. 8c). The fourth simulation retained the input parameters from the third run except that egg production was input as normal distributions rather than the flat distributions established in the egg production studies of Houde et al. (1988a) (Fig. 8d).

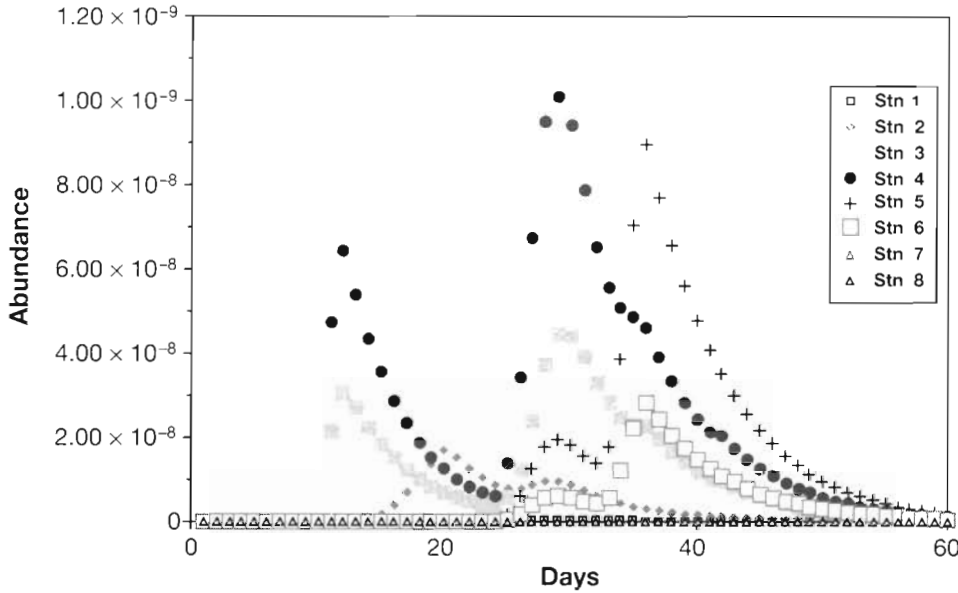


Fig. 9. *Morone saxatilis*. Simulated abundances of striped bass larvae, by station over time. Assigned predation mortality for this simulation was 5.0 % d⁻¹ for eggs and 13.7 % d⁻¹ for larvae

All of the simulated abundances (Fig. 8a, b, c) followed a pattern similar to that observed in the field although peak abundances in the model outputs were lower than the field estimates and lagged it by several days. The discrepancies between the estimated larval abundance and the 2 simulations that assumed low mortality of eggs and larvae from predation (Fig. 8a, b) indicate that predation or 'other' unidentified sources of mortality were higher in the Potomac River in 1987 than in the simulations. Only the Fig. 8c & d output, which included the high assumed predation rate on larvae, closely tracked the actual estimated abundances over most of the spawning season. The Fig. 8c simulated abundances resemble those observed in the Potomac River, except that the peak abundance was lower and lagged the field estimates. With egg production input as normal distribution the lag in peak abundance was eliminated and the simulated peak abundance was increased slightly (Fig. 8d).

Patterns of abundance by station reflected the importance of the middle stations for spawning (Stns 3 to 6) and survival (Stns 2 to 7) (Figs. 9 & 10). Under the assumption that temperature was the principal catastrophic mortality factor acting on striped bass eggs in the Potomac River, percent mortality in the egg stage in 1987 was projected to be highest in river segments 3, 4, 7 & 8. This result was due primarily to the low temperature anomaly that occurred early in the spawning season and the relatively high egg productions at those stations at that time. Egg mortality, mostly due to low temperature effects, killed 54 % of the total simulated egg production compared to an estimated 60 % actually observed in the Potomac River during 1987 (Houde et al. 1988a).

Simulated survival rates of cohorts produced early (Cohorts 1 to 19) and later (Cohorts 20 to 38) in the spawning season differed substantially. Early cohorts experienced poor predicted survivals while those produced later, when temperature and food levels were high, had high predicted survival rates. The highest predicted survival rates were in river segments represented by Stns 1 to 4 for Cohorts 20 to 38, primarily because zooplankton concentrations, light levels and temperatures had increased to more favorable levels in those parts of the river. Although survival rates were low for Cohorts 1 to 19, their best survivals were predicted in river segments represented by Stns 5 & 6,

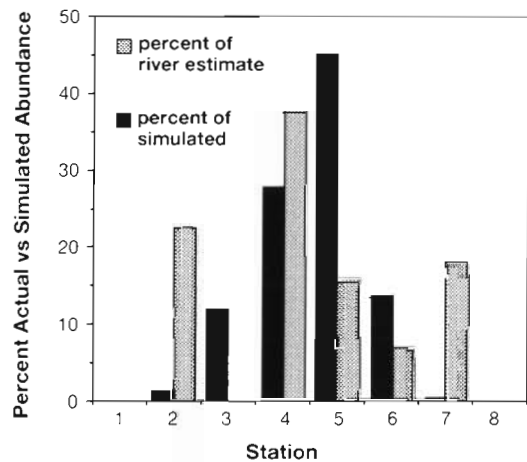


Fig. 10. *Morone saxatilis*. Riverwide comparison from field studies and model simulated percent survival of the total striped bass larvae remaining after the first 60 d of the spawning season in the Potomac River, 1987. Assigned predation mortality for the simulation was 5.0 % d⁻¹ for eggs and 13.7 % d⁻¹ for larvae

primarily because of the relatively high light and food levels that occurred there early in the season.

In the initial run of the model, relatively low values for predation were input. Under the condition where assumed predation mortality on larvae was $2.5\% \text{ d}^{-1}$, the total instantaneous mortality rate (M) in the initial simulation averaged only 0.0361 d^{-1} ($3.5\% \text{ d}^{-1}$) for the last 40 d of simulation. During that period low temperature was not a mortality factor and growth conditions were favorable. Having simulated M and having an estimate of larval abundance in the river (Houde et al. 1988a), the additional mortality that must have occurred from 'other' sources was calculated in order to account for the difference between the field estimate and the model. The additional instantaneous mortality required to account for the difference was estimated to be 0.1220 d^{-1} (11.5%). Total instantaneous mortality rate was 0.1581 d^{-1} (14.6%), i.e. $0.1220 + 0.0361$, and the probable predation or 'other' mortality plus growth-dependent mortality estimated to be 0.1474 ($13.7\% \text{ d}^{-1}$) + 0.0108 ($1.0\% \text{ d}^{-1}$).

DISCUSSION

The model focused on 2 major questions: (1) What are the simulated attrition rates of striped bass due only to factors such as low temperature anomalies and growth-dependent mortality? (2) What rates of mortality must be attributed to other factors, for example predation or toxicant mortality, to account for the larval abundances observed in the Potomac River in 1987? Before the questions could be addressed, it was necessary to determine if laboratory-derived data could predict growth in the field.

There is a degree of uncertainty in estimating growth of striped bass larvae. Consequently, it is difficult to say whether the discrepancy between modeled and estimated growth rates early in the spawning season was caused by unrealistic model assumptions or errors in the field growth estimates or both. In the latest cohorts of the spawning season the modeled and field estimates of growth generally were in close agreement. At that time, larvae were projected to grow at or near their maximum potential rates as previously observed in the laboratory and the field (Chesney 1989, Rutherford & Houde 1992). In the model, mortality of larvae (M) was growth-rate dependent, but limited to a maximum mortality rate of $6\% \text{ d}^{-1}$, but was generally 1 to $2\% \text{ d}^{-1}$. In the field, under conditions that are less than ideal for growth, mortality may be strongly size- or growth-rate dependent (Bailey 1984, Houde 1987). If mortality were strongly growth-rate dependent under poor growing conditions, then estimating growth rates of the survivors would pro-

duce growth rates higher than the mean growth rate that individuals in the population had experienced. Such an effect could also explain some of the discrepancy between modeled and observed estimates of growth in the first half of the 1987 spawning season (Fig. 7). Another possible explanation for the discrepancy is the method used to generate lengths in the model. Length was projected based upon growth-in-weight. Growth in weight could be negative (i.e. fish larvae can lose weight) but not lose length, especially if yolk reserves remain. If fish larvae grew slowly or lost weight as projected in the early season they would still grow in length. The model as presently structured cannot account for that in the length estimates. This could have caused underestimation of growth-in-length of early season cohorts.

In the second half of the spawning season estimated growth rates for the Potomac River larvae and in the simulations were in close agreement. This is the predicted result if growth rate were no longer a factor influencing survival. If all larvae were growing at or near maximum rates then other mortality factors would be less likely to be growth- or size-dependent.

The results show that laboratory data on growth and factors that affect it can be used to effectively estimate growth of striped bass larvae in the field, especially if a better understanding evolves of size-specific influences on mortality. The key to this process may be to properly identify key nutritional and physical factors and account for these in carefully controlled laboratory experiments. Because the lab and field estimates of growth rates appear to be reasonable, we have assumed that the growth-rate-dependent mortality observed in the laboratory also is reasonable and that it accounted for a relatively small percentage of the total field mortality in 1987. Conditions for growth were poor early in the Potomac River 1987 spawning season, but the poor feeding conditions did not have the opportunity to substantially affect survival because of the very high mortality caused by lethally low temperatures during that time frame.

Because of the lack of a reliable set of temperature-dependent growth data from the laboratory, there was no temperature-dependent growth term in the model to account for growth at low temperatures. Growth was modeled based on near optimal conditions from laboratory studies. If significant survival had taken place for the early cohorts, the model, as presently structured, would have probably overestimated growth of those early cohorts. Additional laboratory studies are needed to add a temperature-dependent term to future striped bass models.

The estimated rate of 'other' mortality falls within the broad range of rates reported for mortality of fish eggs and larvae. Some reported daily mortality rates of fish

eggs and larvae range from 0.05 to 0.88 d⁻¹ (McGurk 1986). It is generally believed that much of the mortality of fish eggs and larvae can be attributed to predation (Bailey & Houde 1989), however few good estimates of predation rates exist for field populations. Predation mortality is difficult to estimate and is sometimes estimated in the field by partitioning total mortality.

Assuming that the mortality from sources other than temperature and growth-related mortality is caused by predation, the rate of predation required to account for 'other' mortality can be estimated. The excess between the model estimate of abundance and the Potomac River estimate of abundance on Day 52 of the spawning season (initial run, Fig. 8a) was 2.028×10^9 larvae. If the excess larvae were evenly distributed among Stns 1 to 6 and if they were lost to mortality during the last 40 d of the spawning season, predators would have to consume striped bass larvae at a rate of 1.0 larvae 100m⁻³ d⁻¹ to account for the discrepancy between the field and modeled estimates. A predation rate of that magnitude on striped bass larvae would be reasonable, especially given evidence from laboratory experiments showing that predators from Chesapeake tributaries are capable of capturing significant numbers of striped bass larvae (McGovern & Olney 1988, Monteleone & Houde 1989). McGovern & Olney observed that predators of striped bass eggs and larvae were able to consume 0 to 5 larvae h⁻¹ at concentrations of larvae ranging from 20 to 100 larvae m⁻³. Monteleone & Houde (1989) found that individual white perch juveniles consumed striped bass eggs at a rate of 8 h⁻¹ and larvae at rates up to 60 h⁻¹ in laboratory experiments where stocking densities of striped bass eggs or larvae were 265 m⁻³. These laboratory rates are high, and stocking densities are certainly high compared to densities and rates expected in the field. Nevertheless, it shows that predators that are common within the Potomac River system can easily account for losses observed during 1987 that cannot be attributed to nutrition or temperature anomalies.

The simulated larval abundances followed a pattern similar to that actually recorded in the Potomac River but there were discrepancies and lags, especially in the earlier runs of model. Part of the difference between the model output and observed field result is probably due to assumptions in the egg production and larval abundance estimating methods. Normally distributing the egg production eliminated the lag and reduced the differences between actual and simulated values (Fig. 8c, d). Samples in the Potomac were collected on 2 d cruises at approximately weekly intervals in 1987. Estimated egg productions therefore were calculated from egg abundances observed in a less than 48 h period but expanded to represent weekly intervals. In many cases, spawning periods in the river

probably built to peaks and then declined within several-day periods. It is likely that the weekly field survey missed a major peak of egg production. Abundances of newly-hatched larvae would reflect egg abundances 1 to 3 d earlier; thus the field survey may have observed a peak of larvae that the model could not generate based on the egg production values. These types of errors can explain some of the deviations between the model and field-generated patterns of abundance. Other sources of discrepancy were associated with not knowing actual rates of egg viability and the egg or larval predation rates that were assumed in the model runs.

Some assumptions in the model may have limited its predictive power. Several improvements could be made if better information on striped bass eggs and larvae were available. For example, given that temperatures are favorable for growth, food concentration and light level for feeding are 2 very important factors affecting growth and survival in the laboratory (Chesney 1989). However, a critical but poorly understood factor needed to precisely predict growth in the model is a knowledge of the specific behavior of larvae in response to light in the river system. At what size can a larva regulate its position in the water column? How does this behavior change with size and river conditions? If larval behavior does change and foraging ability increases in older larvae, are growth rates size-specific?

Other information that would improve predictive power of the model is a reliable set of temperature dependent growth data from the laboratory so that growth can be more accurately predicted at sub-optimal temperatures. Finally, more detailed knowledge of the horizontal distribution and concentration of striped bass eggs, larvae and food organisms across each river segment instead of only in the river channel. Those data would have allowed better predictions of egg production, better prediction of conditions that a larva was likely to encounter and better estimation of abundance of larvae located on the flanks of the river. Potomac River field surveys in 1988 included samples from the river flanks. These collections will help to provide better field estimates of abundances and also can improve future modeling efforts.

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