

A Model Analysis of Strategies for Enhancing Stocking Success of Landlocked Striped Bass Populations

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Abstract.—Poor first-year winter survival of stocked fingerling striped bass *Morone saxatilis*, resulting from slow summer growth and small body size in the fall, has limited the sport fishery of Smith Mountain Lake, Virginia. We used an individual-based model to examine different strategies for improving the success of the striped bass stocking program. For two spatially explicit compartments (littoral and pelagic zones) assigned for Smith Mountain Lake, the model simulates daily movement, consumption, growth, and mortality of juvenile striped bass from the time of stocking in early summer until 1 May of the next year. Model predictions of fish prey consumption, predator–prey size relationships, first-year survival, and fall versus spring length–frequency distributions were similar to observed data. Simulations were conducted to examine the effects of fingerling size, stocking density, and day of year at introduction on first-year growth, survival, and recruitment to age 1 and to determine the sensitivity and robustness of the proposed versus the existing stocking strategy to interannual variation in the population dynamics of alewife *Alosa pseudoharengus* and water temperature regimes. Results indicated that stocking striped bass at a median total length of 52 mm on 8 June (rather than 42 mm on 15 June as is presently done) and maintaining the current stocking density at 300,000 fingerlings would result in the largest percent increases in first-year growth, survival, and the number of age-1 recruits. Sensitivity-analysis results indicated that those factors influencing predator–prey size relationships (e.g., timing of alewife spawning, age-0 alewife growth rate, and water temperature) resulted in the largest percentage changes among model prediction variables for all stocking strategies. For these simulations, the proposed stocking strategy was always more robust to variations in alewife population dynamics and water temperature regimes than the existing stocking strategy.

The stocking of striped bass *Morone saxatilis* into southern U.S. lakes and reservoirs has contributed substantially to the pelagic sport fishery in these systems (Axon and Whitehurst 1985). Because inland bodies of water often lack suitable spawning habitat for striped bass, populations are maintained through the annual stocking of fingerlings. Smith Mountain Lake, an 8,343-ha hydroelectric impoundment in south-central Virginia, typifies other freshwater impoundments in which striped bass populations are maintained strictly on a put-grow-take basis. Annual stockings since

1964 have led to the development of an exceptional trophy fishery, displaying growth and harvest rates among the highest reported for landlocked populations (Hart 1978). However, the number of stocked fingerlings and survival to age 1 varied inversely from 1973 to 83 (Moore et al. 1991). As a result, stocking density was reduced and has ranged from 200,000–400,000 fingerlings since 1984. Despite this modification, the inverse relationship still persists and first-year survival remains low, averaging 25% (range 12–40%; Sutton 1997).

Van Den Avyle and Higginbotham (1980) reported that density of stocked fingerling striped bass and first-year survival were inversely related in Watts Bar Reservoir, Tennessee. Although the authors could not determine the cause of the empirical relationship, they believe that size at stock-

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ing, rather than density-dependent mechanisms, was primarily responsible for the observed relationship. Ney and Orth (1986) suggested that piscivore size at stocking relative to available size of fish prey is often a significant factor limiting consumption and, consequently, growth rate during the first year of life. Smaller individuals often cannot consume fish prey and are relegated to a lower quality, invertebrate diet. As a result, these fish grow at a slower rate than larger, piscivorous conspecifics, resulting in differential growth rates and intracohort size divergence (Shelton et al. 1979; Timmons et al. 1980; Keast and Eadie 1985; Olson 1996; Mooij and van Nes 1998). In addition, body size of piscivores at the end of their first growing season has been identified as a critical determinant of overwinter survival because smaller individuals are more likely to deplete limited energy reserves to meet metabolic demands (Oliver et al. 1979; Gutreuter and Anderson 1985; Miranda and Hubbard 1994a; Garvey et al. 1998; Hurst and Conover 1998; Fullerton et al. 2000). Disproportionately lower winter survival by smaller fish has been attributed to greater susceptibility to starvation (Oliver et al. 1979; Post and Evans 1989; Ludsin and DeVries 1997), piscine predators (Miranda and Hubbard 1994b; Garvey et al. 1998), and abiotic stressors (Adams et al. 1982; Johnson and Evans 1996; Hurst et al. 2000). Because these same size-dependent differences in fish prey consumption, growth rate, and winter mortality regulate recruitment of juvenile striped bass in Smith Mountain Lake (Sutton and Ney, in press), improvements in first-year growth and survival may be achieved by modifying the present stocking strategy to favorably alter predator-prey size relationships.

One approach to aid the analysis of recruitment variability in piscivorous fish populations is the use of an individual-based model (Huston et al. 1988; DeAngelis and Gross 1992; Van Winkle et al. 1993). These models have been shown to realistically simulate growth of age-0 largemouth bass *Micropterus salmoides* in U.S. reservoirs (Adams and DeAngelis 1987; Jaworska et al. 1997), first-year growth and recruitment of walleyes *Stizostedion vitreum* within the Laurentian Great Lakes drainage (Madenjian 1991; Madenjian and Carpenter 1991; Madenjian et al. 1991), size- and density-dependent recruitment of age-0 smallmouth bass *M. dolomieu* in boreal North American lakes (DeAngelis et al. 1991, 1993), and population dynamics of larval and juvenile striped bass in the Potomac River, Maryland (Cowan et al. 1993; Rose and Cowan 1993; Rose et al. 1993).

Madenjian et al. (1991) also used an individual-based model to investigate the effects of size and timing of stocking on first-year growth and survival of walleyes in Lake Mendota, Wisconsin. Because individual-based models are especially amenable for depicting size-dependent interactions underlying feeding, growth, and mortality, they provide an important means to examine the effects of different stocking strategies on recruitment variability of age-0 piscivores.

The objective of this study was to evaluate strategies for stocking fingerling striped bass in Smith Mountain Lake. Through simulations using a site-specific, individual-based model, we examined the influence of size at stocking, day of year at stocking, and stocking density to determine which scenario(s) maximized first-year growth, survival, and number of age-1 recruits. From these simulation results, we made recommendations to the striped bass stocking program maintained by the Virginia Department of Game and Inland Fisheries (VDGIF). We also evaluated the effect on model results of interannual variation in alewife *Alosa pseudoharengus* population dynamics and water temperature regime from baseline conditions. These simulations were conducted to determine the sensitivity and robustness of model predictions and efficacy of different stocking strategies.

Model Description

The model used in this study simulates growth and survival of juvenile striped bass stocked into Smith Mountain Lake. The model represents biotic and abiotic dynamics in two well-mixed, connected, spatial compartments: the littoral and pelagic zones. After specifying fingerling density, size distribution, and date at stocking, striped bass are introduced into the littoral compartment. Dispersion to the pelagic compartment occurs later in the growing season and is dependent upon body length. Feeding success is determined by invertebrate and fish prey encounter rates and capture efficiency, and growth is based on a bioenergetics approach in which maximum consumption and metabolic rate are weight- and temperature-dependent processes. Predation and winter mortality are functions of striped bass length, weight, and density. These processes are simulated daily and tracked for each striped bass from the time of stocking until 1 May of the next year.

Environmental conditions considered in each model compartment included daily water temperature and predator-prey dynamics. Temporal and spatial variability of striped bass and their prey

were accurately simulated by using data collected from previous studies conducted at Smith Mountain Lake. These data included abundance, growth, and mortality of age-0 alewives (Tisa 1988) and cyprinids (Sutton 1997), as well as dispersal, growth, food habits, and overwinter survival of juvenile striped bass (Sutton 1997; Sutton and Ney, in press).

Spatial Scaling

Two well-mixed, spatial compartments, which were scaled proportionately to their estimated volumes, were used to represent Smith Mountain Lake. Compartment dimensions for the littoral zone were $990 \times 990 \times 2$ m (deep); pelagic zone compartments measured $7,319 \times 7,319 \times 16.8$ m (deep) before 1 October and $9,129 \times 9,129 \times 16.8$ m after that. The volume of the pelagic compartment was increased after 1 October to simulate dispersal of striped bass throughout pelagic areas of Smith Mountain Lake.

Daily Water Temperature

Daily water temperatures were generated as stochastic deviations from a regression function fit to observed average temperatures. The average was based on weekly temperatures recorded at a 1-m depth from the littoral and pelagic zones of Smith Mountain Lake during the 1994–1996 sampling seasons (Sutton 1997). Because temperature estimates were not significantly different between zones ($\chi^2 = 20.16$, $df = 15$, $P = 0.11$), the temporal temperature regime was considered identical for both compartments. The function defining the annual temperature cycle (T ; °C) in Smith Mountain Lake was

$$T = 15.94 - 9.07 \cdot \cos(0.0172 \cdot D) - 6.10 \cdot \sin(0.0173 \cdot D), \quad (1)$$

where D is the calendar day of year, and 0.0172 was used to convert degrees to radians.

Stocking

Input parameters that defined the striped bass cohort at stocking included fingerling density (number/m³); day of year at introduction; and median, minimum, and maximum total length (mm). The initial shape of the size distribution for each model simulation, which matched that observed at stocking in 1994 and 1995 (Sutton and Ney, in press), was a triangular probability distribution. This three-parameter distribution was defined by the mode, which was set to the median and min-

imum and maximum values (specified to -7 and $+8$ mm, respectively) about the median. For each simulation, the initial length distribution was positioned on its axis to coincide with the median length and range specified for that simulation. Stocking parameters were altered singly and in combination to investigate their effects on subsequent striped bass growth, mortality, and recruitment to age 1 (see the first subsection in the Model Simulations section for a detailed description of these simulations).

Dispersion

Striped bass were stocked into the littoral compartment and remained in this zone until they reached 150 mm, after which they had a daily probability of 0.2 of moving into the pelagic compartment. This dispersal rate was chosen because it allowed the length distribution of juvenile striped bass within and outside the stocking coves to approximate observations in Smith Mountain Lake (Sutton 1997). After 1 October, the pelagic compartment was expanded to simulate dispersal throughout the open-water areas of the lake. Because striped bass greater than 150 mm were not observed within the stocking coves (Sutton 1997), they were not allowed to return to the littoral compartment after dispersing to the pelagic compartment.

Growth

Daily growth of juvenile striped bass was simulated using a bioenergetics approach. A full description of the logic and functions used in this model component is provided in Rose and Cowan (1993). Site-specific modifications were required to obtain realistic growth rates for the warmer waters of Smith Mountain Lake. Daily growth in weight (W_t ; mg dry weight) was represented with a difference form of a bioenergetics equation,

$$W_t = W_{t-1} + (p \cdot C_{\max})(0.7 \cdot K) - R_{\text{tot}}, \quad (2)$$

where p is the proportion of C_{\max} realized, C_{\max} is the maximum consumption rate (mg/d), K is the ratio of prey to striped bass caloric density, R_{tot} is the total metabolic rate (mg/d), and t is time (d). The fraction of ingested food available for growth and metabolism was assumed constant at 0.7 (Brett and Groves 1979). Dry weight (W_t) was converted daily into length (L_t ; mm) using the following relationship for age-0 striped bass (Tuncer 1988):

$$L_t = 9.63 \cdot W_t^{0.31}. \quad (3)$$

For model-simulated growth patterns to parallel empirical observations in Sutton and Ney (in press), the maximum allowable daily increase in length was 1.5%; individuals adding weight that would convert to greater length increases became stouter individuals.

Maximum Consumption

Maximum dry weight daily consumption (C_{\max}) depended on striped bass body weight and temperature (Rose and Cowan 1993 describe C_{\max} estimation). To allow model growth rates of piscivorous striped bass less than 175 mm to match field observations in Sutton and Ney (in press), juveniles were permitted to consume up to twice the fish prey mass allowable in their stomach. Because model growth rates of striped bass greater than 175 mm matched field observations, these individuals were only allowed C_{\max} for fish prey. Fish prey mass in the stomach (XS) of each striped bass was tracked as

$$XS_t = XS_{t-1} \cdot E + p \cdot C_{\max}, \quad (4)$$

where E is the fraction of consumed prey evacuated from the gut in a 24-h period (computed as reported in Rose and Cowan 1993). On each day, striped bass were allowed to consume fish prey less than $2 \cdot (C_{\max} - XS)$. If all fish prey were digested each day, striped bass less than 175 mm were allowed to consume twice their C_{\max} each day. As residual fish prey accumulated in the stomach of each striped bass, fewer new prey could be eaten.

Adjustment for Caloric Density

The ratio of prey-predator caloric density (K) depended on the type of prey consumed by a striped bass. Wet weight caloric densities were 1,143.3 cal/g for juvenile striped bass (Rogers et al. 1980), 972.0 cal/g for invertebrate prey, 1,123.3 cal/g for cyprinids, and 1,464.4 cal/g for alewives (Moore 1988).

Metabolism

Metabolic dry weight loss (R_{tot}) was estimated as the sum of a body weight-dependent and temperature-dependent routine component (R_r) and an activity-dependent component (ACT), which was a multiplier of routine metabolism. The relationship was defined as

$$R_{\text{tot}} = R_r + (\text{ACT} - 1)(R_r \cdot \text{FF}), \quad (5)$$

where FF is the fraction of the day when metab-

olism is active. Routine metabolism (from Eldridge et al. 1982) was determined as a function of weight and a Q_{10} temperature relationship:

$$R_r = 0.096 \cdot W^{0.721} \cdot G(T) \quad (6)$$

and

$$G(T) = e^{0.0405(T-T_r)}, \quad (7)$$

where 0.0405 represents $0.1 \cdot \log_e(Q_{10})$, Q_{10} for juvenile striped bass was set to 1.5 (see Rose and Cowan 1993 for justification), and T_r was the reference water temperature for routine metabolism. In contrast to Rose and Cowan (1993), T_r was increased from 22°C to 25°C to account for the warmer temperatures of Smith Mountain Lake.

Computation of p

The proportion of C_{\max} realized daily by an individual (p) was critical for matching model growth patterns to empirical data. The value of p was fixed at 0.12 for striped bass feeding on invertebrates, allowing the size range of these fish to agree with that observed at the end of the growing season in Smith Mountain Lake (90–120 mm; Sutton and Ney, in press). For piscivorous striped bass, p was based on prey encounter rate and probability of capture. These juveniles received a minimum p equal to 0.3 when feeding on fish resulted in p values less than 0.3. Although young striped bass do not feed at winter temperatures below 10°C (Vladykov and Wallace 1952; Koo and Ritchie 1973), a $p = 0.12$ was assigned to juveniles during winter to allow weight loss and mortality to match spring field observations from Sutton and Ney (in press).

Prey Encounters and Capture

Mean encounter rates were computed as the product of the volume searched (see Rose and Cowan 1993) and density of each prey cohort (cyprinids or alewives; see *Prey types and densities*). The number of individuals encountered from each prey type was estimated from a Poisson distribution, and the number of individuals from a given cohort encountered was estimated from a binomial distribution. The probability of a successful capture (CAP) for an individual prey item declined with increasing ratio of fish prey to striped bass body length (R ; Sutton and Ney, in press), in the following manner:

$$CAP = \begin{cases} 1 & \text{for } R < 0.2 \\ -3.33 \cdot R + 1.66 & \text{for } 0.2 < R < 0.05 \\ 0 & \text{for } R > 0.05. \end{cases} \quad (8)$$

Prey Selection

Striped bass consumed fish prey when available, before switching to less-preferred invertebrate prey. For fish prey, striped bass in the littoral and pelagic compartments would only encounter cyprinids and alewives, respectively (Sutton and Ney, in press). Selection of a prey item depended on encounter rate; prey were ranked in descending order of preference as determined by the product of prey dry weight (PW) and capture probability (PW · CAP; see Rose and Cowan 1993). Ingestible fish prey were consumed until all eligible prey items had been consumed or until consumption exceeded C_{max} .

Prey Types and Densities

Different invertebrate prey consumed by striped bass in Smith Mountain Lake were not incorporated into the model because densities have not been quantified during field studies. As a result, invertebrate prey were represented only through the proportion of C_{max} realized ($p = 0.12$), which remained constant for all simulations and sizes of striped bass.

Cyprinids and alewives represented the fish prey in the littoral and pelagic compartments, respectively, because they were the primary fish consumed by piscivorous striped bass in Smith Mountain Lake (Sutton and Ney, in press). Both prey types were represented by 10 cohorts that were introduced at subsequent periods to simulate the

range of sizes available throughout the growing season (cyprinids from Sutton 1997; alewives from Tisa 1988). Cyprinids were introduced at 5-d intervals beginning on 10 May (Table 1), and alewives were introduced at 10-d intervals beginning on 20 May (Table 2). Mean total length (TL; mm) of each fish prey cohort was represented separately over time and converted to mean wet weight (WT; mg) using the following weight-length regression equations (Sutton 1997):

$$WT = 0.000003311 \cdot TL^{3.21} \quad \text{for cyprinids} \quad (9)$$

and

$$WT = 0.000005623 \cdot TL^{3.10} \quad \text{for alewives.} \quad (10)$$

for alewives. Wet weight was converted to dry weight by using a multiplier of 0.28.

The initial density of each cohort was based on specifying an initial total year-class density (3.5 cyprinids/m³ from Sutton 1997; 2.2 alewives/m³ from Tisa 1988) and allocating the total density among the 10 cohorts such that peak density occurred on 25 May for cyprinids (Jenkins and Burkhead 1993) and 19 June for alewives (Tisa 1988). Total length at hatching for cyprinids and alewives was 5 mm, and daily growth rates were estimated from temporal changes in length-frequency distributions (Tisa 1988; Sutton 1997).

Because daily mortality rates of cyprinids in Smith Mountain Lake were not known, densities of fish prey were reduced using a mortality rate of 0.02/d before 1 December and 0.01/d after 1 December, as estimated for age-0 alewives by Tisa (1988). However, only alewife cohort densities were further reduced due to striped bass consumption. We did not allow consumption to reduce cyprinid densities because this resulted in their

TABLE 1.—Simulated density (number/m³) and growth (mm/d) of 10 age-0 cyprinid cohorts in Smith Mountain Lake. A total instantaneous mortality rate (Z) of 0.02/d and 0.01/d was assumed for before and after 1 December, respectively. Total length at hatching was assumed to be 5.0 mm.

Cohort	Hatch date	Initial density	Growth			25 June	
			Before 1 Sep	1 Sep to 1 Dec	After 1 Dec	Density	Length
1	10 May	0.21	0.35	0.10	0.00	0.10	20.8
2	15 May	0.35	0.35	0.10	0.00	0.18	19.4
3	20 May	0.53	0.30	0.10	0.00	0.30	15.8
4	25 May	0.70	0.30	0.10	0.00	0.54	14.3
5	30 May	0.59	0.25	0.10	0.00	0.39	11.5
6	4 Jun	0.48	0.25	0.10	0.00	0.34	10.3
7	9 Jun	0.39	0.20	0.10	0.00	0.30	8.2
8	14 Jun	0.28	0.15	0.05	0.00	0.24	6.7
9	19 Jun	0.18	0.10	0.05	0.00	0.16	5.6
10	24 Jun	0.11	0.10	0.05	0.00	0.10	5.1

TABLE 2.—Simulated density (number/m³) and growth (mm/d) of 10 age-0 alewife cohorts in Smith Mountain Lake. A total instantaneous mortality rate (Z) of 0.02/d and 0.01/d was assumed for before and after 1 December, respectively. Total length at hatching was assumed to be 5.0 mm.

Cohort	Hatch date	Initial density	Growth			19 August	
			Before 1 Sep	1 Sep to 1 Dec	After 1 Dec	Density	Length
1	20 May	0.13	1.00	0.30	0.00	0.03	96.0
2	30 May	0.22	0.95	0.30	0.00	0.06	82.0
3	9 Jun	0.33	0.90	0.30	0.00	0.11	68.9
4	19 Jun	0.64	0.85	0.30	0.00	0.25	56.9
5	29 Jun	0.44	0.80	0.30	0.00	0.20	45.8
6	9 Jul	0.31	0.75	0.30	0.00	0.16	35.8
7	19 Jul	0.24	0.75	0.30	0.00	0.15	28.3
8	29 Jul	0.18	0.65	0.30	0.00	0.11	18.7
9	8 Aug	0.11	0.60	0.30	0.00	0.08	11.6
10	18 Aug	0.07	0.55	0.30	0.00	0.06	5.6

elimination from the littoral compartment. Age-0 cyprinids were abundant in Smith Mountain Lake throughout the growing (Sutton 1997). Therefore, it appears that empirical estimates underestimated actual densities or that model-simulated cyprinid consumption rates were too high.

Fish Prey Availability

Densities of fish prey were multiplied by a constant in model simulations to adjust their behavioral availability to striped bass. For fish prey, availability factors (0.00065 for cyprinids; 0.0002 for alewives) were adjusted until model predictions of striped bass length distributions on 15 December and 1 May were similar to observed patterns. Availability factors were necessary to help mimic expected behaviors, such as schooling of forage fishes and prey search behaviors of juvenile striped bass.

Mortality

Mortality of striped bass depended on their weight, length, and density. Weight-dependent mortality was based on laboratory data at low food levels without predators and was interpreted as starvation (see Rose and Cowan 1993). Length- and density-dependent mortality were based on regression relationships and represented predation and other losses. Predation mortality consisted of length- and density-dependent components:

$$P_D = (1 - e^{-Z}) \cdot \text{DDM}_t, \quad (12)$$

where P_D is the daily probability of dying, Z is the daily instantaneous mortality rate (dependent on length), and DDM_t is a density-dependent multiplier. If a generated random number from a uniform distribution between 0 and 1 was less than

P_D , the individual died. This mortality component was defined using a regression equation fit to reported mortality rates (d^{-1}) of various size ranges of striped bass (see Figure 7 in Rose and Cowan 1993).

Because first-year survival estimates of striped bass in Smith Mountain Lake from 1973 to 1996 were significantly correlated with fingerling stocking density ($r^2 = 0.42$, $P = 0.002$; Sutton 1997), survival was adjusted to fit this trend. The multiplier for daily mortality (DDM_t), which depended on striped bass density each day (SD_t), used the following sigmoidal function:

$$\text{DDM}_t = a + b/(1 + e^{-(\text{SD}_t - c)/d}), \quad (13)$$

where $a = 0.39$, $b = 4.45$, $c = 334,749.33$, and $d = 138,111.62$ (Figure 1). These coefficients were estimated by adjusting model-predicted survival estimates until they matched the observed trend at increasing stocking densities. Although the degree of interannual variability in survival is not the same as the empirical data, maintaining first-year survival estimates close to the observed trend allows for realistic evaluation of striped bass stocking strategies in Smith Mountain Lake.

Model Corroboration

Model predictions under the existing stocking strategy and baseline conditions for alewife population dynamics and water temperature regimes were compared with empirical data for Smith Mountain Lake. One-year simulation runs were used to portray fish prey consumption and size relationships, and pre and postwinter striped bass length-frequency distributions (data from Sutton and Ney, in press). Multiple series of 1-year simulation runs, using the actual fingerling stocking

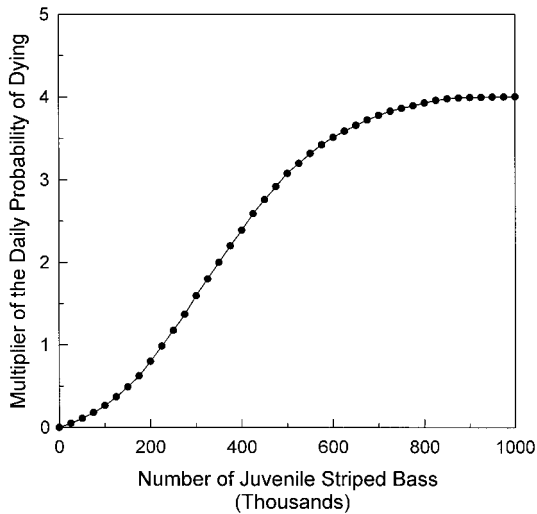


FIGURE 1.—Sigmoidal relationship between the multiplier for the daily probability of dying and fingerling striped bass stocking density.

data from 1973 to 1996 (Sutton 1997), were compared with the observed survival estimates.

Predictions of fish prey consumption and size relationships generally agreed with empirical data (Figure 2). Size-dependent differences in fish prey

consumption were accurate; however, predicted size relationships tended to involve shorter prey lengths than were observed from field data. For example, striped bass less than 130 mm consumed primarily small cyprinids (observed = 9–40 mm; predicted = 6–37 mm), whereas bigger individuals consumed strictly larger alewives (observed = 50–125 mm; predicted = 40–95 mm). Although the observed ratio of prey to predator length declined with predator size, the ratio of alewife to striped bass length was greater than the analogous ratio for cyprinids (range = 25–54% and 10–40%, respectively). However, model-predicted ratios were slightly lower than field observations (alewives = 24–50%; cyprinids = 8–33%).

First-year survival predictions were inversely related to fingerling stocking density, as observed from empirical data (Figure 3). Observed and predicted survival rates were 10.2% and 11.3% at the highest stocking density (809,246 fingerlings) and 9.9% and 28.8% at the lowest stocking density (197,534). Although variability in survival estimates was less for the model (CV = 26.6 for predicted versus 48.1 for observed), regression slopes were not significantly different (slope = -0.04 versus -0.05, respectively; *t*-test between regression coefficients: *t* = 1.52, *P* = 0.07).

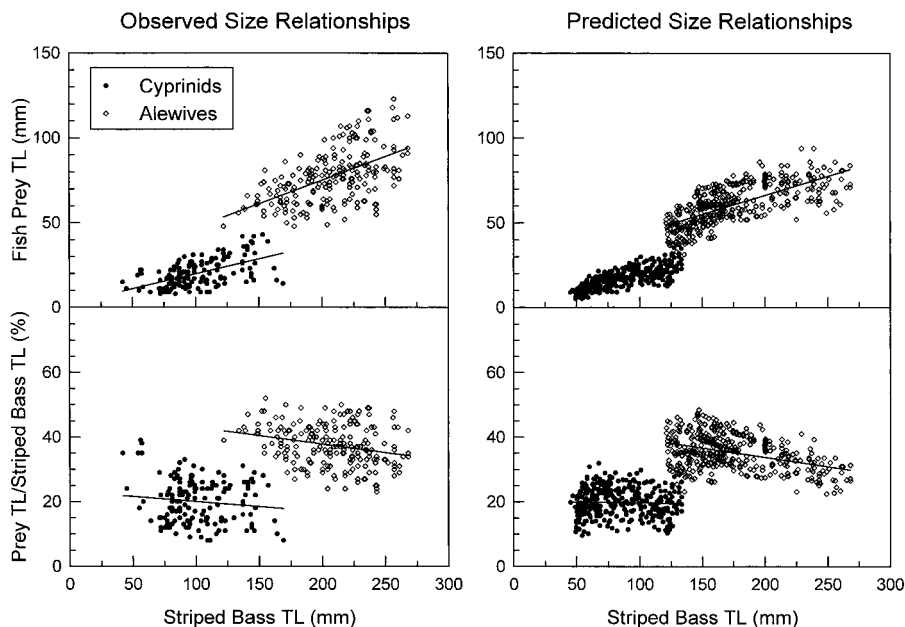


FIGURE 2.—Comparison of observed (left panels) versus predicted (right panels) total length (TL) relationships of cyprinids (solid circles) and alewives (hollow diamonds) consumed by juvenile striped bass. The upper panels represent the relationship between length of fish prey and striped bass length and the lower panels represent the relationship between the ratio of prey length to striped bass length and striped bass length.

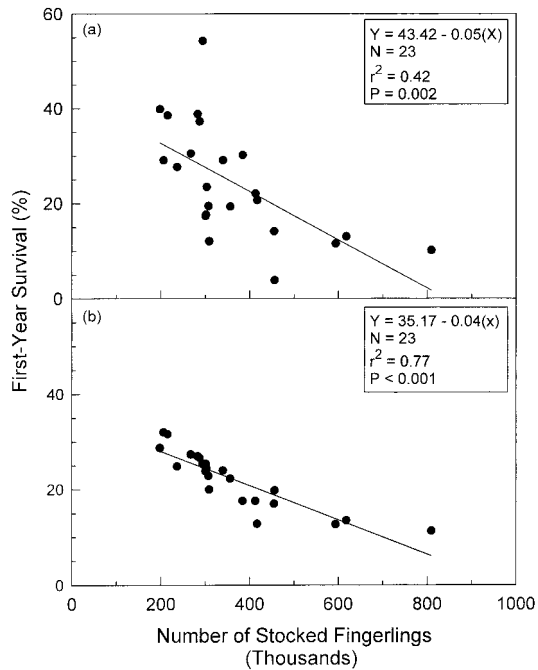


FIGURE 3.—Comparison of fingerling striped bass stocking density and survival to age 1 in Smith Mountain Lake, 1973–1996, as (a) determined from fall gill-net surveys and (b) predicted from model simulations.

Predicted fall and spring length distributions of striped bass were similar to those observed from 1994 to 1996 in Smith Mountain Lake (Figure 4). The model predicted a bimodal length distribution at the end of the first growing season with a range (86–262 mm) similar to December 1994 (84–266 mm) and November 1995 (80–261 mm) observations. The model also predicted that large-mode striped bass (median = 223 mm, range = 182–262 mm) would be twice as long as small-mode juveniles (median = 93 mm, range = 86–144 mm); this agreed closely with field data for large- and small-mode striped bass in 1994 (large, median = 225 mm, range = 182–266 mm; small, median = 94 mm, range = 84–140 mm) and 1995 (large, median = 226 mm, range = 183–261 mm; small, median = 100 mm, range = 80–137 mm). Although predicted spring length-frequency distributions were unimodally distributed, as observed in the empirical data, the predicted distributions had a narrower range (161–262 mm) than that observed in March 1995 (range = 97–268 mm) and April 1996 (range = 128–262 mm).

Model Simulations

Stocking Strategies

Different strategies for stocking striped bass into Smith Mountain Lake were examined by mod-

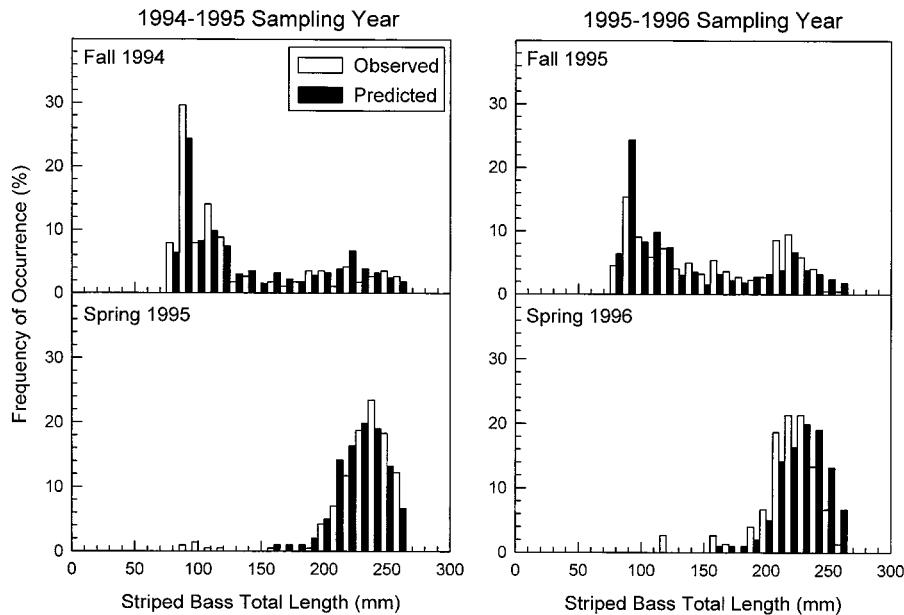


FIGURE 4.—Comparison of observed (hollow bars) and predicted (solid bars) length-frequency distributions of juvenile striped bass before and after winter in Smith Mountain Lake. Observed length distributions were estimated from field collections in late fall (December 1994; November 1995) and early spring (March 1995; April 1996). Predicted length distributions were estimated from model simulations in late fall (15 December) and spring (1 May).

TABLE 3.—Alewife population dynamics and water temperature perturbation simulations used to compare the sensitivity of the existing versus the proposed fingerling striped bass stocking strategies.

Model simulation	Alewife population dynamics				
	Population density (per m ³)	Spawning-day offset	Daily growth-rate multiplier	Daily mortality-rate multiplier	Daily water-temperature offset (°C/d)
Baseline conditions	2.2	0 d	1.00	1.00	0.0°
Population density					
Density doubled	4.4	Baseline	Baseline	Baseline	Baseline
Density halved	1.1	Baseline	Baseline	Baseline	Baseline
Spawning day offset					
Two weeks earlier	Baseline	-14 d	Baseline	Baseline	Baseline
One week earlier	Baseline	-7 d	Baseline	Baseline	Baseline
One week later	Baseline	+7 d	Baseline	Baseline	Baseline
Two weeks later	Baseline	+14 d	Baseline	Baseline	Baseline
Daily growth rate multiplier					
Slow growth	Baseline	Baseline	0.75	Baseline	Baseline
Fast growth	Baseline	Baseline	1.50	Baseline	Baseline
Daily mortality rate multiplier					
High mortality	Baseline	Baseline	Baseline	1.10	Baseline
Low mortality	Baseline	Baseline	Baseline	0.90	Baseline
Daily water temperature offset					
Much cooler	Baseline	Baseline	Baseline	Baseline	-4.0°
Cooler	Baseline	Baseline	Baseline	Baseline	-2.0°
Warmer	Baseline	Baseline	Baseline	Baseline	+2.0°
Much warmer	Baseline	Baseline	Baseline	Baseline	+4.0°

el simulations. Baseline stocking conditions, which represented the existing strategy, were 300,000 fingerlings with a median total length of 42 mm (range = 35–50 mm) introduced on 15 June (day 166); these values were used in simulations unless otherwise noted. Four stocking scenarios were examined: (1) median total length at stocking was allowed to vary from 22 to 112 mm in 10-mm increments; (2) day of year at stocking was allowed to range from 18 May (day 138) to 20 July (day 201) in 7-d increments; (3) stocking density was allowed to vary from 100,000–1,000,000 fingerlings in 100,000-fingerling increments; and (4) median total length and day of year at stocking were allowed to covary over the same ranges and increments as stated in scenarios 1 and 2. Ten simulations were conducted for each of scenarios 1–3 and 100 simulations (10 initial lengths \times 10 d of stocking) were conducted for scenario 4. Although replicate simulations could have been conducted that differed only in random number sequence, the predicted density and survival among replicate simulations varied less than 8%, and predicted median total length varied less than 6%. Therefore, only single simulation results are presented for each stocking strategy reported in this study.

At the end of each simulation trial, number of recruits, median total length, and first-year survival were recorded. Recruits referred to the num-

ber of age-1 striped bass that were greater than 150 mm on 1 May of the year following stocking. This minimum length was chosen because striped bass that do not reach that size by the end of the growing season in Smith Mountain Lake suffer almost complete mortality relative to their larger conspecifics (Sutton and Ney, in press).

Sensitivity and Robustness Analyses

Variability was imposed in model inputs to determine the sensitivity of output predictions to environmental variation. Based on the results of scenarios 1–4, a stocking scheme was identified that led to increased recruitment, size, and first-year survival compare with the presently used strategy. The existing strategy was 300,000 fingerlings with a median length of 42 mm (range = 35–50 mm) introduced on 15 June (day 166). The proposed strategy was 300,000 fingerlings with a median total length of 52 mm (range = 45–60 mm) introduced on 8 June (day 159). For sensitivity analyses, water temperature and alewife population dynamics were varied singly (Table 3) and in combination (Table 4) from baseline values for both the existing and proposed strategies. Combinations represented how inputs would covary during warm or cold years. For example, during a warm year, water temperature would be higher, prompting alewives to spawn earlier and their progeny to exhibit faster growth and higher mortality; the converse

TABLE 4.—Alewife population density and warm and cold year perturbation simulations used to compare the sensitivity of the existing versus the proposed fingerling striped bass stocking strategies.

Model simulation	Alewife population dynamics				Daily water-temperature offset (°C/d)
	Population density (per m ³)	Spawning-day offset	Daily growth-rate multiplier	Daily mortality-rate multiplier	
Baseline conditions	2.2	0 d	1.00	1.00	0
Warm year					
High density	4.4	-14 d	1.50	1.10	+4.0
Baseline density	2.2	-14 d	1.50	1.10	+4.0
Low density	1.1	-14 d	1.50	1.10	+4.0
Cold year					
High density	4.4	+14 d	0.75	0.90	-4.0
Baseline density	2.2	+14 d	0.75	0.90	-4.0
Low density	1.1	+14 d	0.75	0.90	-4.0

would be expected during a relatively cold year. To estimate sensitivity, percent relative change of each prediction variable was computed as $[(Y_i - Y_b)/Y_b] \cdot 100$, where Y_i was the predicted model output value for the i th input perturbed and Y_b was the predicted model output value under baseline conditions. Percent relative change values were computed for both the existing and proposed strategies under environmental variability.

Sensitivity analysis results were also used to compare model output values between the two stocking strategies to determine which stocking strategy was more robust to variability in model inputs. To estimate robustness, percent relative change in each prediction variable was computed as $[(Y_{pi} - Y_{bi})/Y_{bi}] \cdot 100$, where Y_{pi} was the predicted model output value for the i th input perturbed under the proposed stocking strategy and Y_{bi} was the predicted model output value for the i th input perturbed under the existing stocking strategy.

The degree of variation imposed on model inputs was determined from previous Smith Mountain Lake studies. Variability in water temperature regime was based on annual Smith Mountain Lake temperature records (M. Duval, Virginia Department of Game and Inland Fisheries, unpublished data). Changes in the timing of alewife spawning and daily growth and mortality rates of age-0 alewives were estimated from Tisa (1988). Estimates for variability in age-0 alewife density were not based on known values. Tisa (1988) reported that relative abundance of age-0 alewives in Smith Mountain Lake did not vary from 1982 to 1983. Although annual variations in age-0 alewife density in other systems have not been reported, clupeids are often characterized by large fluctuations in year-class strength (Lasker 1985). Therefore,

cohort density was allowed to vary $\pm 200\%/m^3$ from the estimated baseline value of $2.2/m^3$.

Results

Stocking Strategies

Number of age-1 recruits, median total length, and first-year survival of stocked striped bass at the end of the simulation period increased with increasing fingerling size at stocking. Although the greatest increase in age-1 recruits occurred when median total length was increased from 32 to 42 mm (+50%), a similar increase occurred when stocking size was increased from 42 to 52 mm (+49%; Figure 5). However, stocking striped bass larger than 52 mm resulted in lower percent increases in age-1 recruits (less than +5%). Similarly, median total length and first-year survival increased +38% and +44%, respectively, when stocking size was raised from 42 to 52 m; increases were less after 52 mm (less than +9% and less than +4%, respectively; Figure 5).

The number of age-1 recruits, median total length, and first-year survival of the striped bass cohort declined with later day of year at stocking. Although age-1 recruits increased +20% when fingerlings were stocked 1 week earlier (8 June; day 159) than baseline (15 June; day 166), the largest increase (+25%) occurred when stocking was moved two weeks earlier (1 June, day 152; Figure 6). Median total length and first-year survival also increased when stocking occurred 1 week earlier (+7% and +12%, respectively), and exhibited the largest percent increases when stocking was moved 2 weeks earlier (+23% and +28%, respectively; Figure 6).

When fingerling density at stocking was increased, number of age-1 recruits increased,

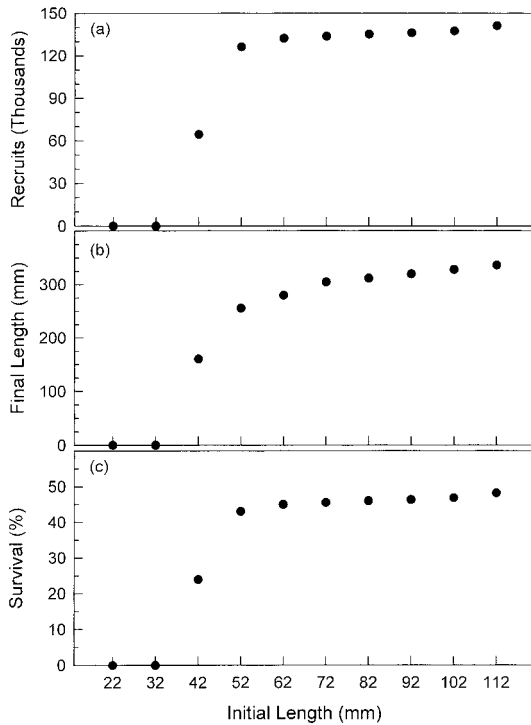


FIGURE 5.—Simulated striped bass responses for (a) number of age-1 recruits, (b) median total length (final length), and (c) first-year survival of juveniles on 1 May to changes in median total length at stocking (initial length).

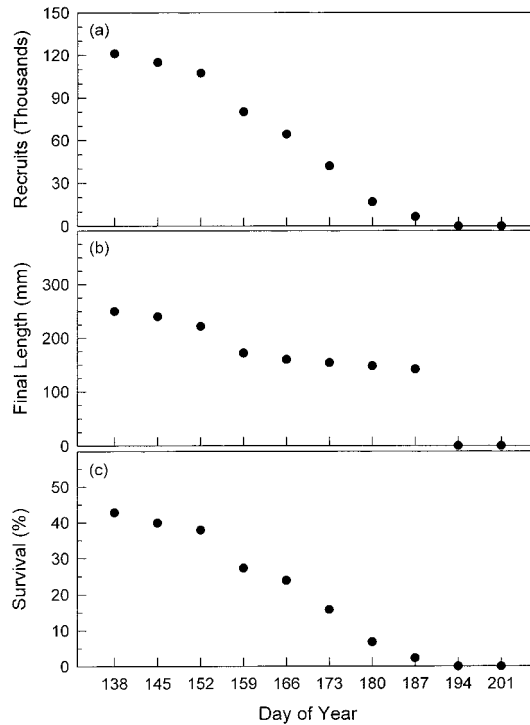


FIGURE 6.—Simulated striped bass responses for (a) number of age-1 recruits, (b) median total length (final length), and (c) first-year survival of juveniles on 1 May to changes in day of year at stocking.

whereas decreases occurred for median total length and first-year survival. Although recruitment increased progressively with stocking density, the largest percentage increase occurred when numbers were increased from 200,000 to 300,000 fingerlings (+22%); percentages leveled off for higher stocking densities (<+6%; Figure 7). Median total length and first-year survival also declined most substantially from 200,000 to 300,000 fingerlings (-14% and -21%, respectively) and to a lesser extent for higher stocking densities (less than -3% and less than -12%, respectively; Figure 7).

Stocking striped bass at a larger size and earlier in the growing season resulted in an increase in number of age-1 recruits, median total length, and first-year survival (Figure 8). Number of age-1 recruits exhibited a steep gradient, especially with respect to initial size (Figure 8a). For this response surface, the greatest percentage increase occurred when size at stocking was increased from 42 to 52 mm and as stocking was moved from 15 June (day 166) to 8 June (day 159). A similar result was

observed for first-year survival (Figure 8c). Although the median total length response surface revealed a less distinct trend, an increase did occur as size at stocking was increased and stocking occurred earlier in the growing season (Figure 8b).

Sensitivity and Robustness Analyses

The number of age-1 recruits, median total length, and first-year survival for striped bass stocked under the existing and proposed strategies were most strongly influenced by alewife spawning day offset, age-0 alewife growth rate multiplier, and water temperature offset (Figure 9). In contrast, simulations involving variations in age-0 alewife density and mortality rate multiplier resulted in smaller percent changes of model predictions (Figure 9). Perturbations in model inputs resulted in greater percent changes in age-1 recruits and first-year survival than for median total length. Although this pattern was similar for both stocking strategies, the existing strategy was more sensitive (i.e., had a greater relative change from baseline) to parameter perturbations than the proposed strategy (Figure 9).

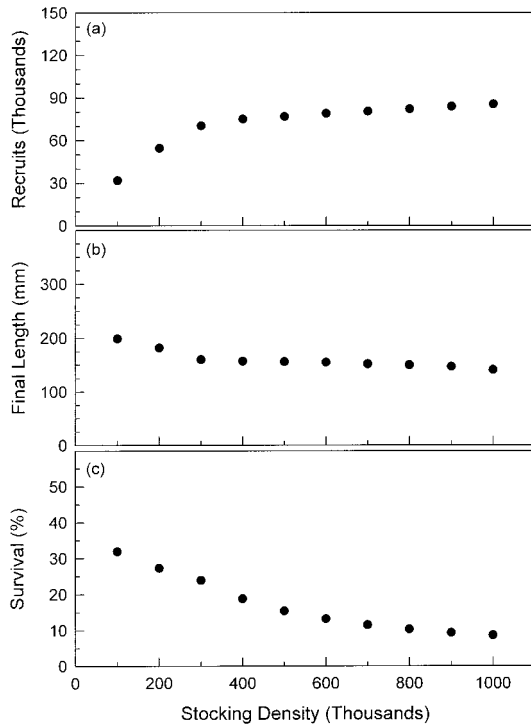


FIGURE 7.—Simulated striped bass responses for (a) number of age-1 recruits, (b) median total length (final length), and (c) first-year survival of juveniles on 1 May to changes in density of stocked fingerlings.

Combined perturbations in alewife and temperature inputs differentially influenced model outputs at the existing and proposed stocking strategy. During warm-year simulations, number of age-1 recruits, median total length, and first-year survival exhibited percentage decreases from baseline for both strategies (Figure 10). Percent change for model predictions increased during warm years as cohort density was reduced from 4.4 to 1.1/m³. During cold-year simulations, age-1 recruits, median total length, and first-year survival exhibited percentage increases from baseline for both stocking scenarios, and percent change for predictions decreased as cohort density was reduced from 4.4 to 1.1/m³ (Figure 10). Although the change was greatest for age-1 recruits and first-year survival, the pattern was identical for both stocking strategies. However, the existing strategy was more sensitive (i.e., had a greater percent change from baseline) to combined parameter perturbations than the proposed strategy (Figure 10).

Comparison of number of age-1 recruits, median total length, and first-year survival between stocking strategies revealed that the proposed strategy

consistently resulted in greater percent increases than the existing strategy in all model prediction variables regardless of the parameter perturbation (Table 5). For model inputs varied singly, the greatest percentage increases were for age-1 recruits (range = 96.8–145.6%) and first-year survival (range = 96.9–145.2%). Median total length also increased, albeit to a lesser extent (range = 53.8–60.6%). Lower cohort density, earlier spawning, faster growth, lower mortality of alewives, and warmer temperatures resulted in the greatest percent increases in model outputs when varied singly. When model inputs were varied together, the greatest percent increases were observed for age-1 recruits (range = 85.7–170.5%) and first-year survival (range = 85.8–170.9%), whereas median total length increased to a lesser extent (range = 48.9–55.5%). Low alewife cohort density during warm years and high alewife cohort density during cold years resulted in the largest (+170.5%) and smallest percent changes (+85.7%) among prediction variables. The proposed strategy always resulted in greater percent returns in model predictions regardless of the parameter perturbation, and the magnitude of percentage changes remained relatively constant (i.e., is robust) under variation in model inputs.

Discussion

A spatially explicit, individual-based model of juvenile striped bass life history dynamics was used to examine various stocking strategies for enhancing first-year growth, survival, and recruitment in Smith Mountain Lake. Results from model simulations demonstrated that stocking striped bass at a larger length (52 mm) than the current average (42 mm) and earlier in the growing season (8 June instead of 15 June), while maintaining the current annual stocking density at 300,000 fingerlings, led to the largest percentage increases in median total length, first-year survival, and number of age-1 recruits. In addition, our proposed stocking strategy was always less sensitive and more robust to variations in alewife population dynamics and water temperature regimes than was the existing strategy. Below, we discuss the ecological significance and implications of these results, weaknesses of the model, areas for future data collection, and utility of individual-based modeling for examining stocking issues for piscivores in lentic systems.

Based on the mechanisms known to regulate recruitment of striped bass in Smith Mountain Lake, increased stocking success would directly arise in

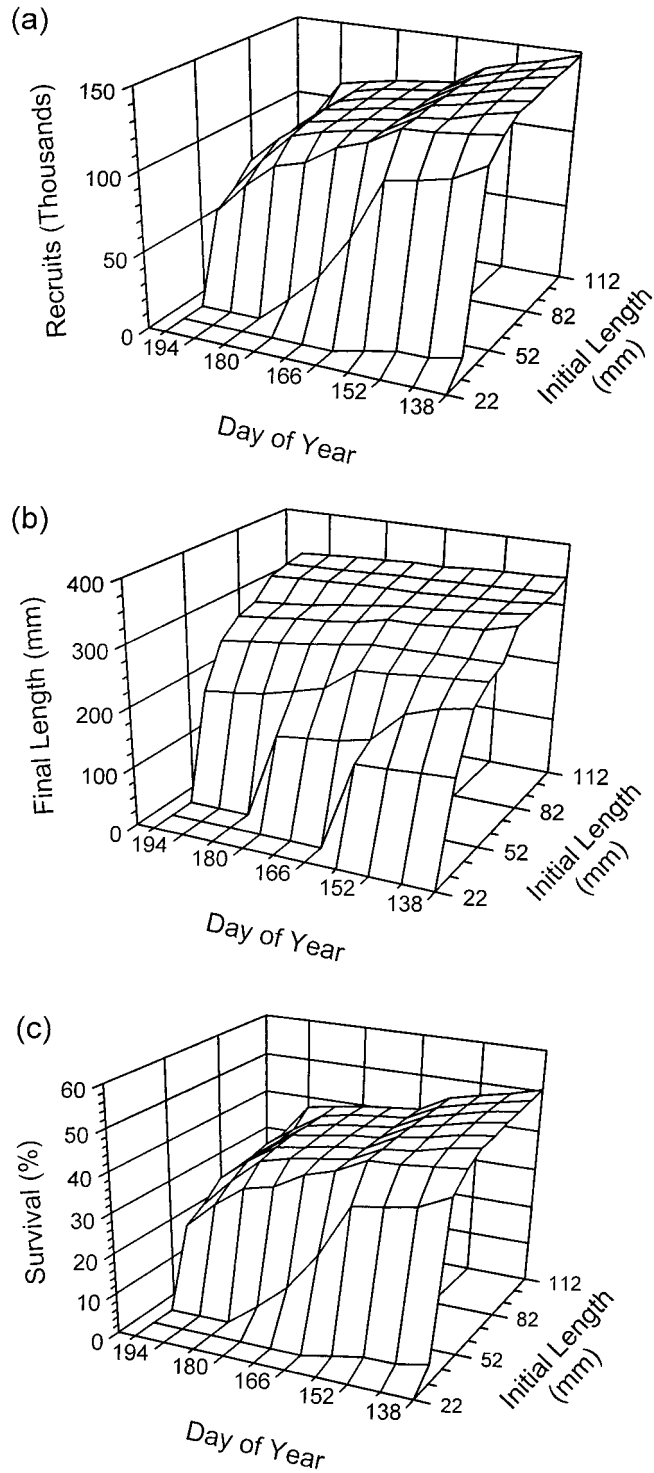


FIGURE 8.—Simulated striped bass response surfaces (a) for number of age-1 recruits, (b) median total length (final length), and (c) first-year survival of juveniles on 1 May to changes in median total length of fingerlings (initial length) and day of year at stocking.

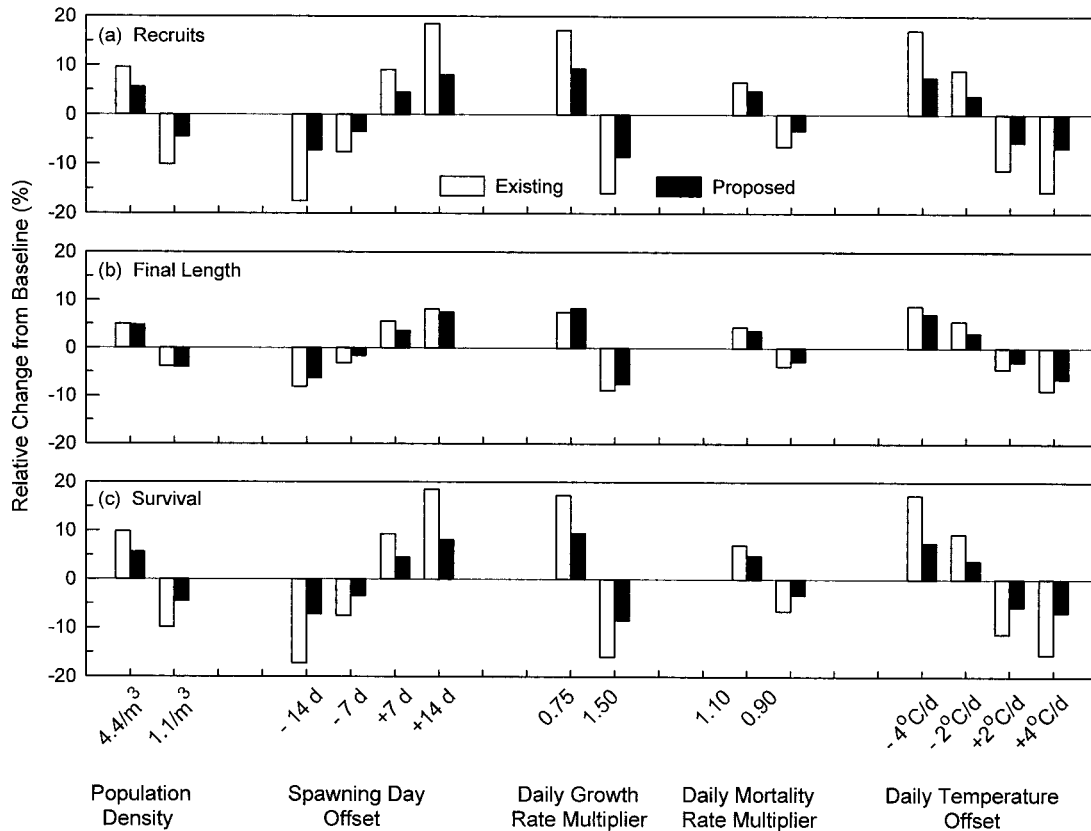


FIGURE 9.—Relative percent changes in striped bass (a) number of age-1 recruits, (b) median total length (mm), and (c) percent survival of juveniles at the end of their first winter from baseline or current stocking practices. Individual perturbations in alewife population dynamics and water temperatures are examined for the existing (hollow bars) and proposed (solid bars) stocking strategies.

response to more profitable feeding opportunities. According to Sutton and Ney (in press), it appears that individuals at the leading edge of the initial length distribution at stocking demonstrate significantly greater growth and survival. Growth divergence within the cohort, resulting in the development of bimodality by the end of the growing season, appeared to be mediated by size-dependent differences in food habits and diet quality. Larger fingerlings were able maintain a higher degree of piscivory by consuming age-0 alewives and grew at a faster rate than smaller striped bass that could not switch to this prey. As a result, smaller juveniles maintained a lower quality invertebrate diet, grew at a slower rate, and attained a smaller size than piscivorous individuals. Striped bass stocked earlier and at a larger size would have a greater length advantage over fish prey, resulting in a larger portion of the age-0 alewife biomass being within their ingestibility limits. Because

small differences in juvenile piscivore size, relative to their fish prey, can lead to large increases in prey availability (Adams and DeAngelis 1987; Madenjian and Carpenter 1991; Olson 1996; Donovan et al. 1997), this change in stocking strategy will allow fingerlings to maintain a higher degree of piscivory, grow at a faster rate, and reach a larger size by winter. Because juveniles greater than 150 mm had accumulated sufficient lipid stores to survive this critical period (Sutton and Ney, in press), the proposed stocking strategy should enhance striped bass recruitment in Smith Mountain Lake.

Our model results demonstrate that improved stocking success would be achieved by introducing larger fingerlings into Smith Mountain Lake earlier in the growing season. To accommodate this recommendation, personnel at the VDGIF Vic Thomas Striped Bass Hatchery (VTSBH; Brookneal, Virginia) have modified their striped bass culture

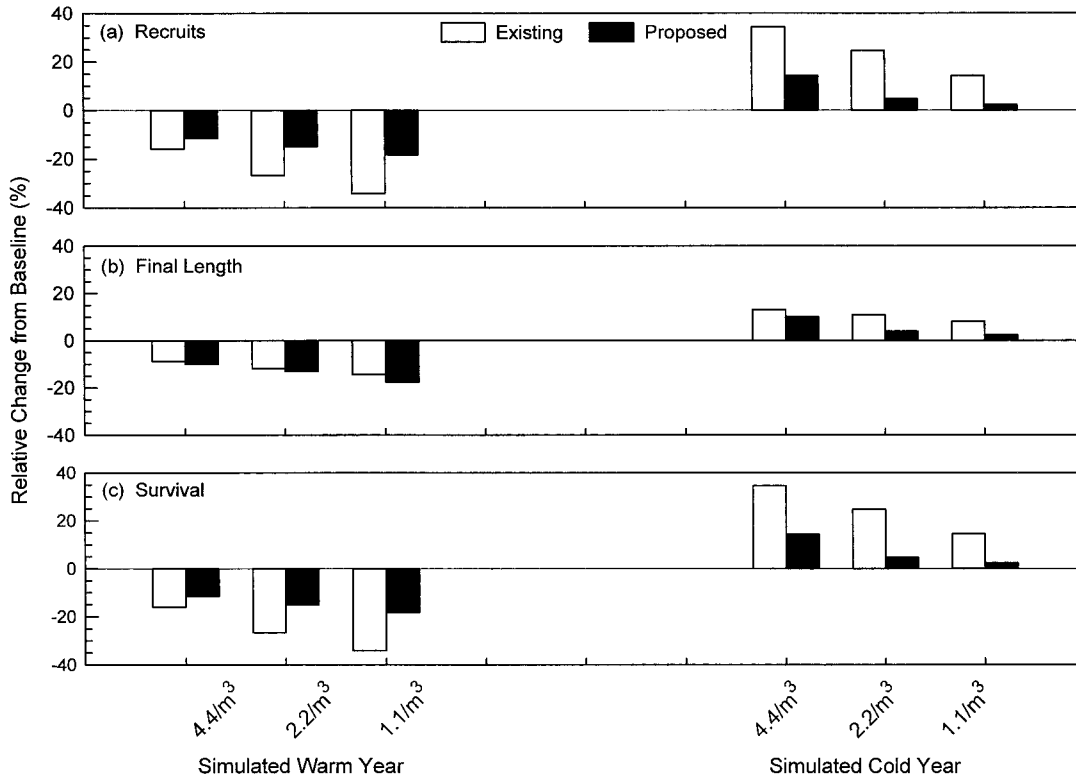


FIGURE 10.—Relative percent changes in striped bass (a) number of age-1 recruits, (b) median total length (mm), and (c) percent survival of juveniles at the end of their first winter from baseline or current stocking practices. Perturbations in alewife population dynamics for simulated warm and cold years are examined for the existing (hollow bars) and proposed (solid bars) stocking strategies.

program. Traditionally, ripe adult broodstock have been collected from an upstream reach of the Roanoke River in Kerr Reservoir from late April to early May and spawned at the hatchery. After hatching, striped bass were reared in 0.4-ha to 1.7-ha ponds on zooplankton and subsequently stocked into Smith Mountain Lake once they had reached 30–40 mm TL (S. Arthur, VT SBH, personal communication). To meet the proposed stocking strategy, adult striped bass will be collected during winter months, maintained indoors at the hatchery in 5,000-L circular tanks, and induced to spawn at the beginning of March by altering photoperiod and water temperature regimes. After hatching, larvae will be reared in 415-L indoor raceways on *Artemia*. At approximately 14 d of age, larval striped bass will be gradually switched to a prepared feed. Once they have completely accepted this diet, they will be graded by length and densities will be reduced as fish are transferred to a series of larger (26,684-L) tanks. This final portion of the grow-out period in these outdoor tanks will

continue until early June when they reach the target stocking size. Therefore, these modifications to striped bass spawning and rearing practices allow for a greater degree of control over the production process than did the previous strategy, and currently represent the most cost-effective and feasible option for this hatchery facility (J. Rudacille, VT SBH, personal communication).

Although the highest period of mortality for fish typically occurs shortly after hatching, when larvae are small and vulnerable (Miller et al. 1988), mortality processes for stocked juveniles, such as size-selective predation and winter mortality, can also substantially impact recruitment (Carline et al. 1986; Santucci and Wahl 1993; Wahl and Stein 1993; Stahl et al. 1996; Ludsin and DeVries 1997). For age-0 fishes, the interaction between biotic and abiotic factors can alter the size relationship between predator and prey, thereby influencing the recruitment process through their combined effects on growth (Adams et al. 1982; Miller and Storck 1984; Adams and DeAngelis 1987; Cargnelli and

TABLE 5.—Percent relative increases in the number of age-1 recruits, median total length, and first-year survival at the end of the overwintering period for the proposed versus the existing fingerling striped bass stocking strategy as a result of perturbations in adult alewife spawning, age-0 alewife population density, daily growth rate, daily mortality rate, and Smith Mountain Lake water temperature varied singly and in combination.

Model simulation	Parameter variation	Recruits (%)	Length (%)	Survival (%)
Baseline conditions		+118.4	+57.5	-118.7
Population density				
Density doubled	4.4/m ³	+110.4	+57.1	+110.2
Density halved	1.1/m ³	+131.8	+57.1	+131.6
Spawning-day offset				
Two weeks earlier	-14 d	+145.6	+60.5	+145.2
One week earlier	-07 d	+128.2	+60.0	+128.3
One week later	+07 d	+109.0	+54.4	+109.0
Two weeks later	+14 d	+96.8	+56.6	+96.9
Daily growth-rate multiplier				
Slow growth	0.75	+103.6	+58.7	+104.0
Fast growth	1.50	+127.4	+59.6	+138.3
Daily mortality-rate multiplier				
High mortality	1.10	+141.6	+56.3	+114.4
Low mortality	0.90	+126.0	+59.1	+126.5
Daily water-temperature offset				
Much cooler	-4°C/d	+100.4	+55.2	+100.4
Cooler	-2°C/d	+108.0	+53.8	+107.7
Warmer	+2°C/d	+137.0	+60.1	+137.4
Much warmer	+4°C/d	+141.4	+61.6	+141.0
Simulated warm year				
High density	4.4/m ³	+129.9	+55.5	+130.6
Baseline density	2.2/m ³	+153.0	+55.3	+153.5
Low density	1.1/m ³	+170.5	+51.8	+170.9
Simulated cold year				
High density	4.4/m ³	+85.7	+53.0	+85.8
Baseline density	2.2/m ³	+88.5	+49.1	+88.7
Low density	1.1/m ³	+95.5	+48.9	+95.5

Gross 1996). Results from sensitivity analyses indicated that alterations in water temperature not only affected the timing of alewife spawning relative to striped bass introduction, but also impacted growth rates of age-0 alewives, which influenced alewife size availability, striped bass growth, and ultimately, the length distribution of the stocked cohort. Size structure is a major determinant regulating recruitment of age-0 piscivores (Adams et al. 1982), including striped bass in Smith Mountain Lake (Sutton and Ney, in press). Environmental conditions that influence juvenile life-stage dynamics can be more important in regulating year-class strength than is typically assumed for many fish populations (Adams et al. 1982; Gutreuter and Anderson 1985; Adams and DeAngelis 1987; Ludsins and DeVries 1997; Kimmerer et al. 2000).

Our model projects first-year striped bass growth, survival, and recruitment as a function of fingerling length and density at stocking, day of year at introduction, water temperature regime, and population dynamics of fish prey. Stocking success may also depend on other environmental

factors not explicitly incorporated into the model; these include availability and dynamics of invertebrate and other fish prey, genetic variability within the striped bass cohort, and size-dependent variation in physiological health of fingerlings from stocking through their first year of life. In addition, the cyprinid component of the model did not allow for realistic characterization of predator-prey dynamics; the best available data resulted in striped bass eliminating cyprinids from the littoral zone. Because cyprinids were abundant in near-shore regions of Smith Mountain Lake throughout the growing season (Sutton 1997), it is unlikely that they could eliminate this prey resource. As a result, cyprinids were not removed from the population by consumption, which allowed the model to accurately portray first-year growth of striped bass.

Because of its limitations, the model could not be used to identify the specific processes resulting in density-dependent mortality. Possible hypotheses include (1) size-selective predation on striped bass by larger piscivores (this may only become significant at higher stocking densities or during

adverse environmental conditions); (2) physiological stress on striped bass during transportation; (3) an artifact of using different sampling gears to collect striped bass over spatial and temporal scales; (4) movement of smaller striped bass into the pelagic zone to avoid predation, resulting in a mismatched length relationship with alewife prey; and (5) density-dependent growth of striped bass in the littoral zone before they dispersed to pelagic areas of Smith Mountain Lake. When specific information becomes available regarding the effects of these factors on juvenile striped bass population dynamics, these data can be incorporated into the model and used to identify the specific mechanisms limiting recruitment in Smith Mountain Lake.

The model presented here could be also used to predict growth, survival, and number of age-1 recruits should environmental conditions change in Smith Mountain Lake. Although the proposed stocking strategy was shown to be robust to stochasticity in alewife population dynamics and water temperature regimes, ecological status could shift due to reservoir aging, watershed perturbation, and exotic species introductions (Strong 1983). Cowan et al. (1993) and Rose et al. (1993) have used individual-based models to investigate the effects of changes in biological factors and environmental quality on early life history dynamics of striped bass in the Potomac River, Maryland. Therefore, the individual-based model presented in this study could be incorporated into a more comprehensive model of Smith Mountain Lake and could be used as a predictive tool to evaluate effects of changes in environmental conditions, stocking strategies, and harvest policies on long-term population dynamics and sustainable yield. Such a model would describe the entire recruitment sequence from stocking through the adult life stage. However, detailed information on adult life-stage dynamics and the striped bass fishery in Smith Mountain Lake would be required to develop and apply a more extensive, site-specific model.

The individual-based model presented in this paper has been used to evaluate strategies for stocking striped bass into Smith Mountain Lake, and the sensitivity and robustness of the proposed stocking strategy to environmental stochasticity. Simulation analyses, such as those conducted in this study, would be appropriate for other age-0 piscivore populations maintained on a put-grow-take basis in lentic systems. The model is necessarily complex to realistically describe the size-

dependent relationships inherent in predator-prey dynamics. The model accurately portrays population variability resulting from individual differences in body size on first-year striped bass growth and survival, both critical determinants of successful stocking programs for piscivorous fishes (Santucci and Wahl 1993). Further, the proposed stocking strategy is robust to environmental variability that might occur annually in Smith Mountain Lake. As a result, individual-based modeling represents a useful tool to evaluate stocking strategies and management plans for juvenile striped bass and other piscivores in temperate freshwater systems.

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