

Use of larval stocking in restoration of Chesapeake Bay striped bass

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After the collapse of striped bass *Morone saxatilis* stocks in the late 1970s, hatchery programs and release experiments were instituted to evaluate the potential to restore striped bass in Chesapeake Bay. Because survival of striped bass larvae to first feeding (7 d after hatch) is low in Chesapeake tributaries, ranging from 0.2 to 5.2% of eggs spawned, it is possible to enhance survival through hatchery propagation of eggs and yolk-sac larvae, and it may be feasible to supplement recruitment by stocking post-yolk-sac larvae. During 1991–1993, otoliths of 31.7 million hatchery-produced striped bass larvae (5–13 d after hatch) were chemically marked and released into two tributaries of Chesapeake Bay. In years of moderate to poor natural larval production (1991, 1992), stocked larvae contributed 20 to 30% to overall juvenile abundance. In 1993, a year of high natural production, stocked larvae contributed only 5% to juvenile abundance, although numbers contributed were higher than in previous years. Using field and hatchery estimates of larval and juvenile growth and mortality, enhancement strategies were compared in which fish were released at three different ages: larvae (7 d post-hatch), summer-stocked juveniles (55 d post-hatch), or fall-stocked juveniles (220 d post-hatch). Based upon hatchery records, reared larvae and juveniles experienced substantially higher rates of growth and survival than did wild larvae and juveniles of similar age. In years of low natural egg production, cohort biomass at 220 d post-hatch was highest when juveniles were stocked in summer or fall. When approximate costs were incorporated into the analysis, the efficacy of stocking 7-d-old larvae was higher than summer and fall stocking of juveniles if stocked larvae encountered favourable conditions. In years of poor natural recruitment, stocking post yolk-sac larvae into estuarine tributaries could supplement stocks of striped bass and possibly other anadromous species which experience high embryo and yolk-sac larva mortality.

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Introduction

Large reductions in landings of striped bass *Morone saxatilis* and declines in recruitment (Fig. 1) prompted a restoration program in Chesapeake Bay (ASMFC, 1995). Tagging and genetic studies had shown that Chesapeake Bay is the major nursery area and source of recruits to coastal fisheries in the mid-Atlantic region of North America (Boreman and Lewis, 1987; Fabrizio, 1987; Wirgin *et al.*, 1993). High rates of exploitation on premigratory juveniles ($z > 2.0 \text{ yr}^{-1}$; Gibson, 1993) throughout the 1970s and degraded nursery habitats (Hall *et al.*, 1993) were believed to have led to recruitment failure in Chesapeake Bay. One of two principal

responses by management to restore striped bass was a hatchery-based stocking program. From 1985–1993, 1.4 million 35–50 mm, total length [TL] juveniles and 6.1 million 150 to 200 mm TL juveniles were stocked into several Chesapeake Bay tributaries during summer and fall, respectively. The other response was to impose fishing moratoria in Chesapeake Bay in Maryland (1985–1989) and Virginia (1989), and restrict exploitation in coastal waters (ASMFC, 1995).

The rationale for hatchery-based restoration was based upon studies that indicated: (1) high mortality rates of eggs and larvae in nursery habitats; and (2) strong environmental and density-independent effects on striped bass recruitment (e.g. Ulanowicz and Polgar,

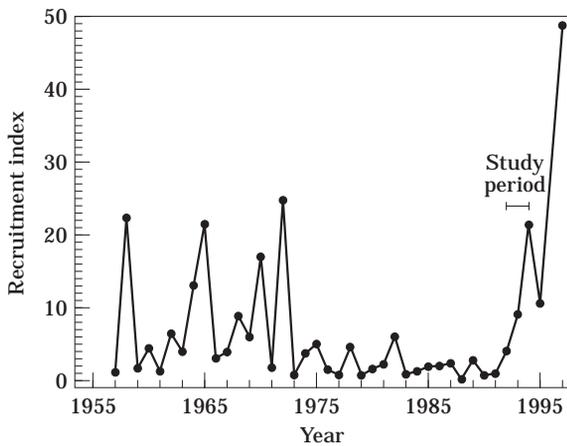


Figure 1. Striped bass recruitment time series for the Nanticoke River (Chesapeake Bay), 1956–1996. Recruitment is indexed by young-of-the-year abundance, estimated as the mean number of juveniles collected in a seine survey of the Nanticoke River (Cosden and Barbour, 1995; Cosden, Maryland Department of Natural Resources, pers. comm.).

1980). In two Chesapeake tributaries, recent estimates of larval mortality from hatching to first feeding (ca. 5 d after hatch) ranged from 94.8–99.8%; larval mortality from first-feeding to ca. 8 mm standard length ranged from 91.6–94.8% (Secor and Houde, 1995a; Kellogg *et al.*, 1996). Striped bass ichthyoplankton studies demonstrated that meteorologically driven variability in water quality (temperature, pH, conductivity) are dominant influences on egg and larval survival and juvenile production (Uphoff, 1989; Rutherford and Houde, 1995; Secor and Houde, 1995a; Kellogg *et al.*, 1996; Bulak *et al.*, 1997). Thus, if survival of embryos, and survival and growth of larvae were high in hatcheries, then released juveniles would have bypassed a bottleneck of critical mortality, whether caused by degraded nursery habitat or fluctuating meteorological conditions.

In this paper, we examine the premise that stocking striped bass juveniles is a strategy superior to that of stocking larvae. We have already conducted larval mark-recapture experiments in 3 years (1991–1993) and in two tributaries, the Patuxent and Nanticoke Rivers (Fig. 2), to examine how growth and mortality rates of larvae are related to meteorological events and associated water quality (Secor *et al.*, 1995a,b; 1996). Our experiments indicated that larvae released under favourable conditions made substantial contributions to juvenile production. Stocking larvae as a replenishment tool might therefore, be a viable alternative to stocking juveniles. Here, we document the contribution of hatchery stocked striped bass larvae to juvenile populations in the Patuxent and Nanticoke Rivers in 1991–1993. We then apply estimated larval growth and survival rates

from past studies and the literature to simulate and compare production rates of striped bass larvae and juveniles in either wild or hatchery environments. Three ages at release were compared: 7-d post hatch, first-feeding larvae; 55-d post hatch, summer-stocked juveniles; and 220-d post hatch, fall-stocked juveniles. Criteria considered were rate of biomass accumulation and cost.

Materials and methods

Larval mark-recapture experiments

Striped bass eggs, obtained from induced spawning in the hatchery of 10 (1991), 9 (1992) and 12 (1993) wild females captured in the Patuxent (1991) or Nanticoke River (1992–1993), were provided to us by Maryland Department of Natural Resources (Table 1). Fertilized eggs were held in either 1 m³ or 2 m³ raceways for incubation and larval rearing at the Manning Hatchery. Larvae were immersed in solutions of alizarin complexone in 1991 and 1992 and tetracycline hydrochloride in 1993 to produce fluorescent marks in their otoliths (Secor *et al.*, 1991a, 1995b). Batches of embryos or larvae were immersed and marked at ages ranging from 0 to 9 d after hatch. Batches of larvae were marked by single or multiple treatments (Table 1). Otolith marks (equivalent to codes) on recaptured individuals provided information on release date, site, and larval age at release.

Five to 13 day-old larvae were transported from the hatchery to release sites and released directly into the rivers in late April/early May. Release sites were chosen based upon occurrences of wild striped bass larvae in collections during the week preceding the initial stocking date in each year. Tests at the Chesapeake Biological Laboratory (CBL) and at an on-site laboratory on the Nanticoke River (1992–1993) indicated that no significant mortality was associated with the stocking procedure (Secor *et al.*, 1995b, 1996). Thus, larvae, were not acclimated to river water prior to their release.

Recaptures of released larvae were obtained in several one-day ichthyoplankton surveys from late April to early June. Sampling gears were a 60-cm diam. 505- μ m mesh plankton net and a 2-m² mouth-opening, 707- μ m mesh Tucker trawl. On each survey date, collections were made at 8 to 11 stations spanning the known nursery area of wild striped bass larvae. Secor *et al.* (1995b, 1996) provide details on methods and analysis of ichthyoplankton samples and water quality datasets. Juvenile striped bass were surveyed by Maryland Department of Natural Resources in 37-m seine collections from 13 July to 15 September in all years. Three surveys were conducted annually at six (Patuxent River) and eight sites (Nanticoke River) that have been sampled historically to index juvenile abundance (Minkinen, 1993).

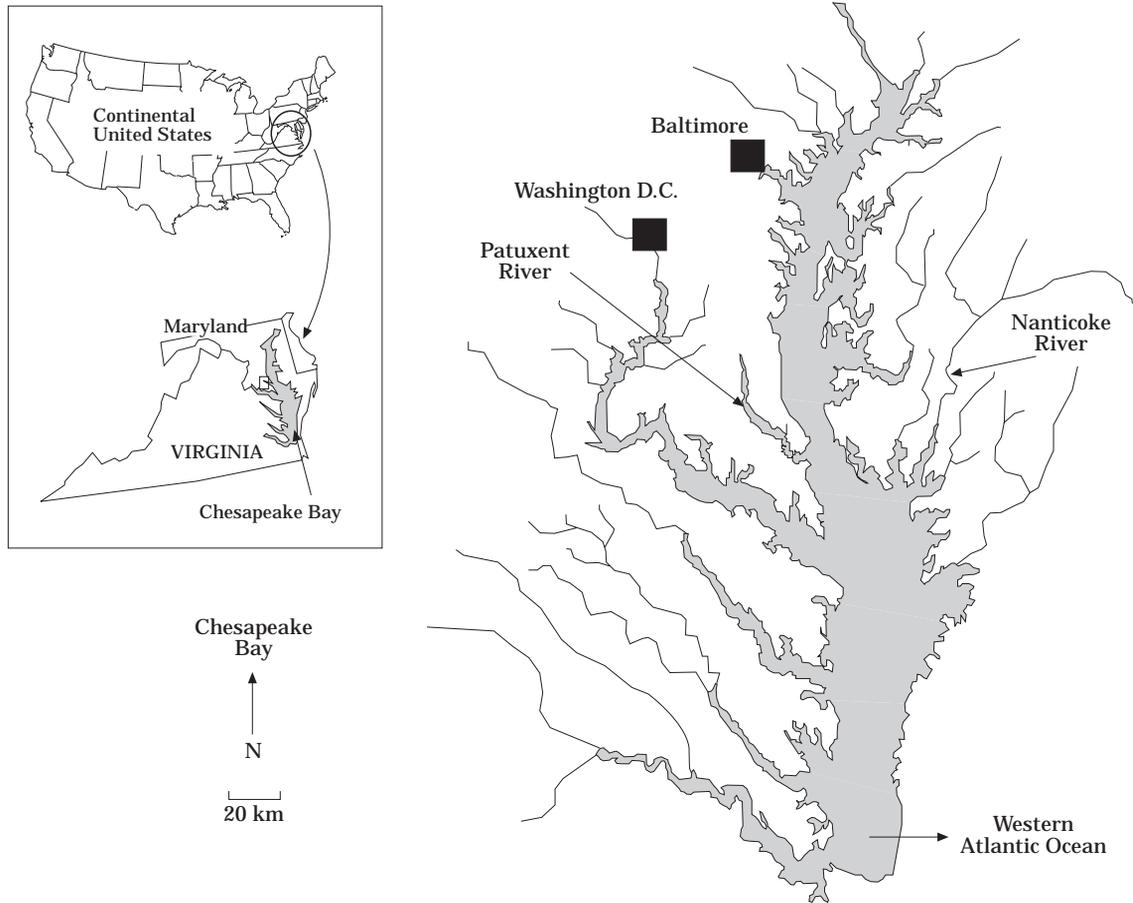


Figure 2. Map of Chesapeake Bay showing Patuxent and Nanticoke Rivers.

Otoliths were examined for subsampled larvae and juveniles (Secor *et al.*, 1991b). Subsample sizes were constrained by our ability to process numerous otoliths and were not proportional to differences in larval or juvenile abundance among years. The presence of chemical marks on otolith increments was determined under an epifluorescence microscope. Identification of specific otolith marks (Table 1) allowed release date, larval age(s) at release, and sites of release (1992 experiment only) to be determined.

Growth and mortality rates of marked larvae were determined based upon their lengths, known ages and estimated abundances. Growth rates of larvae were estimated from exponential regressions of length-on-age (Ricker, 1975). Growth and mortality rates from the exponential models were compared among groups using a Newman-Keuls test (Zar, 1974).

During June, the Maryland Department of Natural Resources released coded wire-tagged (CWT), young-of-the-year (40–60 mm SL) striped bass in 1991, 1992, and 1993, respectively (Minkinen, 1993). The number of juveniles stocked, adjusted for transport mortality and

tag loss, was: 97 611; 71 124; and 209 133 in 1991, 1992 and 1993, respectively. Based upon abundances of recaptured CWT juveniles and juveniles originating from our larval releases, we were able to estimate recruitment potential of our released larvae. Abundances of juveniles from our marked larval releases (N_{CM}) at the time of release of CWT juveniles were estimated (Secor and Houde, 1995b) by:

$$N_{CM} = \sum_{i=1}^x (N_{CWT} R_{CM_i}) R_{CWT}^{-1} \quad (1)$$

where N_{CWT} = number of released juveniles with coded wire tag, adjusted for tag loss and stocking mortality;

$i(1 \dots x)$ = experimental larval release group;

R_{CM_i} = number of recaptured juveniles that had been released as larvae and coded for release i by the unique chemical mark on their otoliths;

R_{CWT} = number of coded wire-tagged juveniles recaptured in the juvenile sampling program.

By applying Equation 1, estimates of abundances of juveniles were obtained for each experimental larval release. The variance of abundance estimates of the

otolith-marked juveniles was calculated based upon an assumed Poisson distribution (Ricker, 1975). In 1991 and 1992, all larval release groups were identifiable based upon the unique marks and mark combinations on their otoliths. In 1993, only one of the individual release groups (second release date, larvae released at 12 d post-hatch) could be confidently distinguished in the juvenile recaptures. Specific identification of other marked groups in 1993 would have depended upon very accurate (± 3 d) ageing, which was not possible based upon analysis of otoliths in juveniles (Secor and Dean, 1989).

Overall survival rate to the 40–60 mm stage for each larval release group (S_i) was estimated by:

$$S_i = N_{CM_i} / (N_o)^{-1} \quad (2)$$

where N_{CM_i} = estimated number of 40–60 mm juveniles from experimental release i (Equation 1) and;

N_o = number of larvae stocked in experimental release i adjusted for mortality associated with the stocking procedure.

Cohort biomass production model

The Chesapeake Bay striped bass stocking program has depended upon releases of juveniles at either ca. 55 d post-hatch or ca. 220 d post-hatch. We compared these strategies with that of releasing larvae at first feeding (7 d post-hatch). To undertake the comparison, stage-specific growth and mortality rates and weights were obtained for the following periods: –2.5 to 6 d post-hatch (embryo), 7 to 55 d post-hatch (larva), and 56 to 220 d post-hatch (juvenile). Hatching was presumed to occur at 2.5 d after spawning (Secor *et al.*, 1992). Estimates of vital rates and wet weights of wild larvae and juveniles were obtained from field studies in the Patuxent River (Minkinen, 1993; Secor and Houde, 1995a; Secor *et al.*, 1995b) and the Nanticoke River (Minkinen, 1993; Kellogg *et al.*, 1996; Secor *et al.*, 1996). Cohort-specific rates of larval-stage growth and mortality were available for all years. Initial egg wet weight was estimated to be 1.0 mg (Secor *et al.*, 1992).

Estimates of growth and mortality rates and weights for hatchery-produced fish were calculated from data provided by staff of the Potomac Electric Power Company, who produced the juveniles stocked into the Patuxent and Nanticoke River (PEPCO, 1987–1995). Pond-specific rates of larval growth, mortality, and weight were available for several ponds in the period 1987–1995. Only mean values of juvenile survival and growth were reported in PEPCO documents. Wet weights at 7-d post-hatch of hatchery-produced larvae stocked into the Nanticoke River were measured by Kellogg (1996).

Cohort, stage-specific biomass (B_S) was estimated as:

$$B_S = B_{S-1} [(W_S / W_{S-1})^{1 - (M_S / G_S)}] \quad (3)$$

where B_{S-1} represents biomass at the end of the previous stage, W_S and W_{S-1} are median weights at the end of stages S and $S-1$, and G_S and M_S are daily instantaneous growth-in-weight and mortality rates for stage S . This method, which was adapted from Houde's (1996) model of biomass proliferation, allowed cohort biomass proliferation to be adjusted according to expected stage-specific weights. To reduce the effects of outliers, median values were chosen to represent stage-specific vital rates and weights. In cases where three or fewer data were available, mean values were used.

In our comparison, we adopted a model that depended upon stocking a maximum biomass of juveniles (at 55 or 220 d) in a year of poor natural reproduction. B_o , the initial spawned biomass, was specified as 2×10^6 g for natural cohorts (egg production = 2×10^9 , ca. 1000 spawning females). Field estimates of spawned egg biomass in the Patuxent and Nanticoke Rivers ranged between 0.7 and 6.7×10^6 g (Secor and Houde, 1995a,b; Kellogg *et al.*, 1996). Thus, the model represented a year of low egg production. Initial egg production in the hatchery was stipulated at 10×10^6 , ca. five spawning females, egg biomass = 10^4 g. Ten million eggs, or ca. 2.5×10^6 first-feeding larvae, represents the maximum number which PEPCO can stock into its ponds for production of juveniles (PEPCO, 1987–1995).

Striped bass larval mortality rates are dependent upon environmental influences and vary by >4-fold in nature (Houde, 1996). Therefore, three possible larval mortality rates were used in the model: $Z=0.05$, 0.12, or 0.20 d^{-1} . These rates were similar in range to mortality rates experienced by larvae stocked into the Patuxent and Nanticoke Rivers in our release–recapture experiments. Hatchery estimates of larval mortality in ponds were dependent upon their initial abundance estimates of larvae. Hatchery personnel had visually approximated the densities of striped bass larvae that were transported to ponds for grow-out. Based upon volumetric estimates that we obtained in our larval mark-recapture experiments, we believe that actual abundances had been underestimated by at least 2-fold. Therefore, reported pond survival rates were probably overestimated by at least a factor of two. In our analysis, we chose two estimates, $Z=0.025$ or 0.05 d^{-1} , to bracket what we believe were likely pond mortality rates. A survey of South Carolina hatchery-pond survival rates by Secor and Dean (1989) indicated a mean larval mortality rate of 0.039 d^{-1} .

Costs of larval and juvenile production were estimated using current commercial values: \$0.003, \$0.10, and \$0.45 each for larvae, and 55 d and 220 d juveniles,

Table 1. Striped bass larval mark-recapture experiments, Patuxent River (1991) and Nanticoke River (1992–1993). Release records for striped bass larvae by year. Broods are designated according to Maryland Department of Natural Resources hatchery records. Release site indicates batches of larvae which were released at downriver and upriver sites within the striped bass nursery. "Ages marked" indicate the ages at which larvae were chemically immersed for 6 h to mark their otoliths. Numbers released were estimated volumetrically (i.e. number m⁻³) in rearing troughs 6 h before release.

Broods	Larval release date	Release site	Age at release (d)	Ages marked (d)	Millions released	g ± s.e. (d ⁻¹)	G (d ⁻¹)	M ± s.e.
1991 – Patuxent River								
P-8	26 April	Downriver	9	0	0.72	—	—	—
P-9, 10, 11, 12, 13	26 April	Upriver, Downriver	9	8	3.24	0.037 ± 0.003	0.157	0.154 ± 0.049
P-12, 13	30 April	Upriver, Downriver	13	6	1.44	0.032 ± 0.001	0.139	0.085 ± 0.039
P-14, 16, 17, 18	30 April	Upriver, Downriver	9	2	1.14	0.036 ± 0.008	0.153	0.188 ± 0.084
Total released					6.54	0.032 ± 0.001	0.150	—
1992 – Nanticoke River								
N-13	24 April	Downriver	8	7	0.65	0.028 ± 0.0028	0.121	0.091 ± 0.024
N-13	24 April	Upriver	8	5	1.13	0.007 ± 0.0033	0.028	0.159 ± 0.038
N-15, 17, 20	25 April	Downriver	5	1, 3	1.55	0.025 ± 0.0024	0.106	0.075 ± 0.022
N-14, 16	25 April	Upriver	5	1	0.93	0.031 ± 0.0023	0.133	0.103 ± 0.032
N-15, 17, 20	28 April	Downriver	8	1, 3, 6	1.72	0.028 ± 0.0030	0.118	0.149 ± 0.021
N-14, 16	28 April	Upriver	8	1, 6	2.72	0.014 ± 0.0017	0.061	0.145 ± 0.118
N-18, 21	1 May	Downriver	10	0, 7	2.40	—	—	0.161 ± 0.399
N-19, 22	1 May	Upriver	10	0, 9	2.12	0.025 ± 0.0038	0.106	0.135 ± 0.051
Total released					13.22	0.026 ± 0.0013	0.111	—
1993 – Nanticoke River								
N-1, N-3, N-4	21 April	Upriver, Downriver	10	8	2.18	—	—	—
N-5, N-7	25 April	Upriver, Downriver	12	8	1.07	0.035 ± 0.0029	0.153	0.068 ± 0.019
N-11, N-13	25 April	Upriver, Downriver	9	5	2.48	0.034 ± 0.0023	0.147	0.108 ± 0.021
N-16, N-17, N-18	29 April	Upriver, Downriver	6	4	3.98	0.030 ± 0.0022	0.128	0.047 ± 0.032
N-19, N-20	3 May	Upriver, Downriver	6	4	2.18	0.030 ± 0.001	0.130	0.039 ± 0.009
Total released					11.89	0.032 ± 0.0015	0.136	—
Total released					31.65			

g = Length-specific growth coefficient; G = weight-specific growth coefficient. G coefficient was based upon converted lengths using a weight-length relationship (Houde and Lubbers, 1986). M = Daily instantaneous larval mortality rate.

respectively. These are 1996 cost estimates (profit excluded) provided by Keo Fish Farms in Arkansas, USA (T. M. Freeze, P.O. Box 166, Keo, AR, USA, pers. comm.).

Results

Larval release recapture experiments

Total numbers of marked larvae released were 6.54, 13.22, and 11.89 million larvae in 1991, 1992, and 1993, respectively (Table 1). From 1.78 to 4.52 million larvae were released on each stocking date. The proportion of larvae that were of hatchery origin and sampled in ichthyoplankton tows was four times higher in 1991 and 1992 than in 1993. In 1991 ichthyoplankton surveys, 37.5% (134/357 marked/total larvae) of all subsampled larvae contained a chemical mark. In 1992, the recapture proportion was similar: 32.5% (88/271 marked/total larvae). However, in 1993 only 8.6% (42/488 marked/total larvae) of subsampled larvae were marked.

Growth and mortality rates of released larvae

Mean weight-specific growth estimates for released larvae were 0.15 (16% d⁻¹), 0.11 (12% d⁻¹), and 0.14 (15% d⁻¹) in 1991, 1992, and 1993, respectively (Table 1). Specific growth rates of individual groups ranged between 3 to 17% d⁻¹. Analyses of covariance indicated significantly lower weight-specific growth rate in 1992 than in 1991 or 1993 (p < 0.001). Analyses of covariance did not detect significant differences (p > 0.05) among growth rates of release groups within each year.

Mortality rates (M) of the released larvae ranged from 8 to 17% d⁻¹ in 1991, 7 to 15% d⁻¹ in 1992 and 4 to 10% d⁻¹ in 1993. The rates were nearly twice as high in 1991 and 1992 as in 1993. Mean mortality rates were 0.14, 0.13, and 0.07 d⁻¹ in 1991, 1992, and 1993, respectively and differed significantly (ANCOVA, p > 0.05). Three of the four releases in 1993 experienced significantly lower mortality rates than all release groups in 1991. Mortality rates of three of the four combined-site releases made in 1992 also exceeded 1993 rates. Predicted survivorships at 55 d post-hatch (based upon

Table 2. Striped bass larval mark-recapture experiments, Patuxent River (1991) and Nanticoke River (1992–1993). Petersen population estimates for juveniles on 14 July 1992 and 13 July 1993. Total wild population estimate from Minkinen (1993) and Minkinen (pers. comm.) does not include hatchery-stocked juveniles with coded wire tags. n=Number of recaptured juveniles that originated from release of hatchery-produced larvae.

Release date	Release site (RK)	n	Petersen estimate	95% Confidence intervals	Survival (%)
1991 – Patuxent River					
26 April	Up-, Downriver	5	22 184	5385–39 381	0.56
1 May	Up-, Downriver	2	8874	387–18 849	0.34
All releases	Up-, Downriver	7	31 058	9425–48 469	0.48
Total wild			110 922		
Released contribution (%)			23.5		
1992 – Nanticoke River					
24 April	Upriver	0	0	—	0.0
24 April	Downriver	0	0	—	0.0
25 April	Upriver	4	15 025	2682–55 428	0.97
25 April	Downriver	8	30 050	9068–85 824	3.23
28 April	Upriver	3	11 269	1660–47 765	0.65
28 April	Downriver	14	52 588	20 689–127 714	1.93
1 May	Upriver	5	18 781	4342–63 601	0.78
1 May	Downriver	0	0	—	0.0
All releases	Up-, Downriver	34	127 714	88 273–178 424	0.97
Total wild			315 528		
Released contribution (%)			28.8		
1993 – Nanticoke River					
25 April (12-d larvae)	Up-, Downriver	2	120 809	12 081–434 913	11.29
All releases	Up-, Downriver	8	483 237	205 376–954 392	4.06
Total wild			9 132 141		
Released contribution (%)			5.3		

average age at release=8 d post-hatch) were 0.14% in 1991, 0.22% in 1992, and 4.71% in 1993.

Juvenile recaptures

In juvenile subsamples, 20 of 87 (23%), 34 of 148 (23%), and 8 of 131 (6%) individuals bore hatchery marks on their otoliths in 1991, 1992, and 1993, respectively. Lower proportions of marked fish occurred in juvenile collections than in larval samples due to exclusion of samples of wild larvae taken prior to the period of larval releases. Presumably, these early spawned cohorts were included in the juvenile sample. Estimated abundance of otolith-marked juveniles in mid-July was four times higher in the Nanticoke 1992 experiment (127 714) than in the 1991 Patuxent experiment (31 058). The Nanticoke 1993 abundance estimate (483 237) was 3.8 times higher than the 1992 estimate and 15 times higher than the 1991 Patuxent estimate (Table 2). Confidence intervals were broad but supported the inferences of: (1) positive contributions from the larval releases to overall (wild+hatchery) juvenile abundances; and (2) differing levels of contribution among years. Overall survival rate (S_j) from the time that larvae were released until their

recapture as juveniles in mid-July was higher in 1993 (4.06%) than in 1991 (0.48%) or 1992 (0.97%).

Biomass model

The estimates of stage-specific mortality rate for hatchery-produced larvae and juveniles were substantially lower than mortality rates for wild larvae and juveniles (Table 3). Mean survival from spawning to first-feeding larvae was 0.7 and 26.8% for wild and hatchery groups, respectively. Median survival rates during the larval stage of wild striped bass were much lower (0.13%) than those reared in hatchery ponds (31%). Juvenile survival rates were estimated to be 71.9 and 11.7%, for hatchery and wild groups, respectively. Overall survival until 220 d post-hatch was estimated to be 0.0001% for wild fish and 6.0% for hatchery fish.

Growth rates were negative during the embryo stage for both hatchery and wild groups, due to the utilization of endogenous yolk and oil reserves (Zastrow *et al.*, 1989). Approximately 30 to 40% of original egg biomass was lost during the embryo stage (ending at first feeding), indicating a 4.2 to 6.0% rate of weight loss per day.

Table 3. Striped bass stocking biomass model. Estimates of stage-specific mortality and growth rates and masses used to model biomass in hatchery and naturally produced striped bass.

Source	Mean \pm s.e.	Median	n	Mean \pm s.e.	Median	n	Mean \pm s.e.	Median	n
	M_1 (d^{-1})			M_2 (d^{-1})			M_3 (d^{-1})		
Pax-91	<u>0.348</u>	—	1	0.226 ± 0.079	<u>0.149</u>	8	<u>0.012</u>	—	1
Nan-92	<u>0.706</u>	—	1	0.191 ± 0.037	<u>0.182</u>	7	<u>0.005</u>	—	1
Nan-93	<u>0.690</u>	—	1	0.125 ± 0.018	<u>0.131</u>	8	<u>0.021</u>	—	1
PEPCO	—	—	—	0.025 ± 0.003	0.017	61	0.002	—	8
SC	0.155 ± 0.026	—	3	0.039 ± 0.009	0.020	12	—	—	—
Wild	<u>0.581 ± 0.117</u>	—	3	0.183 ± 0.031	<u>0.141</u>	23	<u>0.013 ± 0.005</u>	—	3
Hatch	<u>0.155 ± 0.026</u>	—	3	0.025 ± 0.003	<u>0.017</u>	73	<u>0.002</u>	—	8
	G_1 (d^{-1})			G_2 (d^{-1})			G_3 (d^{-1})		
Pax-91	—	—	—	0.126 ± 0.005	<u>0.126</u>	7	<u>0.020</u>	—	1
Nan-92	—	—	—	0.165 ± 0.011	<u>0.171</u>	8	<u>0.021</u>	—	1
Nan-93	—	—	—	0.159 ± 0.009	<u>0.159</u>	9	<u>0.023</u>	—	1
PEPCO	—	—	—	0.190 ± 0.003	0.188	62	0.025 ± 0.0001	0.025	24
Wild	—	—	—	0.151 ± 0.006	<u>0.146</u>	24	<u>0.021 ± 0.0001</u>	—	3
Hatch	—	—	—	0.190 ± 0.003	<u>0.188</u>	62	0.025 ± 0.0001	<u>0.025</u>	24
	Wt_1 (mg)			Wt_2 (mg)			Wt_3 (mg)		
Pax-91	0.582 ± 0.069	<u>0.611</u>	6	184.58 ± 68.91	<u>102.71</u>	7	<u>10 250.50</u>	—	—
Nan-92	0.725 ± 0.027	<u>0.705</u>	8	787.81 ± 280.18	<u>350.80</u>	7	<u>10 205.50</u>	—	—
Nan-93	0.630 ± 0.053	<u>0.651</u>	9	675.57 ± 249.92	<u>275.26</u>	9	<u>10 205.50</u>	—	—
PEPCO	—	—	—	370.67 ± 54.25	<u>332.09</u>	24	$24 783.30 \pm 1917.45$	<u>23 785.90</u>	24
CBL	0.586 ± 0.169	—	2	—	—	—	—	—	—
Wild	0.650 ± 0.030	<u>0.673</u>	23	560.30 ± 136.76	<u>275.26</u>	23	<u>10 205.50</u>	—	1
Hatch	<u>0.586 ± 0.169</u>	—	2	370.67 ± 54.25	<u>332.09</u>	24	$24 783.30 \pm 1917.45$	<u>23 785.90</u>	24

Pax-91=Patuxent River 1991, Nan-92=Nanticoke River 1992, Nan-93=Nanticoke River 1993, PEPCO=Potomac Electric Power Company Aquaculture Program, SC=South Carolina Department of Natural Resources hatchery (Secor *et al.*, 1992), CBL=Chesapeake Biological Laboratory, Wild=pooled data from 1991–1993 ichthyoplankton surveys, Hatch=pooled data from PEPCO, SC, and CBL. M_1 =Embryo mortality rate, M_2 =larval mortality rate, M_3 =juvenile mortality rate, G_1 =embryo growth rate, G_2 =larval growth rate, G_3 =juvenile growth rate, Wt_1 =larval weight at 7 d post-hatch (mg), Wt_2 =juvenile wet weight at 55 d post-hatch, Wt_3 =juvenile wet weight at 220 d post-hatch. Values underlined are those used in the biomass model.

Weight-specific growth rates (Table 3) estimated for hatchery-reared larvae ($20.7\% d^{-1}$) and juveniles ($2.5\% d^{-1}$) were slightly higher than those of wild larvae ($15.7\% d^{-1}$) and juveniles ($2.1\% d^{-1}$). At 220 d after hatch, median weight of hatchery fish (23.8 g) was ca. twice the mean weight of wild fish (10.2 g).

Wild striped bass cohorts in the Patuxent and Nanticoke Rivers experienced nearly a three order of magnitude loss of biomass during the embryo stage. Two of the three cohorts continued to lose biomass during the larval stage. All cohorts showed a gradual accumulation of biomass during the juvenile stage (Fig. 3). Interestingly, annual cohort biomass at 220 d after hatch was substantially lower than the spawned egg biomass in all years. Although actual juvenile abundances were highest in 1993 (Table 3; Minkkinen, 1993), when the modelled initial biomass of eggs was standardized to 2000 kg, the relatively low juvenile mortality rates estimated in 1991 and 1992 resulted in higher modelled (standardized) biomasses than in 1993.

Under all scenarios of larval mortality rates, hatchery fish had high rates of biomass accumulation during the larval stage (Fig. 4). At a low hatchery mortality rate ($M=0.025$), biomass at 55 d substantially exceeded that

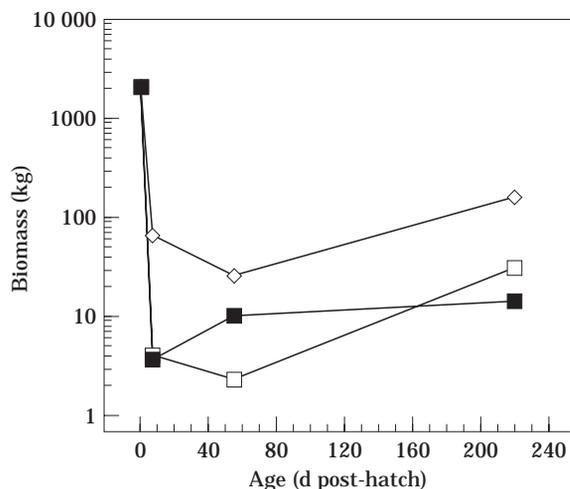


Figure 3. Ontogenetic changes in striped bass cohort biomass for wild larvae and juveniles in the Patuxent (1991) and Nanticoke (1992, 1993) Rivers. Note that for the purpose of comparison, initial cohort biomass was specified at 2000 kg, despite observed differences in egg productions among years. Data used to determine annual cohort biomasses are presented in Table 3: Pax-91 (\diamond); Nan-92 (\square); Nan-93 (\blacksquare).

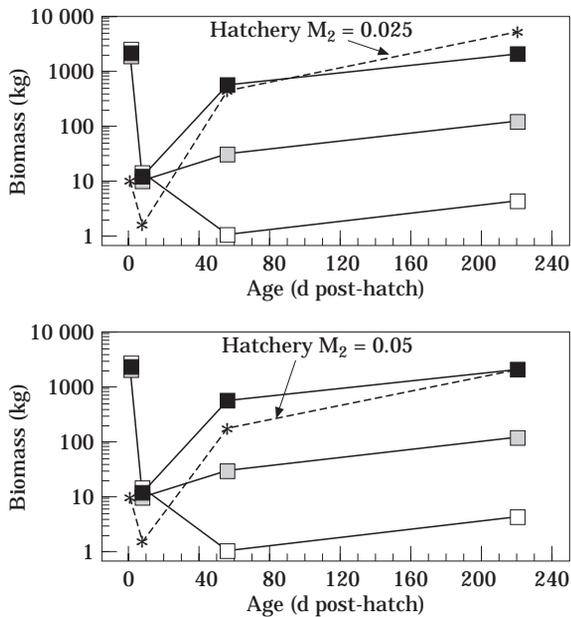


Figure 4. Ontogenetic changes in striped bass cohort biomass for wild larvae and hatchery larvae and juveniles. Hatchery larval stage mortality is specified at low ($M_2=0.025 \text{ d}^{-1}$) or high ($M_2=0.05 \text{ d}^{-1}$) levels. Within each plot, three levels of wild larval-stage mortality are specified: Hatchery (*); Wild, $M_2=0.20$ (\square); Wild, $M_2=0.12$ (\square); Wild, $M_2=0.05$ (\blacksquare).

of wild juveniles that had experienced high and intermediate levels of larval mortality and was equivalent to that of wild juveniles that had experienced low rates of larval mortality. At a higher hatchery mortality rate ($M=0.05$), biomass at 55 d remained much higher than wild juveniles that experienced high and intermediate mortality rates but was three times lower than wild juvenile biomass when wild larvae experienced their lowest mortality rate. Rates of biomass increase during the larval stage were similar between hatchery and wild groups under the scenario of high ($M=0.05$) hatchery larval mortality and low ($M=0.05$) wild larval mortality.

Relative biomass estimates for hatchery larvae and juveniles at the higher larval mortality rate ($M=0.05$) indicated a 22-fold biomass accumulation between spawning and 55 d post-hatch, and a 220-fold increase from spawning to 220 d post-hatch. At $M=0.025$ for hatchery larvae, biomass accumulation from spawning to 55 d and 220 d post-hatch was 33-fold and 364-fold, respectively.

Hatchery stocking contributed >80% to levels of juvenile biomass when 55 d or 220 d juveniles were stocked under scenarios of high or intermediate levels of wild larval mortality rate (Fig. 5). Under the scenario of lowest mortality rates of wild larvae, stocked 55 d juveniles would comprise <43% of the total juvenile population and stocked 220 d juveniles would comprise <70% of the population at low rates of larval survival in the

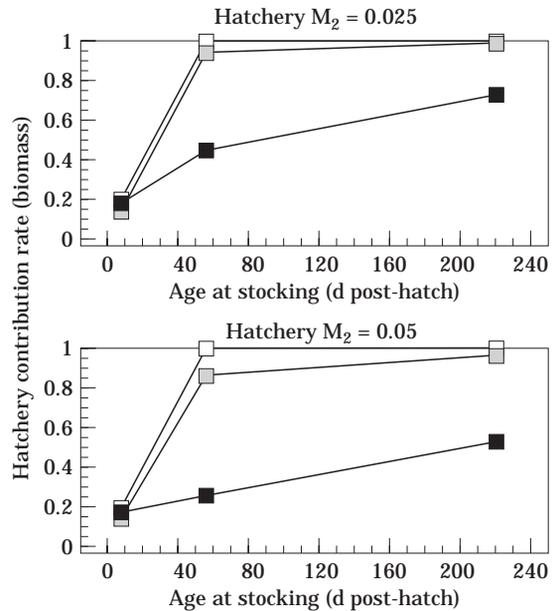


Figure 5. Hatchery contribution rates (hatchery biomass/hatchery+wild biomass) of striped bass stocked at 7, 55 or 220 days after hatch. Scenarios of wild and hatchery larval mortality rates are shown: Wild, $M_2=0.20$ (\square); Wild, $M_2=0.12$ (\square); Wild, $M_2=0.05$ (\blacksquare).

hatchery environment. Stocked larvae would comprise 17% of the total population. Because stage-specific weights were similar between hatchery and wild juveniles, numerical contributions of hatchery fish at 55 and 220 d post hatch under various scenarios of larval mortality were essentially identical to contribution rates based upon biomass.

Stocking juveniles at 55 days and 220 days post-hatch would cost \$0.23 and \$0.45, respectively for each 220 d old "recruit" under all larval mortality rate scenarios. Under favourable larval conditions ($M_2=0.05$), stocking 7 d old larvae would cost \$0.18 per 220 d old recruit. Costs per recruit for larval stocking at intermediate and high natural larval mortality rates were \$2.21 and \$103.00, respectively.

Discussion

Contribution of stocked larvae to juvenile abundances

Larval stocking can be an effective method to enhance striped bass stocks during years of low egg production or unfavourable nursery conditions. In the Nanticoke River during 1992, marked juveniles, originating from the 13.2 million released larvae, comprised nearly 30% of the juvenile population (not counting nearly 100 000 stocked juveniles). In the Patuxent River during 1991, a similar contribution (20–35%) to the juvenile population

was made by larval stocking. In the Nanticoke River during 1993, when natural egg production and embryo survival was high, only 5% of juveniles originated from the 11.9 million larvae that were stocked. However, while the relative contribution was small in 1993, numbers of juveniles originating from released larvae were nearly four times higher in 1993 than in 1992 (Table 2). Results suggest that larval releases may contribute substantially to recruitment of striped bass in years of poor (e.g. 1991) and "average" natural juvenile production (e.g. 1992).

Stocked larvae made a substantial contribution to natural abundances because egg and yolk-sac larval mortality was greatly reduced in the hatchery. Most of the wild striped bass cohort's biomass was lost during these stages. In 1992, for example, the juveniles produced from larval releases into the Nanticoke River were survivors from ca. 40 million hatchery-produced eggs. In contrast, wild juveniles in 1992 were survivors from a natural egg production estimated to be 2.44×10^9 eggs (Kellogg *et al.*, 1996). Considering estimated juvenile abundances (Table 2), an approximately 20-fold reduction in egg-to-juvenile mortality was achieved through hatchery incubation of eggs and rearing of yolk-sac larvae prior to release, relative to average mortalities experienced by wild cohorts. In 1993, increased egg production in the Nanticoke (6.39 billion; Kellogg *et al.*, 1996) and improved survival of yolk-sac larvae (Table 3) "swamped" the numbers of stocked larvae. Although relative contribution of juveniles from the stocked larvae was diminished in 1993, numbers of juvenile survivors were higher than in 1991 or 1992.

A central issue in stocking programs is whether hatchery fish enhance or replace natural production (Svasland and Kristiansen, 1990; Watanabe, 1990; Yamaoka *et al.*, 1991; Nordiede and Fossa, 1992; Whalen and LaBar, 1994). Chesapeake Bay striped bass show very large annual fluctuations in juvenile abundance with infrequent dominant year-classes (Fig. 1) due to variability in early survival rates (Uphoff, 1989; Rutherford and Houde, 1995; Secor and Houde, 1995a). Therefore, in most years juvenile abundance does not exceed the carrying-capacity of the environment. Rutherford (1992), using the model of Shepard and Cushing (1980), analysed survival and abundance data for the Potomac River (Chesapeake Bay) and found that density-dependent survival during the larval stage was unlikely in striped bass.

Finding the right spot

Because stocked striped bass larvae were retained within a limited estuarine region, larval stocking as an enhancement strategy should be especially effective if larvae can be released at times and places that are favourable for their growth and survival. For instance, in 2 out of 3

years (1991 and 1992), the average annual cohort lost biomass during the larval stage (Fig. 3). However, several "weekly" larval cohorts (larvae hatched within the same 4–6 d period) during these years increased in cohort biomass (Secor and Houde, 1995a; Houde, 1996; Kellogg *et al.*, 1996). Further, in the Patuxent River (1991) Secor and Houde (1995a) showed that high survival rates occurred when weekly cohorts experienced mean temperatures of 16–20°C during their first 25 d after hatch. In that year, larvae were stocked during a period of favourable temperatures. Complete losses of release groups in our experiments also provide critical insight on times and places not conducive to survival of stocked larvae. In 1993 (Nanticoke River), a storm event apparently caused complete loss of larvae stocked on 24 April; no larvae or juveniles were recovered from this release group (Secor *et al.*, 1996). Similarly, in 1991, complete loss of a group of stocked larvae occurred when the release site was downstream from the maximum turbidity zone and salt front, which may serve as a retention feature, delimiting the downstream boundary of striped bass nurseries (Van den Avyle and Maynard, 1994; Secor *et al.*, 1995b, 1996). Overall, results from three years of ichthyoplankton surveys and larval mark-recapture experiments indicated that survival of released larvae could be substantially higher than that of average weekly cohorts of wild larvae if larvae were strategically released under favourable conditions. These conditions include: (1) periods of stable and rising temperatures between 16 and 20°C alkalinity >15 mg/L as CaCO₃; pH>6.9; and (2) storm-free weather, especially during dry years (Secor *et al.*, 1996).

Meteorological forecasting and surveys of nursery water quality could increase the probability of stocking larvae into favourable conditions. However, weather during April and May is variable and not easily predicted, and hatchery-produced larvae of appropriate ages may not always be available to stock during favourable conditions. Despite these uncertainties, we believe that a long-term larval stocking program could, on average, augment natural striped bass juvenile abundances in poor to average years of natural recruitment.

Stocking strategy: larvae or juveniles?

How efficient is larval stocking in comparison to stocking hatchery-produced juveniles? We addressed this question by assembling available data, estimating stage-specific vital rates and weights, and analysing rates of biomass accumulation and hatchery contributions under scenarios of releasing larvae, 55 d juveniles or 220 d juveniles. Larval mortality rate estimates were the most variable (wild larvae) or uncertain (hatchery larvae). Therefore, these rates were deliberately varied to evaluate larval vs. juvenile stocking strategies.

We believe that biomass estimates of wild striped bass at 55 d, post-hatch (Fig. 3) for the 1991–1993 annual cohorts may have been underestimated. Estimates (Secor and Houde, 1995a; Kellogg *et al.*, 1996) of cohort abundances at 55 d post-hatch were 14 930, 5435 and 28 387 for 1991, 1992, and 1993, respectively. These estimates were one to nearly three orders of magnitude less than mid-July abundance estimates for juveniles at ca. 85 d post-hatch (Table 3). Late-stage larvae of striped bass are difficult to sample and estimates of mortality rates are uncertain during the late larval and early juvenile period because of an ontogenetic habitat shift from freshwater pelagic to brackish benthic habitats. If mortality rates were lower during this period than we had estimated, substantially higher biomass gains compared to those predicted may have been realized. Finer scale resolution of ontogenetic changes in mortality and growth rates during the larval stage would probably result in higher biomass estimates at 55 d post-hatch because the ratio M/G is expected to decline with size (see Equation 3). Because of these uncertainties, a prudent approach was to consider several possible mortality rates in the field (Fig. 4).

Patterns of biomass accumulation indicated that under a scenario of low natural egg production, hatchery releases of larvae and juveniles could make >10% contributions to overall abundances (Fig. 5). If larvae occur in favourable conditions (intermediate or low mortality rates), then positive rates of biomass increase were expected during the larval stage (Fig. 4). However, under all scenarios, the highest biomass accumulations were predicted for larvae held in hatchery environments. From the perspective of maximizing striped bass production rates, hatchery contribution would be highest if juvenile striped bass were stocked.

When costs were factored into hatchery contribution rates, stocking 55 d old juveniles was predicted to be the most cost effective strategy if: (1) hatchery larval mortality rate was low ($M=0.025\text{ d}^{-1}$); and (2) wild larval survival was poor or intermediate ($M=0.20$ or 0.12 d^{-1}). However, in years of high survival rates of wild larvae, the cost per unit hatchery contribution was 28–250% lower for released larvae than for juveniles released at 55 d or 220 d post-hatch. Rearing larvae and juveniles under such situations is inefficient because hatchery-pond environments do not increase rates of biomass accumulation over that which would occur in the wild. The model did not consider how production costs at hatcheries would increase with decreasing pond production rates (i.e. hatchery $M_2=0.05$) because data was unavailable. However, cost-effectiveness of stocking juveniles would be sensitive to hatchery larval mortality rate, and future efforts should be aimed at refining this estimate and reducing larval-stage mortality in hatchery environments.

Larval stocking as a strategy to enhance juvenile production and recruitment of striped bass has other advantages over juvenile stocking. We believe that stocked larvae will adopt behaviours that lead to successful feeding, growth, and survival in the natural environments into which they are released. Released larvae had similar growth and mortality rates and dispersal patterns compared to contemporary wild cohorts (Secor *et al.*, 1995a,b, 1996). Larvae reared in ponds and stocked as juveniles, may develop behaviours that are favourable in the “artificial” pond environment but not in juvenile nurseries. For example, Andreassen (1995) found that hatchery-origin 220 d old juveniles suffered high predation mortality ($M=0.16$ to 0.36 d^{-1}) during the first 4 d after stocking in the Patuxent River, apparently because their behaviour promoted cannibalism by older wild striped bass. It is probable that fish stocked as larvae and surviving to the juvenile stage will behave more appropriately in the natural environment and will have increased survival.

Application of approach to other species

Comparisons of ontogenetic patterns of cohort biomass accumulation or loss between hatchery and natural environments could provide perspective on the efficiency of stock enhancement strategies in other anadromous and coastal fishes. Salvanes *et al.* (1994) used a similar approach, which considered the ratio M/G as an index of cohort biomass production to evaluate stocking different age (size) cod (*Gadus morhua*) juveniles into fjords after pond production. Approaches described here require accurate estimates of vital rates in natural and hatchery environments. Otolith-based ageing of larvae and juveniles, and larval-mark recapture experiments, can provide estimates of vital rates in the field (Tsukamoto *et al.*, 1989; Secor *et al.*, 1995a). However, hatchery-based estimates of embryo and larval-stage abundances may require more accurate methods than are currently employed.

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