A mark-release experiment on larval striped bass *Morone saxatilis* in a Chesapeake Bay tributary

D. H. Secor, E. D. Houde, and D. M. Monteleone


A larval mark-recapture experiment was undertaken to compare dispersal patterns and vital rates of hatchery-produced and wild larvae. The potential of larval stocking to enhance recruitment in an estuarine tributary was also evaluated. Approximately 6.5 million striped bass *Morone saxatilis* larvae (5-7 mm, SL) were marked by immersion in 25 mg l\(^{-1}\) alizarin complexone, which was deposited in their otoliths. Following release on two dates, the dispersal of marked larvae from release sites was rapid and their distribution 4 days after release resembled that of wild larvae. Growth rates of four release groups ranged from 0.20 to 0.25 mm day\(^{-1}\) and mortality rates ranged from 0.09 to 0.19 day\(^{-1}\). The rates were similar to those of wild larvae. More than 70% mortality of released groups occurred from 0 to 3 days after release and larvae stocked at one down-river site apparently suffered complete mortality due to advective down estuary loss. Hatchery produced larvae were released during a period when temperatures were favorable for growth and survival. Survivors of released larvae were estimated to account for 10 to 35% of the age 0+ juvenile striped bass in the Patuxent River in 1991. The success of this experiment indicated that marked larvae can serve as “probes” to examine environmental and habitat factors that affect recruitment of striped bass and other anadromous species. In the case of striped bass, large-scale stocking of larvae could contribute significantly to recruitment in Chesapeake Bay tributaries.

Key words: estuary, stocking, striped bass, larvae, mark-recapture, recruitment.

Received 4 May 1994; accepted 30 September 1994.

D. H. Secor, and E. D. Houde: Chesapeake Biological Laboratory, Center for Environmental and Estuarine Studies, The University of Maryland System, PO Box 38, Solomons, Maryland 20688, USA. D. M. Monteleone: Environmental Compliance, 1515 Broadway, 51st Floor, New York, 10036, USA.

Introduction

Stocking larval-stage fishes has played an important and controversial historical role in the development of fisheries research (McHugh, 1970; Solemdal *et al.*, 1984). If marked larvae can be identified upon recapture, stocking potentially could be an important tool in research on recruitment processes. Otolith-based marking methods have recently been employed to evaluate larval and juvenile stocking programs for marine, anadromous, and freshwater fishes (Tsukamoto *et al.*, 1989; Volk *et al.*, 1990; Hendricks *et al.*, 1991; Bergstedt *et al.*, 1990). Millions of fish larvae can be marked routinely and economically by immersion in chemicals such as tetracycline or alizarin complexone (Tsukamoto, 1985; Secor *et al.*, 1991a) or through thermal induction (Volk *et al.*, 1990). Chemical or thermal treatments can be applied repetitively at different ages during hatchery rearing to induce fluorescent or microstructural patterns on larval otoliths which result in unique marks (codes). Detection and retention studies have demonstrated that otoliths are permanently encoded on the increment corresponding to the day of chemical or thermal treatment (Tsukamoto, 1985; Volk *et al.*, 1990; Secor *et al.*, 1991a).

Larval mark-release experiments could be employed to investigate population dynamics of fish larvae and recruitment mechanisms (Tsukamoto *et al.*, 1989; Secor and Houde, 1995). Marked larvae can serve as “probes” to examine and evaluate factors that affect recruitment. In striped bass, *Morone saxatilis*, abundances at ca. 100 days post-hatching provide an index of recruitment (Goodyear *et al.*, 1985). Measures of juvenile abundance have indicated high variability in year-class success, with poor recruitments occurring in most years (NMFS, 1993). The largely density-independent causes of recruitment variability in striped bass are related to environmental factors that affect growth and survival of...
larvae (Stevens et al., 1985; Uphoff, 1989; Rutherford and Houde, in press; Secor and Houde, in press).

We designed larval mark-release experiments in which groups of larval striped bass were deliberately released to encounter varying environmental conditions in an attempt to develop a method to determine the influence of environmental factors on larval-stage vital rates. Hatchery-produced larval striped bass were stocked into a small sub-estuary of Chesapeake Bay, USA (Fig. 1) to determine if they had vital rates and dispersal patterns similar to those of wild larvae. Verification of this assumption would support additional efforts to use larval stocking experiments to investigate recruitment mechanisms. Stocked larvae might have different vital rate and dispersal behaviors due to maternal effects (Zastrow et al., 1989; Secor et al., 1992), hatchery rearing practices (Secor et al., 1992), or stocking procedures. Our specific objectives were to: (1) estimate larval growth and mortality rates of experimental release groups and compare them with rates of wild larvae; (2) compare dispersal patterns of released and wild larvae; (3) evaluate how larval attributes (age at release) and environmental variables (release site and date) affected survival of released larvae; and (4) evaluate the potential of larval stocking to enhance striped bass populations.

Methods
Larval marking
Striped bass eggs from 10 hatchery-spawned females of Patuxent River origin were provided by the Maryland Department of Natural Resources. Eggs were incubated and larvae were reared in 1-m³ raceways. To mark embryos or larvae, batches of 0.5 to 3.0 million were immersed for 6 h in 25 ppm alizarin complexone (ALC) adjusted to 1 ppt NaCl salinity. No adjustment of pH was necessary. Some of the embryos and larvae were treated at ages 0, 2, 6, or 8 days after hatching (Table 1). Otolith marks on recaptured individuals from these treatments provided information on release date, site and location, and larval age at release.

Release of marked larvae
In April and May 1991, 6.5 million, 9 to 13-day-old striped bass larvae were stocked into tidal freshwaters of
the Patuxent River (Fig. 1). The spawning and nursery area of the Patuxent River is 20–30 km long and ranges from 30–40 × 10^6 m^3 in volume (Secor and Houde, in press). Numbers of larvae that were to be released were estimated in hatchery raceways 1 to 3 h before transport to release sites (Table 1). Five to seven 250-ml samples were taken from three sections of a raceway with 2.0-cm-diameter plastic tube. The tube sampled larvae from surface to bottom of the raceway. Mean densities of larvae in each raceway section were estimated, multiplied by section volumes, and summed to estimate total number of larvae in a raceway.

On 26 and 30 April 1991, 9 and 13-day-old larvae were dipped into 15-l plastic bags of oxygenated water at densities of 50 000 to 100 000 per bag, placed in insulated boxes and transported by vehicle to release sites. An up-river (RK54) and a down-river release site (RK49) (Fig. 1) were selected based upon occurrence of naturally-produced larvae in concurrent ichthyoplankton surveys and upon historical descriptions of the larval nursery areas (Mihursky et al., 1980). Larvae were acclimated for 10 to 20 min to Patuxent River water in 200-l tanks at the release site before being siphoned through a 2.5-cm diameter hose into the river channel. All releases were made in the evening, within 2 h after sunset.

Mortality associated with the stocking procedure was evaluated within a 48-h period after stocking by a variety of tests on larvae released on 30 April. At the time of stocking, 15-l plastic bags (within insulated boxes) were filled with river water from the release sites (RK54 or RK49). Larvae (RK54, n=292; RK49, n=455) were placed in the bags and were held for 48 h at constant temperature. During this period, aeration, but no food, was supplied. In a second test, 100 larvae were held at the Chesapeake Biological Laboratory in a 76-l aquarium with river water from release site RK54. A third test consisted of deployment in the river of 19-l plastic carboys stocked with approximately 400 larvae at each release site. The carboys, which were fitted with a 500-μm screen over their tops to expose larvae to ambient water-quality conditions, were removed from the water and survivors counted at 42 h after stocking.

**Ichthyoplankton and juvenile surveys**

Ichthyoplankton was collected from 4 April to 30 May 1991 in 11 1-day surveys after the first release of marked larvae on 26 April. Sampling gears were 60-cm-diameter plankton nets (505-μm mesh) and 2-m² mouth-opening Tucker trawls (700-μm mesh). Collections were made at nine stations (Fig. 1). Two or three 5-min oblique tows from 1 m above bottom to surface were made. The 60-cm plankton nets were used on 27, 29 April and 1, 2, 3, 6, 9, and 17 May. The Tucker trawl was deployed on 14, 21, and 30 May to increase capture rates of late-stage larvae and early juveniles. Zooplankton was sampled in a 40-cm-diameter plankton net (53-μm mesh), which was lifted vertically from near-bottom to surface. Zooplankton taxa known to be important first foods for striped bass larvae (Uphoff, 1989; Setzler-Hamilton and Hall, 1991) were identified and categorized broadly as microzooplankton (copepod nauplii and rotifers). Measurements of temperature, salinity, conductivity, pH, and dissolved oxygen were made at all stations. The freshwater tidal portion of the Patuxent River is vertically well-mixed and bottom measures did not differ substantially from surface measures of water chemistry (Secor and Houde, in press). The surface-water measurements at RK54 (Fig. 1), a site located centrally within the spatial distribution of released and wild larvae, were taken as representative of environmental conditions that released larvae encountered. Juvenile striped bass were collected in a 37-m seine from 15 June–15 September 1991 during four 4-day surveys at seven sites that have

<table>
<thead>
<tr>
<th>Brood(s)</th>
<th>Hatch date</th>
<th>Age at marking* (d)</th>
<th>Release date and site</th>
<th>Millions released (± 1 S.D.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P-8</td>
<td>17 April</td>
<td>0</td>
<td>26 April – RK49</td>
<td>0.72 ± 0.21</td>
</tr>
<tr>
<td>P-9, 10, 11</td>
<td>17 April</td>
<td>8</td>
<td>26 April – RK49, RK54</td>
<td>2.37 ± 0.28</td>
</tr>
<tr>
<td>P-12, 13</td>
<td>17 April</td>
<td>8</td>
<td>26 April – RK49, RK54</td>
<td>0.87 ± 0.16</td>
</tr>
<tr>
<td>P-12, 13</td>
<td>17 April</td>
<td>6</td>
<td>30 April – RK49, RK54</td>
<td>1.44 ± 0.27</td>
</tr>
<tr>
<td>P-14, 18</td>
<td>21 April</td>
<td>2</td>
<td>30 April – RK49, RK54</td>
<td>0.35 ± 0.06</td>
</tr>
<tr>
<td>P-16, 17</td>
<td>21 April</td>
<td>2</td>
<td>30 April – RK49, RK54</td>
<td>0.79 ± 0.14</td>
</tr>
<tr>
<td>Total= 6.55</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*The ages at marking also designate “release groups” cited in text.
been sampled historically (Minkkinen and Stence, 1992) to index juvenile abundance (Fig. 1).

**Analysis**

Otoliths of larvae and juveniles were removed and prepared following methods described by Secor et al. (1991b). Otoliths were viewed under an epifluorescence microscope to determine presence of marks. Identification of specific otolith marks (Table 1) allowed larval release groups and sites of release to be determined. One wild cohort of larva was selected for comparison with released larvae. This cohort, designated group W, had a range of hatch dates (based upon otolith aging) similar to released larvae (Secor and Houde, in press). Environmental factors presumably affected group W and released groups similarly, allowing a meaningful comparison.

Riverwide abundances of released and wild larvae were estimated as the product of mean densities (no./volume sampled) at stations and estimated river volumes (Cronin, 1971) for river segments corresponding to sampled stations. River segment boundaries were defined as mid-distances between adjacent stations. Dispersal patterns of the released larvae were charted relative to stocking locations and dates. Growth and mortality rates of marked larvae were determined based upon their known ages and estimated abundances in samples. Growth rates during the first 45 days after hatching were fit with an exponential model, \( L_t = L_0 e^{gt} \) (where \( L_t \) = length at age \( t \); \( L_0 \) = length at hatch, and \( g \) = instantaneous growth coefficient. Linear and power growth models were tested as alternatives but rejected based upon coefficients of determination, residual analysis, and predicted y-axis intercepts that did not approximate expected lengths-at-hatch. Growth rate during the juvenile stage was estimated from a von Bertalanffy equation. Mortality rates were estimated from a Pareto model (Lo, 1985; Loos and Perry, 1991). The more common exponential mortality model was rejected based upon residual analysis and poorly estimated y-axis intercepts. The Pareto model is:

\[
\log N_t = \beta t + C,
\]

where \( N_t \) = larval abundance at age \( t \) and \( \beta, \alpha, \) and \( C \) are coefficients estimated by least squares. The constant \( C \) is an estimate of \( \log N_0 \), where \( N_0 \) is initial number of released larvae adjusted for stocking mortality; \( \beta \) is an estimator of the overall rate of decline in abundance with age; and \( \alpha \) indicates the shape of the curve. A Marquadt, non-linear least-squares, iterative method was used to estimate coefficients of the von Bertalanffy and Pareto functions. Data to determine mortality of released larvae included the number of larvae released in each group, and subsequent estimates of riverwide abundance. The riverwide abundances of juveniles at 92 and 88 days after hatching were derived from Petersen estimates based upon recaptured juveniles (see below).

Growth and mortality rates during the first 45 days after hatching were compared between released and wild groups using analysis of covariance. The exponential coefficients (\( g \)) for fitted growth models were compared between groups. To compare coefficients in Pareto mortality models between groups, we assumed and stipulated that \( \alpha \) was constant among groups, and defined \( t'=t\alpha \). We then compared \( \beta \) coefficients in the linear model, \( \log N_i = \beta_i t' + C_i \), where \( i \) indicates group. The mean value of \( t' \), which was used to estimate \( t' \), was 0.21.

Recaptures of the known-age marked larvae also allowed us to estimate accuracy of aging naturally-produced striped bass larvae. Validation of otolith-aging was dependent upon the assumption that known-age (marked) larvae laid down otolith increments in a similar or identical pattern to wild larvae. Otoliths from 21 recaptured, marked larvae (SL>8 mm) were randomly selected for the validation analysis and increments were counted. At the temperatures in which hatchery larvae were reared (16°C), first increment formation occurs at 4 days after hatching (E. Houde, pers. obs.; thus, 4 days were added to increment counts to estimate age.

We used the known numbers of coded-wire-tagged (CWT) striped bass juveniles (40–60 mm, SL) released by the Maryland Department of Natural Resources to estimate the numbers of juvenile survivors from our experimental releases. In the period 1–18 July 1991, 105 915 CWT young-of-the-year striped bass were stocked into the Patuxent River (Minkkinen and Stence, 1992). The number stocked, after adjustment for transfer mortality and tag loss, was 97 611. Abundance of 40–60-mm juveniles from our marked larval releases \( (N_A) \) was estimated by (Ricker, 1975):

\[
N_A = \sum_{i=1}^{N} (N_C R_{A_i}) R_C^{-1},
\]

where \( N_C = \) number of released juveniles with coded wire tags, adjusted for tag loss and stocking mortality; \( i (1 \ldots x)=\) experimental larval release group; \( R_{A_i} = \) number of captured juveniles that were released as larvae and coded for release \( i \) by the unique alizarin mark on their otoliths; \( R_C = \) number of coded wire-tagged juveniles collected in the juvenile sampling program.

The variance of the juvenile abundance estimate for those juveniles originating from larval releases was estimated from a Poisson distribution (Ricker, 1975). Overall survival rate (\( S \)) from time of release to recapture as 40–60-mm-stage juveniles was estimated by:

\[
S_i = e^{-\frac{r_i}{i}}
\]

where:

\[
Z_i = (\text{log}_e N_{A_i} - \text{log}_e N_0) t_i^{-1}
\]
and \( N_i \) = estimated number of 40–60-mm juveniles from experimental release \( i \) (as calculated above); \( N_0 \) = number of larvae stocked in the experimental release, adjusted for mortality associated with the stocking procedure; and \( t_i \) = days after release.

**Results**

**Stocking mortality**

Totals of 3.96 million and 2.58 million larvae were stocked on 26 April and 30 April 1991, respectively. Coefficients of variation on estimated numbers in individual release groups ranged from 12% to 29% and averaged 19% (Table 1). The tests to estimate stocking mortality in the shipping boxes or aquaria indicated survival rates of 80–99%, while the carboy tests at the two release sites indicated survival rates of 32% and 45%. In retrospect, it was realised that the carboy experiment exposed larvae to extreme tidal fluctuations in temperature, pH, dissolved oxygen, conductivity, and salinity that were not experienced by the released larvae and which could have caused high mortality rates. Based upon the laboratory aquaria and shipping box tests, we conservatively assumed that 80% of the released larvae survived the stocking procedure. Thus, numbers stocked, adjusted for stocking mortality, were 3.17 million and 2.06 million for release dates 26 April and 30 April, respectively.

**Environmental conditions**

At the time of stocking, river temperatures were approximately 2 degrees and 1 degree lower on 26 April and 30 April, respectively, than temperatures in the shipping boxes. On both dates, river conductivity (26 April = 400 \( \mu \)mhos/cm (usiemens/cm), 30 April = 650 \( \mu \)mhos/cm) was lower than hatchery water conductivity (1000 \( \mu \)mhos/cm) at the up-river stocking site (RK54) but river and hatchery conductivities were similar at the down-stream stocking site (RK49) (26 April = 1000 \( \mu \)mhos/cm, 30 April = 1350 \( \mu \)mhos/cm). Conductivities at RK49 were slightly higher than levels where naturally-produced striped bass eggs and larvae usually occurred (Secor and Houde, in press). In the acclimations to river water immediately before release, larvae showed no signs of stress and there was no immediate mortality.

Temperatures at the time of stocking exceeded 16°C, which is well above sublethal (ca. 14°C) (Setzler-Hamilton and Hall, 1991), and continued to rise thereafter (Fig. 2). The rate of increase was rapid and reached 30°C by the end of May. Rainfall was moderate (<3 cm) and evenly distributed in the 3 weeks following releases. Dissolved oxygen decreased and pH increased in the 3 weeks after release, but were within ranges considered favorable for striped bass growth and survival (Setzler-Hamilton and Hall, 1991). Microzooplankton densities ranged from 50 to >100 individuals l\(^{-1}\) (Fig. 2).

**Recapture rates of released larvae**

In 11 surveys conducted within 34 days of the first larval release, 37.5% (134/357 marked/total larvae) of all sampled striped bass larvae >9 days old (5.5 mm) contained a mark (Table 2). The majority of recaptures (90%) were of the early-released group 8 larvae. No group 0 early-release larvae, which had been coded uniquely for the down-river release site, were recaptured. Experimental groups which were released as 9-day-old (group 2) and 13-day-old (group 6) larvae on 30 April contributed 8% and 2% of the recaptures, respectively.

Recapture rates (uncorrected for stocking mortality) for group 8 ranged between 0.0018% (18 per million stocked) at 1 day after release to 0.00006% (0.6 per million stocked) at 34 days after release (Table 2; Fig. 3). Recapture rates may have been affected by gear avoidance. As larvae grew, they apparently became less vulnerable to the 60-cm plankton net (Houde and Rutherford, 1992). Recapture rates were lower on 6, 9, and 17 May (0 to 1.23 per million stocked), when a 60-cm diameter plankton net was deployed, than on 14 and 21 May (1.54 and 2.47 per million stocked), when a 2-m\(^2\) Tucker trawl was used. Also, because the Tucker trawl filtered four times more water than the 60-cm plankton net, higher recapture rates were expected.

**Dispersal of released larvae**

More than half (55%) of the released larvae, the fraction stocked at RK49 (first and second releases), the down-river site, may not have had any potential to survive. A portion (28%) of larvae stocked at the downriver site (RK49) during the first release had a mark unique for that site (Group 0, Table 1), and none were ever recaptured.

Marked larvae from the RK54 releases dispersed quickly throughout the nursery area of the Patuxent River already occupied by wild larvae (Fig. 4). Under the assumption that only larvae stocked at RK54, up-river site, were retained, larvae dispersed >5 km up- and down-river within 4 days of release. The pattern of spatial occurrence of released larvae was similar to that of wild larvae (Fig. 4). During April–May, larvae appear to have been retained up-river of the salt front, which was defined by the 800 \( \mu \)mhos/cm conductivity contour.

**Age validation**

The mean discrepancy between increment counts and known ages of released larvae did not differ significantly from zero (paired t-test; mean difference=0.333;
Growth rates and growth models of released larvae

Released larvae grew at 0.20 to 0.25 mm day\(^{-1}\) in the period up to 25 days after hatching (Fig. 5; Table 3). The exponential coefficients of the release or wild groups did not differ significantly (ANCOVA, p=0.39). However, at 25 days after hatching, predicted lengths and weights of wild group W larvae were substantially less than predicted lengths and weights of larvae from release groups 2 and 8 (Table 3).

The substantial number of recaptures of group 8 individuals as juveniles provided data for growth models to be fitted to both the larval and juvenile stages (Fig. 6). The best fits were obtained by an exponential model for the larval period (0 to 57 days; \(r^2=0.92\)) and a von Bertalanffy model for the juvenile period (57–151 days; \(r^2=0.50\)). The overlapping age (57 days) between larval and juvenile periods was specified because of uncertainty in the age at larval–juvenile transition. Other attempts were made to model growth during the entire
Table 2. Numbers of recaptured marked larval and juvenile striped bass from different release groups, Patuxent River, 1991. Release groups (see Table 1) were group 8, released on 26 April at 9 days after hatch; group 2, released on 30 April at 9 days after hatch; and group 6, released on 30 April at 13 days after hatching. Wild (unmarked) post-yolk-sac larvae >5.5 mm SL are included for comparison. Recapture rates are uncorrected for stocking mortality or probable advection loss of larvae stocked at the downriver site. NA—not applicable.

<table>
<thead>
<tr>
<th>Date</th>
<th>Days after first release (26 April)</th>
<th>Early release, group 8</th>
<th>Late release, group 2</th>
<th>Late release, group 6</th>
<th>Wild post-yolk sac larvae (&gt;5.5 mm SL)</th>
<th>Total number marked larvae</th>
<th>Recapture rate early release, group 8 (per million)</th>
<th>Recapture rate late release, group 2 (per million)</th>
<th>Recapture rate late release, group 6 (per million)</th>
</tr>
</thead>
<tbody>
<tr>
<td>27 April</td>
<td>1</td>
<td>59</td>
<td>0</td>
<td>0</td>
<td>16</td>
<td>59</td>
<td>18.21</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>29 April</td>
<td>3</td>
<td>22</td>
<td>0</td>
<td>0</td>
<td>13</td>
<td>22</td>
<td>6.79</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>1 May</td>
<td>5</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>12</td>
<td>15</td>
<td>3.09</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>2 May</td>
<td>6</td>
<td>5</td>
<td>9</td>
<td>1</td>
<td>23</td>
<td>5</td>
<td>1.54</td>
<td>7.89</td>
<td>0.69</td>
</tr>
<tr>
<td>3 May</td>
<td>7</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>46</td>
<td>1</td>
<td>1.54</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>6 May</td>
<td>10</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>42</td>
<td>5</td>
<td>0.31</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>9 May</td>
<td>13</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>28</td>
<td>0</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>14 May</td>
<td>18</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>42</td>
<td>5</td>
<td>1.54</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>17 May</td>
<td>21</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td>5</td>
<td>1.23</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>21 May</td>
<td>25</td>
<td>8</td>
<td>1</td>
<td>1</td>
<td>14</td>
<td>10</td>
<td>2.47</td>
<td>0.88</td>
<td>0.69</td>
</tr>
<tr>
<td>30 May</td>
<td>34</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>18</td>
<td>2</td>
<td>0.62</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>12 June</td>
<td>47</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>25</td>
<td>4</td>
<td>0.62</td>
<td>0.88</td>
<td>0.69</td>
</tr>
<tr>
<td>18 July</td>
<td>83</td>
<td>5</td>
<td>2</td>
<td>0</td>
<td>25</td>
<td>7</td>
<td>1.54</td>
<td>1.75</td>
<td>0.00</td>
</tr>
<tr>
<td>15 August</td>
<td>111</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>16</td>
<td>8</td>
<td>2.47</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>16 September</td>
<td>142</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0.31</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>
larval-juvenile period of group 8 recaptures, applying Gompertz or logistic models; these either fit the data poorly for the larval stage (Gompertz model) or gave an unrealistic estimate of $L_{\infty}$ (logistic model). In all models, growth-in-length was positively exponential from 0 to 60 days after hatching and negatively exponential thereafter. The $L_{\infty}$ parameter in the von Bertalanffy model (67.50 mm) may have underestimated the length which would be achieved by group 8 juveniles when they entered the winter no-growth period. Length-at-age data were highly variable for recaptured group 8 juveniles (Fig. 6).

Mortality rates of released larvae

Instantaneous mortality rates of released larvae, estimated from the Pareto model, from stocking to 41 days after hatching were 0.11, 0.20, and 0.10 day$^{-1}$, for groups 2, 6, and 8, respectively. The estimated instantaneous mortality rate for wild group W from 9-41 days after hatching was 0.05 day$^{-1}$. The fitted Pareto models provided similar estimates of $\alpha$ for most groups (group W, $\alpha=0.13$; group 2, $\alpha=0.21$; group 6, $\alpha=0.29$; group 8, $\alpha=0.19$). Comparison of $\beta$s estimated for the first 45 days after hatching (group W, $\beta=-5.61$; group 2, $\beta=-6.60$; group 6, $\beta=-5.81$; group 8, $\beta=-4.81$) indicated no detectable differences among released or wild groups ($p=0.21$).

The first 3 days after release accounted for losses of 75%, 86%, and 73% for groups 2, 6, and 8, respectively (Fig. 7). The Pareto model for group W data indicated that high mortality had occurred during the yolk-sac larval stage (0 to 6 days), followed by lower mortality during the feeding-larva stage.

Recaptures of juveniles

In the period 83–111 days after release, 15 of 84 collected juveniles (18%) bore an alizarin mark (Table 4). The high juvenile recapture rate (0.00022%; Table 2) was similar to recapture rates of larvae. Individual growth rates, calculated from known ages of recaptured juveniles, varied from 0.45–0.87 mm day$^{-1}$ and were similar to rates reported previously for juvenile striped bass (Secor and Dean, 1989).

Total abundance of alizarin-marked juveniles on 18 July (the final day of CWT juvenile stocking) was estimated to be 31,058. In collections on that date, 22 juveniles had a coded wire tag, five had an alizarin mark specific to group 8, two had a mark specific to release group 2, and 25 had no mark or tag (Table 4). The estimated abundance of alizarin-marked juveniles in group 8, from collections on 15 August, was nearly six times higher (130,148) than on 18 July. The wide 95% confidence intervals for alizarin-marked juveniles collected on the two dates overlapped broadly, ranging from 8232 to 101,854 on 18 July and from 25,334 to 701,024 on 15 August. Although abundance could not be estimated precisely, the released larvae clearly made a significant contribution to the juvenile population. The contribution of released larvae apparently was between 13% and 35% of overall juvenile abundance and between 25% and 50% of the wild juvenile abundance. The estimated mortality rates ($Z_i$) from release to 18 July for
Mark-release on larval striped bass

Figure 4. Spatial occurrences of released and wild striped bass larvae in the Patuxent River, 1991. Abundances at stations are plotted by date and river km. The conductivity contour is given for 800 μhos/cm which is indicative of the salt front. The two release sites and dates are indicated by the symbols on the bottom panel.

groups 2 and 8 were both 0.06 day⁻¹ (5.8% per day). Mortality rate from release to 15 August for group 8 was 0.03 day⁻¹ (2.8% per day). These results indicated that from 0.7 to 4.0% of released larvae survived to the juvenile stage.

Discussion

Dispersal of released larvae

We believe that larvae stocked at the down-river site were advected down-river and out of the striped bass nursery area. The down-river site (RK49) was located near the estuarine salt front, as indicated by conductivity (Secor and Houde, in press), above which striped bass eggs and larvae are apparently retained in Chesapeake Bay tributaries (Houde and Rutherford, 1992; Secor and Houde, in press). Evidence for loss of down-river stocked larvae were: (1) no recaptures of group 0 larvae which were released only at the down-river site, and (2) the very high apparent mortality rates observed for groups 2, 6, and 8 from one to three days after release, which could have been the consequence of large advective loss of the fractions of these releases made at the down-river site. Group 0 larvae which were released only at the down-river site comprised 11% of the total number of released larvae (Table 1). If this group had survived at a rate similar to the other released groups, the probability of observing 0 recaptures for this group \( p = (1 - 0.11) = 0.89 \) among plankton samples \( (n = 137) \) is \( 0.89^{137} \) or \( 1.2 \times 10^{-7} \), a highly unlikely result. Rates of loss in the first 3 days after release were estimated to be 73%, 86%, and 75% for release groups 2, 6, and 8, respectively. Most of this mortality could be attributable to complete loss of larvae in these groups stocked at the down-stream site. Consequently, the effective release number (i.e. those released above the salt front) was approximately 45% (i.e. 2.91 \times 10^6) of the actual release number (Table 1).

Down-river advection would have resulted in displacement of larvae into habitats not typically utilized by striped bass larvae. Although rearing studies indicate that larvae have enhanced survival in slightly brackish water (1 to 5 ppt salinity) (Setzler-Hamilton and Hall, 1991), wild larvae are uncommonly observed in oligohaline habitats (Uphoff, 1989; Houde and Rutherford, 1992). We speculate that several factors related to down-estuary advection could cause high mortality of striped bass larvae. Euryhaline species of fishes, which are potential predators (juvenile Morone spp. and Leiostomus xanthurus, and adult Fundulus heteroclitus, and Menidia menidia), are more abundant in oligohaline habitats (Funderburk et al., 1991). Oligohaline habitats also have higher densities of macroinvertebrate species (e.g. mysids, isopods, calanoid copepods), which may compete with or prey upon small larvae. Increased dispersion and flow rates in regions down river from the salt front and maximum turbidity zone (Ulanowicz and Flemer, 1978) could cause larvae to be advected into mesohaline salinities which presumably would result in osmotic stress. The complete lack of juvenile recaptures from group 0 also supports our view that down-river advection of the released larvae resulted in complete mortality.

Hatchery vs. wild larvae

Larvae were released into the river during a period when temperature was increasing, which we believe coincided with conditions favorable for growth and survival (Fig. 2). Secor and Houde (in press) estimated higher mortality rates \( Z > 0.15 \) for wild cohorts of larvae spawned during periods preceding and following the larval release period. Temperatures during the first 25 days after hatching were shown to have a strong effect on mortality rates, and a temperature window between 16 and 20°C supported good survival of striped bass larvae (Fig. 8). Early (groups 0 and 8) and late (groups 2 and 6) released
larvae experienced average temperatures of 19.1 and 20.1°C, respectively, during the first 16 days after release. Thus, their low mortality rates are believed to be attributable to favorable temperatures.

In mark-recapture experiments, an important assumption is that marked-released fish and wild fish behave similarly (Ricker, 1975; Begon, 1979). In our study, hatchery-produced larvae were fed *Artemia* nauplii in the hatchery for a few days before release. It is possible that during this period hatchery-produced larvae might have experienced a nutritional advantage or disadvantage compared with wild larvae. Also, larvae from hatcheries might not have acquired behavior required to regulate their position in the water column and thus might be selectively transported or dispersed from favorable nursery areas.

Any nutritional advantage or disadvantage that hatchery larvae may have had over wild larvae was not tested. But, there was evidence that growth rates of release groups 2 and 8 were higher than that of wild group W (Table 3). On the other hand, release group 6 larvae experienced a growth rate similar to group W and also experienced a higher apparent mortality rate than other release groups. Group 6 was comprised of larvae released at 13 days after hatching; all other groups were released at 9 days after hatching. The longer period of hatchery rearing experienced by group 6 larvae could have had a detrimental effect, either by selecting unnatual behaviors or by detrimentally affecting ontogenetic processes such as swimbladder inflation (J. Van Tassel, Maryland Department of Natural Resources, PO Box 1136, Prince Frederick, MD 20678, pers. comm.).

Growth rates of released larvae (0.20 to 0.25 mm day⁻¹) were typical of growth rates (0.20-0.29 mm day⁻¹) observed for natural cohorts of striped bass larvae in the Potomac River and Upper Bay (Rutherford and Houde, in press), but were higher than rates (0.15-0.22 mm day⁻¹) estimated for most co-occurring natural larvae in the Patuxent River in 1991. Mortality rates of the released larvae tended to be lower than mean daily mortality rates reported for the Potomac River (Z=0.22 X 0.34 day⁻¹), Upper Bay (Z=0.73 1.14 day⁻¹) (Rutherford and Houde, in press), and the Patuxent River (Z=0.24), but were similar to those reported for the Choptank River (Z=0.06-0.21 day⁻¹) (Uphoff, 1989).

Abundance estimates

Relatively high rates of recapture were observed for juvenile striped bass released as larvae. The habitat of juvenile striped bass is primarily shallow areas along river banks (Weisberg *et al.*, 1991) and sampling for juveniles may have been more efficient than for larvae.

---

![Graphs showing exponential regressions of standard length on age for release groups 2, 6, and 8, and naturally-produced group W, Patuxent River, 1991.](image-url)
Table 3. Growth coefficients and size-at-age among release groups and naturally-produced group W. Length (mm) at 25 days estimated from length-at-age regressions (Fig. 5) for ages 9 to 45 days after hatching; weight (mg) at 25 days estimated from the weight-length relationship of Houde and Lubbers (1986). G=weight-specific growth coefficient.

<table>
<thead>
<tr>
<th>Group</th>
<th>mm day⁻¹ at 25 days</th>
<th>Length (mm) at 25 days</th>
<th>G (day⁻¹) at 25 days</th>
<th>mg day⁻¹ at 25 days</th>
<th>mg at 25 days</th>
</tr>
</thead>
<tbody>
<tr>
<td>Release 2</td>
<td>0.25</td>
<td>10.54</td>
<td>0.157</td>
<td>0.59</td>
<td>15.06</td>
</tr>
<tr>
<td>Release 6</td>
<td>0.20</td>
<td>8.58</td>
<td>0.153</td>
<td>0.23</td>
<td>6.00</td>
</tr>
<tr>
<td>Release 8</td>
<td>0.20</td>
<td>9.21</td>
<td>0.139</td>
<td>0.35</td>
<td>8.98</td>
</tr>
<tr>
<td>Group W</td>
<td>0.17</td>
<td>8.42</td>
<td>0.120</td>
<td>0.23</td>
<td>5.92</td>
</tr>
</tbody>
</table>

Figure 6. Growth models for larval and juvenile striped bass from release group 8, Patuxent River, 1991. Larval growth was modeled from 0 to 57 days by fitting data to an exponential model. Data on juvenile growth from 57 to 151 days were modeled with a von Bertalanffy equation.

Assuming a Poisson distribution, the overlapping confidence intervals of 8200 to 102 000 alizarin-marked juveniles, based upon 18 July collections, and 25 000 to 701 000, based upon 15 August collections, indicated that estimates were imprecise but that a large contribution of juveniles was derived from the larval releases. Considering the possible sources of error, it is probable that the true abundance of alizarin-marked juveniles in July 1991 lay between 31 000 and 130 000, the point estimates of abundance given in Table 4. The alizarin-marked juvenile abundance estimate of 130 148, based upon the 15 August collection, seems unrealistically high considering the estimated abundances in plankton collections of late-stage larvae from released groups. The Pareto mortality models (Fig. 7) predicted abundances of 33 087, 3810, and 109 672 alizarin-marked larvae at 40 days after hatching for groups 2, 6, and 8, respectively. Assuming a very conservative daily mortality rate, Z=0.01 for the period 40 to 92 days after hatching (Dorazio et al., 1991), expected abundance of marked larvae would decline from 146 569 to 87 138 juveniles. The juvenile abundance estimate of otolith-marked fish, based upon 18 July collections (31 058) might be an underestimate because the CWT juveniles, which were released from 1–18 July, may not have dispersed adequately. They were released in close proximity to collection sites and, consequently, might have been over-represented relative to alizarin-marked juveniles in 18 July collections.

Larval stocking and fishery enhancement

Our data indicate that larval stocking could contribute significantly to enhancement of striped bass stocks. If larval releases were planned to coincide with dates and sites favorable for growth and survival, large enough releases could be made to enhance recruitment significantly in all but the largest of Chesapeake Bay's
Figure 7. Pareto mortality models for striped bass larval release groups 2, 6, and 8, and naturally-produced group W, Patuxent River, 1991.

Table 4. Juvenile abundances estimated on 18 July and 15 August, based upon collections of coded wire-tagged juveniles stocked by Maryland Department of Natural Resources.

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Proportion collected</th>
<th>Estimated abundance</th>
<th>Overall survival</th>
</tr>
</thead>
<tbody>
<tr>
<td>18 July</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coded wire tagged</td>
<td>22</td>
<td>0.4074</td>
<td>97 611</td>
<td></td>
</tr>
<tr>
<td>Alizarin marked</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group 8</td>
<td>5</td>
<td>0.0926</td>
<td>22 184</td>
<td>0.68%</td>
</tr>
<tr>
<td>Group 2</td>
<td>2</td>
<td>0.0370</td>
<td>8874</td>
<td>0.78%</td>
</tr>
<tr>
<td>Wild</td>
<td>25</td>
<td>0.4630</td>
<td>110 922</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>54</td>
<td></td>
<td>239 591</td>
<td></td>
</tr>
<tr>
<td>15 August</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coded wire tagged</td>
<td>6</td>
<td>0.2000</td>
<td>97 611</td>
<td></td>
</tr>
<tr>
<td>Alizarin marked</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group 8</td>
<td>8</td>
<td>0.2667</td>
<td>130 148</td>
<td>4.01%</td>
</tr>
<tr>
<td>Group 2</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wild</td>
<td>16</td>
<td>0.5333</td>
<td>260 296</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>30</td>
<td></td>
<td>488 055</td>
<td></td>
</tr>
</tbody>
</table>
Mark-release on larval striped bass

A = Wild cohorts
\( \triangle = \text{Release groups} \)

Figure 8. Mortality rates of natural cohorts and release groups in relation to temperature encountered during the first 25 days after hatching. Quadratic model fit to natural cohorts:

\[ Z = 6.042 - 0.665 \text{ temperature} + 0.0184 \text{ (temperature)}^2; \quad n = 7; \quad r^2 = 0.99. \]

Standard error bars for mortality rates are shown. "W" = group W. Figure modified from Secor and Houde (in press).

To release may have reduced expected mortality from the egg to juvenile stage by approximately an order of magnitude compared with the average mortalities experienced by wild cohorts.

The success of a larval stocking program in a given year will depend upon the environmental conditions and natural recruitment level. For striped bass, we expect that favorable environmental conditions will occur upriver from the 800 \( \mu \text{hos/cm} \) conductivity contour. Meteorological forecasting could increase the probability of stocking larvae into temporally favorable conditions. However, weather conditions in April and May are quite variable and not easily predicted and hatchery-produced larvae may not always be available to stock during favorable periods. Despite these concerns, we believe that a long-term larval stocking program could, on average, augment natural striped bass larvae under favorable conditions. It is possible that poor or no survival of stocked larvae could occur in some years when environmental conditions were poor. In 1991, hatchery larvae were released into very favorable conditions for growth and survival in the Patuxent River. If numbers stocked had been three to four times higher in 1991 (e.g. 9–12 million larvae stocked at the upriver site), and assuming that compensatory mortality was unimportant, a two-fold increase in riverwide juvenile (marked + wild) abundance might have been achieved. The abundance of wild juveniles in 1991 was relatively low compared with historic abundances in the Patuxent River (Minkkinen and Stence, 1992). The substantial relative contribution of stocked larvae to the juvenile population in 1991 was a consequence of poor production of wild larvae. Juvenile abundance in the Patuxent River has varied by more than an order of magnitude from 1987 to 1992 (Dorazio et al., 1991, Minkkinen and Stence, 1992). In a relative sense, stocking larvae will be most effective during poor recruitment years.

Larval mark-release experiments for anadromous fishes

Research on population dynamics and recruitment mechanisms can be enhanced by larval mark-release experiments. Because aging is not a source of error, growth rate estimates of released larvae are very accurate and estimates of mortality rates will be more accurate than those for naturally produced larvae. Larval distributions and dispersal can be tracked from recaptured marked larvae (Tsukamoto et al., 1989; Lehton et al., 1992; this study). However, sampling error is still important in larval mark-release experiments, which can bias estimates of vital rate and dispersal rate. Because recapture rates are expected to be low, these errors can be important, and due consideration should be given to determine if sufficient numbers of recaptures can be expected. Using releases of marked larvae, we envisage experiments to evaluate size-specific mortality rates, predation, dispersal, and hatchery contribution rates, as well as determination of anthropogenic effects on nurseries and impacts of introduction of genetically altered fish (Secor and Houde, 1995).

Acknowledgements

Research was supported by the Governor's Council on Chesapeake Bay Research, administered through the Chesapeake Bay Research and Monitoring Division, Maryland Department of Natural Resources, Contract CB90-007-004. We are indebted to the Manning Hatchery staff of Maryland DNR, who collected and spawned adult striped bass to provide larvae for our experiments. In this regard, we especially thank B. Florence and J. Van Tassel. We thank Capts J. Crane and W. Keefe, and the crews of the RVs “Orion” and “Aquarius” for competent assistance. Many people assisted in the research. We acknowledge L. Bean, C. Cooksey, J. Cowan, S. Dorsey, L. Linley, J. MacGregor, P. Miller, T. Newberger, E. Rutherford, and C. Zastrow. Statistical procedures for comparing Pareto models were suggested by E. Perry. L. Fernandez assisted with manuscript preparation. Publication No. 2593 of the Center for Environmental and Estuarine Studies, The University of Maryland System.

References


Rutherford, E. S., and Houde, E. D. In press. The influence of temperature on cohort-specific growth, survival and recruitment of striped bass, Morone saxatilis, larvae in Chesapeake Bay. Fishery Bulletin, US.


Secor, D. H., and Houde, E. D. In press. Temperature effects on the timing of striped bass egg production, larval viability and recruitment potential in the Patuxent River (Chesapeake Bay). Estuaries.


