Effect of Egg Sampling Efficiency on Estimates of Historic Striped Bass Egg Production in the Savannah River Estuary, Georgia-South Carolina

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Abstract: The striped bass (*Morone saxatilis*) population of the Savannah River estuary declined in the 1980s, likely because of the operation of a tide gate that increased salinity on spawning grounds and accelerated seaward transport of eggs and larvae. Following discovery of this negative effect, periodic egg sampling monitored striped bass reproductive effort and documented a 96% decline in egg density (n/100m^3) from pre-tide gate levels. The decline in egg density was concomitant with a similar decline in the adult striped bass population. An intensive stocking program eventually restored the adult population, but reproductive output remained low through the 1990s. Previous estimates of egg density allowed only relative comparisons between areas and/or years. Estimates of actual egg production for the system have not been attempted but would be helpful in understanding reproductive levels needed to set recovery goals (i.e., to pre-tide gate levels). Recent estimates of sampling efficiency now make back-calculation of egg production possible for this system. We used these estimators to back-calculate a minimum level of egg production at two historic spawning areas to 1978. Estimated minimum egg abundance the year before tide gate operation (1978) was 220 million eggs. After tide gate installation and operation, estimated annual egg abundance was variable, peaking in 1986 (486 million) but declined to as low as 4.5 million by 1998 (1990–1998 average: 33.4 ± 22.0 million SD). In 1999 and 2000, however, the minimum estimated egg production was over 60 million each year (60.3 and 63.1 million eggs, respectively). With continued recovery of the adult population, egg abundance should continue to rise and may eventually return to levels estimated to exist prior to the decline.

Key words: striped bass, reproduction, estimation, Savannah River, recovery

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The Savannah River estuary supported Georgia's most popular sport fishery for striped bass (*Morone saxatilis*) during the 1960s and 1970s and was the source of broodstock for the Georgia Department of Natural Resources (GA-DNR) state-wide stocking program. Subsequent declines in the catch-per-unit-effort (CPUE) of adults alerted the resource agency to potential recruitment problems. From 1980 to 1988, total CPUE of adult striped bass declined by 97% (Reinert et al. 2005). Egg sampling from 1986–1989 served as an index of reproductive effort and confirmed a concomitant 96% decline in striped bass egg density (measured as n/100m^3). This decline was linked to operation of a tide gate that increased salinity on spawning and nursery grounds and altered egg transport pathways, shunting eggs to areas of harmful or lethal salinity (Van Den Avyle and Maynard 1994).

Restoration initiatives included stock enhancement and habitat restoration. Stock-recovery efforts for striped bass began in 1988 with a fishing moratorium and continued with the inception of an annual stocking program in 1990. Stocking resulted in striped bass adult CPUE increasing to levels near those reported prior to the decline (Reinert et al. 2005). Downstream of river kilometer (rkm) 45, the Savannah River divides into three channels: the Front, Middle, and Back rivers (Figure 1). The Back River was considered the primary striped bass spawning and nursery ground, primarily because of high adult CPUE and egg abundances in that reach (Smith 1970, Dudley and Black 1978). Thus, habitat restoration focused on restoring the habitat quality of the Back River, while development continued in the Front River, including a deepening of the channel in 1993–1994 (and subsequent maintenance dredging). Back River spawning and nursery habitat remediation included cessation of tide gate operation in 1991 and filling in of a diversion canal in 1992 (see Figure 1). Back River salinity levels and flow pathways recovered almost immediately after completion

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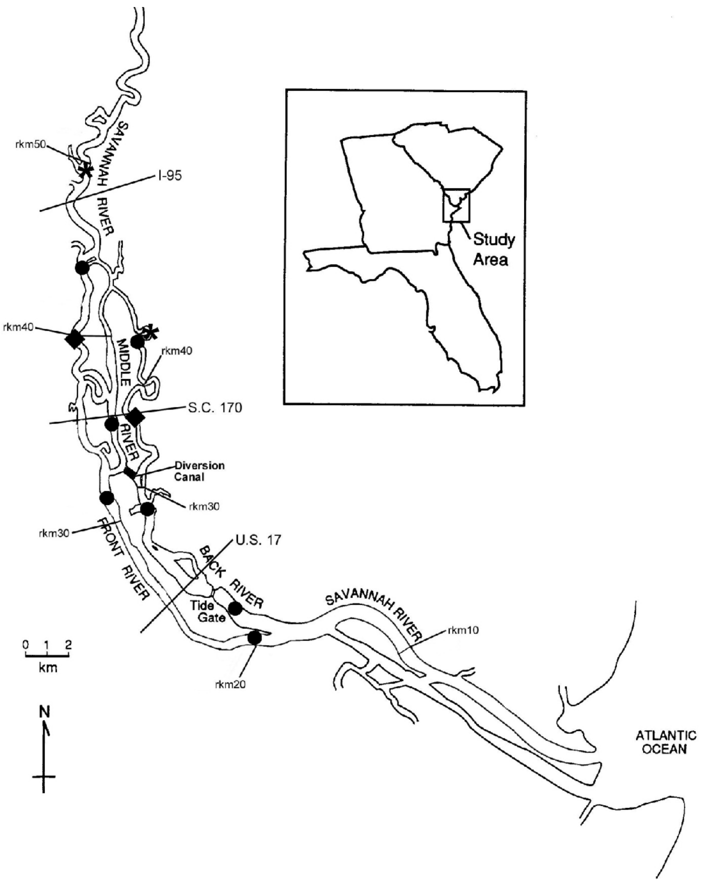

Figure 1. Map of the Savannah River estuary including Front, Middle, and Back river channels, major highways, tide gate, and diversion canal. Gellan bead release locations (*) and sampling stations (●) are shown. Historic sampling stations where individual efficiencies were calculated denoted by (◆). RKM = river kilometer.

of remediation activities (Pearlstine et al. 1993). Despite increased adult abundance from the stocking program and restored salinity patterns in historic spawning locations, however, egg density did not increase substantially and remained far below that of the late 1970s, especially in the historically productive Back River (Reinert et al. 2005).

Historically, density of striped bass eggs at certain fixed sampling stations in the Savannah River was used to determine the location of spawning grounds and as a relative index of the amount of egg production; it was used most intensively from the mid-1980s through the 1990s (Larson 1985, Van Den Avyle et al. 1990, Wallin and Van Den Avyle 1995, Reinert et al. 1996, 1998, Will et al. 2000). The methods employed to estimate density of striped bass eggs were dependent on the assumptions that capture efficiency of eggs was constant among stations and years. Thus, if striped bass egg density increased or decreased relative to previous years, the assumption was that total egg abundance increased or decreased as well. Initial results from an egg-sampling efficiency study in the Savannah River, in effect a mark-recapture study of egg surrogates, suggested that sampling efficiency was an order of magnitude greater in the Back River than the efficiency calculated for the estuary as a whole (Reinert et al. 2004). This unequal capture efficiency would result in biased conclusions about egg abundance if egg density is used as the informative index (Reinert et al. 2004). Based on Reinert et al.'s (2004) conclusions, actual egg abundance historically may have been much higher in the Front River than previously suspected.

To investigate historical abundances of striped bass eggs, we employed sampling efficiency estimators developed by Reinert et al. (2004) for our egg sampling methods. The objectives for this study were to: 1) refine the sampling efficiency estimators developed by Reinert et al. (2004) to discern individual sampling efficiencies at two of the historically most productive sampling stations in the Front and Back rivers, and 2) use the less-biased estimates of sampling efficiency on historic egg density estimates to back-calculate a minimum egg abundance for each historic sampling station. The overall goal of this study was to use these adjusted estimates of egg abundance to better understand the historic trends in striped bass egg distribution within the Savannah River estuary and provide direction to guide future estimation of striped bass reproductive effort and ultimately management and policy decision making.

Methods

Historically, sampling for striped bass eggs in the Savannah River estuary was conducted with bow-mounted, 0.5 m-diameter, conical plankton nets with 505-µm mesh and mesh-windowed sample cup. Samples were collected on ebb tides with the boat driven upstream at an oblique angle from bank to bank, at an approximate velocity of 1 m/sec. The net was fished 1 m below the surface for eight minutes or until approximately 100 m^3 of water was sampled. A General Oceanics flow meter in the mouth of each net estimated the water volume sampled, and captured eggs were standardized to number per 100 m^3. Until 1990, a sampling event consisted of a single pass of paired nets (Dudley and Black 1978, Van Den Avyle et al. 1990, Wallin and Van Den Avyle 1995). Beginning with the 1991 sampling season, sample collection was standardized to one net fished for three consecutive passes (considered subsamples; Brown and Austen 1996, Kelso and Rutherford 1996) during each sampling event. Stations typically were sampled daily or every other day from about mid-March through mid-May (see Figure 1 for sampling stations).

In an effort to understand the implications of egg density measurements and to potentially back-calculate egg abundances, Reinert et al. (2004) used egg surrogates to investigate the sampling efficiency of the standardized egg sampling procedures. These egg surrogates (hereafter, 'beads') were considered to be a reasonable model for striped bass eggs in these transport studies (Reinert et al. 2004). Beads were released at two locations: one in the Savannah River upstream of the channel divisions and one in the Back River (Figure 1). Based on historic captures of broodfish from these locations and opinions and observations of GA-DNR biologists, we selected these areas as they coincided with the known spawning grounds of striped bass in the Savannah River estuary. A total of six releases were performed (three roughly concurrent releases at each station) and were used to estimate individual sampling efficiencies at the historic sampling stations (Table 1). Different colored beads distinguished each release location. Bead release times generally coincided with times and conditions when striped bass were known to be spawning. All releases occurred at the start of the flood tide. Previous standardized egg sampling protocols after each bead release were followed, with all stations sampled on the two days following each release. Since striped bass eggs hatch in 44 to 48 h under prevailing water temperatures in the Savannah River estuary (Bayless 1972), sampling longer than two days post-release was not deemed necessary.

To estimate the number of Savannah River-released beads that traveled into the Back and Middle rivers, we applied the average Back River capture efficiency (from Reinert et al. 2004) to the total number of Savannah River-released beads captured in the Back and Middle rivers (Table 1). Middle River captures were included with Back River captures because, based on hydrographic charts and average channel width throughout each reach, the Middle River is more similar hydrographically and hydrologically to the Back River than to the Front River. Therefore, we make the assumption that sampling efficiency will be similar along these two reaches of the estuary (although did not test this empirically). The estimated number of Savannah River-released beads that traveled into the Back and Middle rivers and were available for capture was calculated as:

$$1. \qquad \hat{N}_B = \hat{E}_B (C_B + C_M)$$

where $\hat{E}_B$ is the sampling efficiency estimator for Back and Middle rivers (0.0058%, from Reinert et al. 2004), and C_B and C_M are Savannah River-released beads captured in the Back and Middle rivers, respectively. Because we now had an estimate of the proportion of beads that traveled into the Back and Middle rivers, we subtracted that estimate ($\hat{N}_B$) from the total number of beads initially released in the Savannah River to obtain the amount of Savannah River-released beads available for capture in the Front River ($\hat{N}_F$). The sampling efficiency estimator for the Front River station (rkm 40; see Figure 1) was then estimated as,

$$2. \qquad \hat{E}_F = \frac{C_F}{\hat{N}_F}$$

where C_F = total number of Savannah River-released beads captured at the Front River station. Sampling efficiency for both stations was estimated as the mean of the three bead releases, and standard error (SE) from the mean sampling efficiency was used to calculate 95% confidence intervals around the estimated egg abundance. Our estimated efficiencies were applied to historic captures of striped bass eggs at these two stations. Unfortunately, the selected Front River station was only partially sampled in 1978 and not sampled in 1984 and 1986. For these years, we used egg captures at a nearby station (rkm 43.3) with the efficiency developed for the station at rkm 40. Because of potential independence problems with the paired-net samples (1977–1990) and high variability with the three replicate single net samples (1991–2000), we summed egg captures throughout each season by station rather than treating each sample or replicate independently.

Table 1. Capture of striped bass egg surrogates (gellan beads) released upstream of the Savannah River estuary, 1999–2000. The estimated number of beads in the Back (BR) and Middle (MR) rivers is used to adjust the remaining number of beads in the Front River (FR) available for capture, and to calculate an adjusted sampling efficiency specifically for the Front River sampling station (river kilometer 40). Mean efficiency and standard error (SE) are calculated.

	n released	Bead captures	Efficiency %	Estimated *n* beads	Adjusted *n* beads	Bead captures	Adjusted efficiency %
Date	**SR**	**BR+MR**	**BR**[a]	**BR + MR**	**FR**	**FR station**	**FR station**
19 May 1999	2.1×10^6	10	0.0018	562,500	1.54×10^6	3	0.00019
27 Mar 2000	3.5×10^6	23	0.0070	328,571	3.17×10^6	2	0.00006
31 Mar 2000	7.0×10^6	8	0.0088	90,688	6.91×10^6	28	0.00041
						$\bar{x}$ =	0.00022
						SE =	0.00010

a. Back River sampling efficiency is from Reinert et al. (2004).

Results

During the 1999 and 2000 bead releases, the estimated number of beads that traveled from the Savannah River release location into the Back and Middle rivers ranged from about 90,000 to over 500,000 (out of a possible 2.1 to 7 million, Table 1). Adjusting the number of beads available for capture at the Front River station yielded an adjusted sampling efficiency of 0.00022% (± 0.001% SE, Table 1). From Reinert et al. (2004), sampling efficiency at the Back River station averaged 0.0058% (± 0.0021% SE, Table 2).

Estimated egg abundances at the two stations differed greatly, but consistently, over time. In all years, estimated egg abundance at the Front River station was at least one order of magnitude greater than the estimated abundance at the Back River station (Table 3). Estimated Front River abundance ranged from 4.5 million (in 1998) to

Table 2. Estimated sampling efficiency at the historic egg sampling station in the Back River (river kilometer 35), Savannah River estuary, 1999–2000. Striped bass egg surrogates (beads) were released in the Back River, river kilometer 43.3. Mean efficiency and standard error (SE) are calculated.

Date	*n* released	*n* captured	Station efficiency %
19 May1999	1.8×10^6	32	0.0018
29 Mar 2000	9.0×10^5	63	0.0070
31 Mar 2000	2.8×10^6	241	0.0086
		$\bar{x}$ =	0.0058
		SE =	0.0021

Table 3. Minimum egg abundance estimates at the Front River (FR; river kilometer [rkm] 40) and Back River (BR; rkm 35) reference stations, Savannah River estuary, 1978–2000, based on mean capture efficiencies for each reach. Confidence interval (95%) is ± 1.96*SE of efficiency and expanded. Note: Front River egg captures in 1978 and 1986 (denoted by "*") are from rkm 43.3 because the reference station (rkm 40) was either partially or not sampled at all those years.

Year	*n* of eggs FR	Est. FR abundance	95% CI (± 1.96 SE)	*n* of eggs BR	Est. BR abundance	95% CI (± 1.96 SE)
1978	455*	2.06×10^8	$1.67 \times 10^7 – 4.32 \times 10^8$	844	1.46×10^7	$5.99 \times 10^6 – 6.27 \times 10^7$
1984	100*	4.52×10^7	$3.68 \times 10^6 – 9.48 \times 10^7$	1259	2.17×10^7	$8.92 \times 10^6 – 9.35 \times 10^7$
1986	1023*	4.63×10^8	$3.67 \times 10^7 – 9.70 \times 10^8$	1345	2.32×10^7	$9.53 \times 10^6 – 9.98 \times 10^7$
1987	315	1.42×10^8	$1.16 \times 10^7 – 2.99 \times 10^8$	31	5.38×10^5	$2.21 \times 10^5 – 2.32 \times 10^6$
1988	66	2.98×10^7	$2.43 \times 10^6 – 6.26 \times 10^7$	179	3.08×10^6	$1.27 \times 10^6 – 1.33 \times 10^7$
1989	240	1.09×10^8	$8.83 \times 10^6 – 2.28 \times 10^8$	42	7.25×10^5	$2.98 \times 10^5 – 3.12 \times 10^6$
1990	126	5.70×10^7	$4.63 \times 10^6 – 1.19 \times 10^8$	32	5.50×10^5	$2.26 \times 10^5 – 2.37 \times 10^6$
1991	11	4.97×10^6	$4.05 \times 10^5 – 1.04 \times 10^7$	0	0	0 – 0
1994	196	8.86×10^7	$7.21 \times 10^6 – 1.86 \times 10^8$	4	7.08×10^4	$2.91 \times 10^4 – 3.04 \times 10^5$
1995	82	3.71×10^7	$3.02 \times 10^6 – 7.78 \times 10^7$	16	2.67×10^5	$1.10 \times 10^5 – 1.15 \times 10^6$
1996	27	1.22×10^7	$9.93 \times 10^5 – 2.56 \times 10^7$	2	3.45×10^4	$1.42 \times 10^4 – 1.48 \times 10^5$
1997	16	7.24×10^6	$5.88 \times 10^5 – 1.52 \times 10^7$	3	5.18×10^4	$2.13 \times 10^4 – 2.23 \times 10^5$
1998	10	4.52×10^6	$3.68 \times 10^5 – 9.48 \times 10^6$	1	2.30×10^4	$9.43 \times 10^3 – 9.87 \times 10^4$
1999	132	5.97×10^7	$4.85 \times 10^6 – 1.25 \times 10^8$	32	5.50×10^5	$2.26 \times 10^5 – 2.37 \times 10^6$
2000	139	6.29×10^7	$5.11 \times 10^6 – 1.32 \times 10^8$	14	2.40×10^5	$9.85 \times 10^4 – 1.03 \times 10^6$

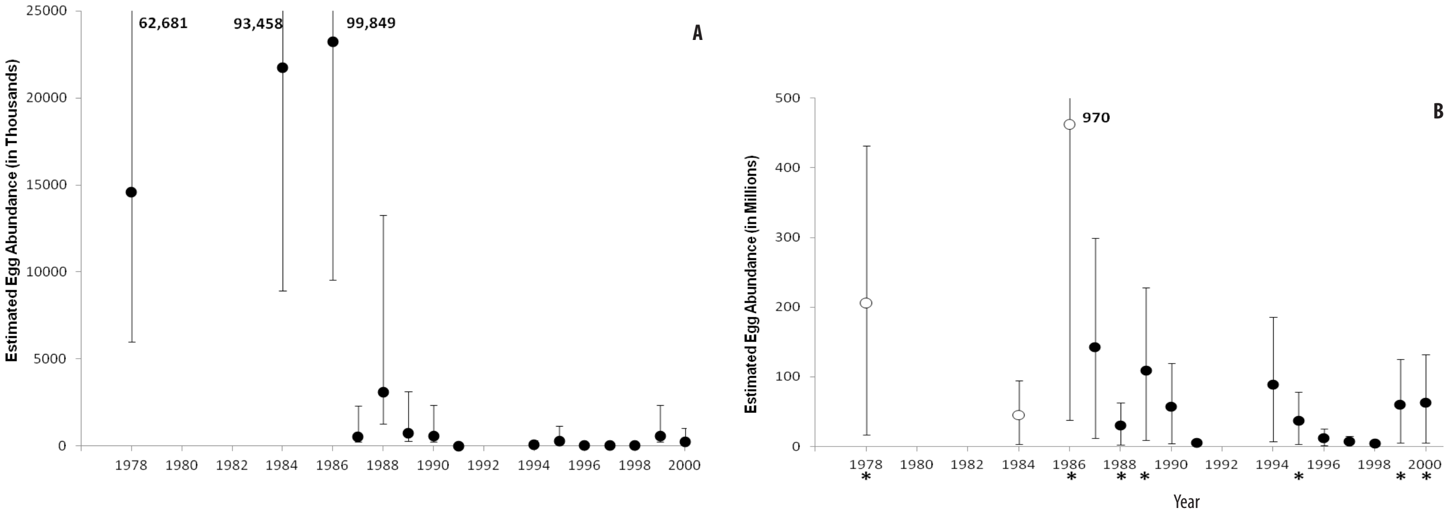

Figure 2. Estimated minimum striped bass egg abundance in the Savannah River estuary, 1978–2000. A) Abundance (in 1000s) at the Back River reference station (river kilometer [rkm] 35). B) Abundance (in millions) at the Front River reference station (rkm 40). Note: abundances from 1978, 1984 and 1986 (denoted by open circles) are from rkm 43.3 because the reference station was not fully sampled those years. Asterisks (*) denote years of comparable river discharge (± 100 cms) to 1999–2000, when sampling efficiencies were developed. Error bars are 95% Confidence Intervals (±1.96*SE of mean sampling efficiencies). Where error bars disappear, end points are denoted.

over 460 million eggs (1986), whereas estimated Back River abundance ranged from 0 (in 1991) to just over 23 million (in 1986).

April river discharge was highly variable (437 ± 281 m^3/sec) during the historic study period (1978–2000), but was low and stable (186 ± 35 m^3/sec) during the period we established sampling efficiencies (1999–2000). Discharge may have an impact on sampling efficiency and years of similar discharge (± 100 m^3/sec of the 1999–2000 April average) are most directly comparable using these methods (Figure 2).

Discussion

Reinert et al. (2004) used egg surrogates to investigate the sampling efficiency of standardized egg sampling procedures used historically in the Savannah River to estimate relative abundance of striped bass eggs. These egg surrogates were considered to be adequate representations of natural striped bass eggs and should provide a reasonable model for striped bass egg transport studies. Beads had a specific gravity of 1.0015 to 1.0018 and were 4.4 to 4.8 mm in diameter (see Reinert et al. 2004 for more specific details). Although larger than Savannah River striped bass eggs (2.77 mm ± 0.19 mm;

Bergey et al. 2003), beads were very similar to Savannah River striped bass eggs in regards to specific gravity (1.001; Bergey et al. 2003), which we considered the more critical of the two metrics. Location in the water column (largely controlled by specific gravity) was more important than relative travel speed (likely more dependent on drag and thus egg diameter). Similar-sized but denser beads would have distributed lower in the water column and would not have been an appropriate surrogate for the standardized sampling methodology. Because the beads had a similar specific gravity and would be similarly located within the water column, we felt they were equally susceptible to our gear as were natural striped bass eggs, which made them adequate surrogates for these studies. Whether striped bass eggs are uniformly distributed throughout the water column is unknown; therefore, using surrogates of similar specific gravity should reduce this potential source of bias, as the surrogates should travel at the same level in the water column as naturally-spawned eggs.

River discharge likely affected sampling efficiency by increasing dispersion or more rapidly moving eggs (and beads) through the system, although we were unable to evaluate this effect during our study. Our sampling efficiency estimates were calculated under relatively low discharges ($<225\,m^3$/sec) and thus may not be applicable to all years and discharge levels. Higher discharge rates may negatively affect sampling efficiency through increased dispersion or flushing rates, which may reduce the applicability of our calculated efficiencies (and hence abundance estimates) during those years of exceptional discharge. During such years, we may be overestimating sampling efficiency, and hence, underestimating egg abundance. Conducting additional egg surrogate studies under a variety of flows (e.g., average and high flows) would reduce the variance in our estimates and better predict the relationship between discharge and sampling efficiency. Only a small range of discharges was available to us during our sampling window, and the narrow range of testable discharges was unavoidable. However, several years throughout the span of our back-calculations had mean April discharges similar to 1999–2000 (Figure 2); estimated egg density during these years are directly comparable and do provide insight into the decline of striped bass reproduction in the Savannah Estuary.

Previous estimates of striped bass reproductive effort were limited to reporting average egg density for stations and years and provided a relative index of striped bass reproduction in the estuary. Historic data show that densities of striped bass eggs in the Back River seem to be higher than those in the Front River during 1978, 1984, and 1986 (Figure 3); however, because of a previously unknown bias in sampling efficiencies between reaches of the Savannah River estuary, those egg densities may not be a valid index for directly comparing egg catches between reaches. Sampling efficiency at our Front River station was much lower than that of the Back River station and resulted in abundance estimates for those stations that contradict interpretations based solely on egg density comparisons. By determining sampling efficiencies for our egg sampling methods, we were able to address this bias and further translate egg density estimates into estimates of egg abundance at these stations (Table 3).

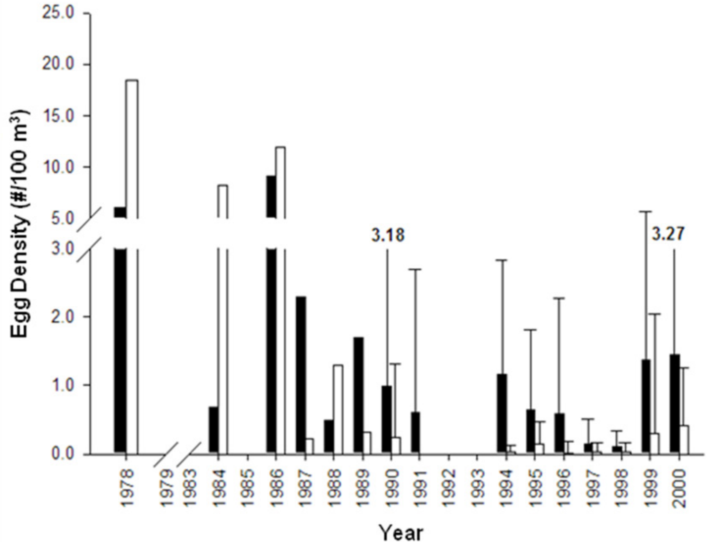

Figure 3. Historic egg densities (number/100m^3) in the Savannah River estuary, 1978–2000. Front River egg densities (black bars) are from river kilometer (rkm) 43.3 in 1978, 1984, and 1986 and from the reference station (rkm 40) for the remaining sample years. Back River egg densities (open bars) are from the Back River reference station (rkm 35). Error bars (where available) are standard deviations. Where error bars disappear, end points are denoted. Data are from Dudley and Black (1978), Larson (1985), Van Den Avyle et al. (1990), Wallin and Van Den Avyle (1995), Reinert et al. (1996, 1998), and Will et al. (2000, 2001).

Because we did not sample at multiple depths, whether eggs (and beads) were evenly distributed throughout the water column is unknown. If such were known to be the case, our sampling efficiencies, coupled with egg captures and the cross-sectional area of the sampling sites would allow for a total egg abundance estimate for each site. Without this information, however, our estimates of production should be viewed as minimum egg production estimates. Additional sampling at depth to determine egg (and bead) distribution would allow bathymetric and geomorphic data to be coupled with our sampling efficiency estimates to create a more accurate estimate of total production in the estuary. Egg captures at multiple stations were summed throughout each sampling year, and sampling efficiencies applied to estimate the minimum amount of egg production occurring in the Savannah River estuary and how that production was distributed throughout the multi-channeled system. Minimum egg abundances at the Front River station far exceeded estimated egg abundances at the Back River station (Table 3) and suggests that the Front River likely received most of the eggs produced in the system in any given year.

The importance of the Front River as a spawning and nursery ground may have been underestimated in the past. Current minimum abundance estimates indicate that the vast majority of striped bass eggs occurred in the Front River. Previous studies found that egg density was highest in the Back River and thus concluded that the Back River area was the primary spawning location for striped bass (Smith 1970, Dudley and Black 1978, Larson 1985). Under this interpretation, managers suggested that habitat restoration efforts should concentrate on the Back River, potentially at the expense of the Front River (i.e., if the Back River could be restored and historic spawning levels returned, additional development could be allowed in the Front River). Our study suggests that sampling efficiency is one order of magnitude greater in the Back River than in the Front River and may have created the false conclusion that more eggs occur there than in the Front River. Egg surrogates, released above where the estuary divides into separate reaches, traveled into both Front and Back rivers; presumably, striped bass eggs do the same. Additionally, striped bass larvae are rarely captured in our egg samples, but when they have occurred, they were captured primarily in upper Front River areas (Van Den Avyle et al. 1990, Jennings and Weyers 2003). Thus, the upper Front River portion of the estuary may be more important to striped bass recruitment than previously considered. The Back River, however, has supported known spawning aggregations of striped bass in the past, and its importance should not be diminished by these results. Indeed, the area has been shown to be an important nursery area for juvenile striped bass (Sinclair 1996) as well as other species (Collins et al. 2003, Jennings and Weyers 2003). Clearly, as far as potential striped bass recruitment is concerned, the Savannah River estuary must be considered in its entirety.

Recovery efforts for the Savannah River striped bass population have taken the two-faceted approach of environmental restoration and stock-enhancement, with the ultimate goal of restoring a self-sustaining population. To rectify the environmental issues thought responsible for the population collapse, the tide gate was removed from operation and the diversion canal was filled in (1991 and 1992, respectively). Salinity has since decreased in the areas thought to be important striped bass spawning and nursery areas (Pearlstine et al.1993), and original pathways for egg distribution have been restored. The stock-enhancement program also has been successful, as indicated by increasing adult CPUE to levels similar to pre-tide gate levels (Reinert et al. 2005). With increased adult abundance, reproductive effort also should be expected to increase. Estimating the number of actual eggs present (even a minimum count as presented here) will be more meaningful to managers and decision makers than were the earlier estimates based on the relative (and biased) metric of egg densities.

Based on our estimates, the minimum striped bass egg abundance in the Savannah River estuary was over 200 million eggs in 1978 and was at least as high as 485 million in 1986. Reproductive effort at our two reference stations in 2000 (the last year sampled) was estimated at a minimum of 63 million eggs. Although considerably less than minimum production prior to the alterations inflicted upon the system, this estimate is nearly twice that of the most recent year of comparable discharge (1995), when minimum production was as low as 37 million eggs (Table 3). Estimates of reproductive effort have been used in the past to dictate management efforts in this system, and our efforts here seek to refine those estimates. Further, our efforts also seek to correct previously unknown biases affecting those estimates and, ultimately, policy decisions. Our results are a reasonable first step toward recognizing the importance of how location and sampling efficiency may have biased historic estimates of striped bass reproductive effort in the Savannah River estuary. Additional research could further refine these estimates and allow a means to more accurately estimate historic egg production in the system. Regardless, the apparent increased production during the final two years of this study is encouraging. Striped bass have been shown to be year-class dependent and high egg production in any given year will not guarantee a successful year class (Ulanowicz and Polgar 1980, Boreman and Austin 1985, Secor and Houde 1995). Thus, if the adult population increases to a point where such reproductive output can be maintained over several years, at least one successful year-class might be ensured and thereby provide the population a reasonable chance of regaining self-sustainability.

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