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ENVIRONMENTAL ASSESSMENT

Modeling the Effects of Potential Salinity Shifts on the Recovery of Striped Bass in the Savannah River Estuary, Georgia–South Carolina, United States

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Abstract Increased salinity in spawning and nursery grounds in the Savannah River estuary was cited as the primary cause of a 97% decrease in adult striped bass (*Morone saxatilis*) and a concomitant 96% decrease in striped bass egg production. Restoration efforts focused on environmental remediation and stock enhancement have resulted in restored salinity patterns and increased egg and adult abundances. However, future water needs or harbor development may preclude further recovery by reducing freshwater inflow or increasing salinity intrusion. To assess the effect of potential changes in the salinity regime, we developed models relating discharge, tidal phase, and salinity to striped bass egg and early larval survival and recast these in a quantitative Bayesian belief network. The model indicated that a small upstream shift (≤1.67 km) in the salinity regime would have the least impact on striped bass early life history survival, whereas shifts >1.67 km would have progressively larger impacts, with a 8.33-km shift potentially reducing our estimated survival probability by >28%. Such an impact could have cumulative and long-term detrimental effects on the recovery of the Savannah River striped bass population. The available salinity data were collected during average and low flows, so our model represents some typical and some extreme conditions during a striped bass spawning season. Our model is a relatively simplistic, "first-order" attempt at evaluating potential effects of changes in the Savannah River estuarine salinity regime and points to areas of concern and potential future research.

Keywords Bayesian belief network · Decision analysis · Early life history survival · *Morone saxatilis* · Salinity · Striped bass

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Introduction

The Savannah River estuary, Georgia–South Carolina, United States, once hosted Georgia's largest and most economically important striped bass (*Morone saxatilis*) fishery. This population also served as the source of brood stock for a state-sponsored aquaculture program during the 1960s and 1970s that focused on stocking reservoirs and riverways throughout the state with striped bass and striped bass–white bass (*M. chrysops*) hybrids. Historically, striped bass spawning occurred in the upper-estuary reaches of the Savannah River between river kilometers (rkm) 40 and 50 of both the Front and Back Rivers (Fig. 1). The Georgia Department of Natural Resources (GA-DNR) annually collected brood stock by way of electrofishing in the upper estuary, particularly the Back River. In the early 1980s, GA-DNR biologists noted reductions in the catch-per-unit-effort (CPUE; number of fish/h) of large striped bass (≥9.0 kg); those reductions eventually made brood fish collections in the estuary impractical. By 1989, CPUE of

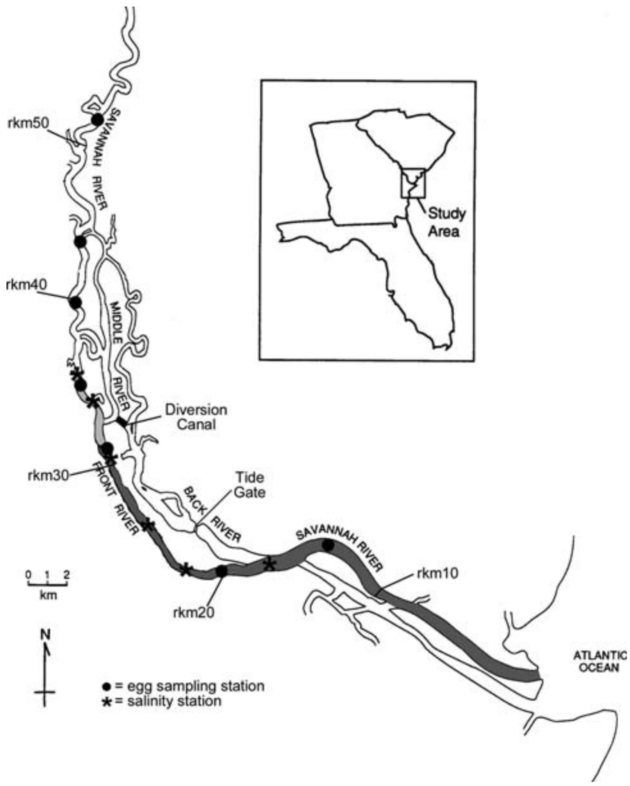

Fig. 1 Map of the Savannah River estuary, Georgia–South Carolina, showing the maintained river channel (harbor), tide gate, and diversion canal (filled). *Salinity-measurement stations. •Egg-sampling stations. Dark grey channel depth is 12.8 m MLW, and light grey channel depth is 11.6 m MLW. Proposed deepening will occur along the current 12.8 m channel. MLW = mean low water

adults had decreased by 97%, and egg production had decreased by 96% (Reinert and others 2005).

Striped bass adults typically spawn in freshwater habitats within or just upstream of the tidally influenced sections of estuaries (Setzler and others 1980). In Georgia, spawning typically occurs from mid-March through early May when water temperatures are between 12 °C and 21°C. Because striped bass are broadcast spawners (i.e., gametes are released into the water column, and eggs float for a brief period, typically 44 to 48 hours in Georgia's waters, before hatching), and larvae have limited motility until at least 5 days after hatching, fish in early life history stages are susceptible to downstream changes in habitat and water quality. Loss of tidal-freshwater spawning and nursery habitat brought about by increases in salinity and accelerated seaward transport of eggs and larvae were cited as the primary causes of the decrease in the Savannah striped bass population (Van Den Avyle and Maynard 1994). These altered conditions were caused by the installation of a tide gate on the Back River and a diversion canal that enhanced flushing sediments from Savannah Harbor (see Fig. 1). Flood tides were captured by the tide gate and forced through the diversion canal during ebb flow. Entrapment of the flood tide increased salinity at important spawning and nursery areas, and transport through the diversion canal exposed eggs and larvae to harmful or lethal salinity levels in the industrial harbor. During tide gate operation, the saltwater wedge moved 3.33 to 10 km upstream, depending on tidal and discharge conditions (Pearlstine and others 1993), and increased up to 8‰ in some areas (Reinert and others 2005). For Savannah striped bass, salinity >10‰ is harmful to eggs and lethal to larvae (Winger and Lasier 1994).

Efforts to restore the population began with a fishing moratorium in 1988 and the inception of a state-sponsored restoration-stocking program in 1990 (Reinert and others 2005). Environmental remediation included decommissioning the tide gate (1991) and filling the diversion canal (1992). To date, the restoration-stocking program has released almost 2 million fish into the estuary, and in recent years, egg production and CPUE of large striped bass have increased. Salinity levels in historic spawning and nursery habitats are similar to those before the decrease (Reinert and others 2005). In addition, during recent trawl surveys, captures of wild-spawned larvae and juveniles indicate that natural reproduction is occurring and is successful (Collins and others 2003, Jennings and Weyers 2003). The increasing abundance of larger fish should result in continued increases in egg production and future recruitment. However, a proposed deepening of the harbor would directly affect the Front River channel to rkm 32 (Fig. 1) and may have indirect effects further upstream if additional salt water is conveyed into the estuary by way of the deeper channel. Such changes may preclude striped bass recovery by again allowing saltwater intrusion into upstream spawning and nursery habitats.

To assess possible anthropogenic changes in the Savannah River estuary, we developed a model to predict the changes in striped bass reproductive success in response to upstream shifts in the salinity regime. Our model was parameterized using published data of striped bass early life history survival, river discharge, tidal phase, and unpublished data characterizing the distributions of striped bass eggs and larvae and salinity gradients in the estuary. Because our model is based on changes in salinity and not a specific environmental impact or management decision, it may be applied to a variety of freshwater habitat loss situations, including deepening and mitigation scenarios. Specifically, our objectives were (1) to develop a predictive relation between salinity conditions and survival of early life history stages of striped bass in the Savannah River estuary and (2) to incorporate these relations into a model to evaluate the potential effects of upstream salinity shifts on early life history survival probability (ELHS).

Methods

Study Area

The Savannah River basin drains an area of approximately 28,750 km^2. Its headwaters originate in the Blue Ridge Mountains of North Carolina, South Carolina, and Georgia. The Seneca and Tugaloo Rivers join near Hartwell, GA, to form the Savannah River. From there, the river flows approximately 500 km in a southeasterly direction to the Atlantic Ocean and serves as a boundary between Georgia and South Carolina. The estuary spans roughly the lower 50 km of the river and is characterized by a distributary network of three main channels: the Front, Middle, and Back rivers (Fig. 1). Annual mean stream flow to the estuary is approximately 359 m^3/s (United States Geological Survey [USGS] 2003) and is regulated by a series of upstream dams, the furthest downstream of which is located at rkm 302. Discharge to the estuary is measured at Clyo, GA (station ID 02198500), the nearest USGS gauge (rkm 103) and includes 88.7% of total watershed drainage area. Mean tidal range for the Savannah River mouth is approximately 2.5 m and spring tides can exceed 3.0 m (NOAA 2003).

Field Collections

Striped bass eggs and larvae were sampled from March through May 1990 through 2000, with the exception of 1992 to 1993 (Wallin and Van Den Avyle 1995a, Reinert and others 1996, 1998, Will and others 2000, 2001). Front River samples were collected at least every two days from seven stations located between rkm 15 and 52 (Fig. 1). Five of the seven stations were sampled each year. The station at rkm 35 was sampled for two years, and the station at rkm 40 was sampled for seven years. These stations represent a range of salinity conditions in the estuary from entirely fresh (rkm 52) to oligohaline (rkm 15). Sampling consisted of pushing bow-mounted 0.5-m diameter, 505-μm mesh plankton nets 1 m below the water surface. Sampling primarily occurred during daylight hours on the ebb tide. A General Oceanics, Inc. (Miami, FL) flow meter in the mouth of each net measured the volume sampled, and captured eggs were standardized to number per 100 m^3. Discharge (measured at the Clyo gauge) during egg sampling ranged from 171 to 922 m^3/s, and samples were collected during all tidal phases (i.e., neap, spring, and mixed).

Environmental Data

Daily discharge data for the lower Savannah River were obtained from USGS records for the Clyo, GA, gauging station. Daily discharge was lagged by two days, reflecting the amount of time a water mass takes to reach the upper estuary (approximately rkm 50; P. Conrads, USGS Water Resources Discipline, personal communication, August 2003). Daily tidal amplitude in the estuary was calculated from tidal heights as measured at a National Oceanographic and Atmospheric Administration (NOAA) gauging station (Ft. Pulaski; station ID 8670870) near the Savannah River mouth.

Applied Technology and Management (ATM; a consulting firm hired by the Georgia Ports Authority) collected surface-salinity measurements from multiple stations in the estuary as part of a three-dimensional hydrodynamic modeling effort. The data were collected during July through October 1997 and 1999 at three and six stations, respectively, located between rkm 18.3 and 35.8 (Fig. 1; ATM). These stations were downstream of three egg-sampling stations and overlapped three egg-sampling stations, and they were 3.3 km upstream of the furthest downstream egg-sampling station. Surface-salinity measurements were recorded at 15- and 5-minute intervals in 1997 and 1999, respectively, using in situ Hydrolab DataSondes (Hach Environmental, Loveland, CO). ATM provided this large and unique data set for our model-building exercise. River discharge during salinity sampling ranged from 154 to 326 m^3/s, and tides ranged from 1.5 to 3.1 m.

Model Overview

Adult striped bass in the Savannah River generally use the entire run of the river and rarely venture into the open ocean. During winter and spring, they occur primarily in estuarine environments, whereas during summer, they move to cooler, upstream areas (Dudley and others 1977). Young-of-year (YOY) and subadult Savannah River striped bass tend to prefer brackish or freshwater habitats in the lower estuary near the freshwater–saltwater interface (Wallin and others 1995). Because juveniles and adults are highly mobile (as are their prey), we assume that changes to the salinity character of the estuary will not substantially influence survival for fish at these life stages. Eggs (up to two days old) and prolarvae (i.e., larvae with a yolk sack; <5 to 7 days old) have little or no active control over their place in the water column and are systematically transported seaward during their brief time in these life stages. We assume then that these fish in early life history stages are likely to be more sensitive to changes in the salinity regime. Therefore, our model focuses on estimating egg and prolarval survival in response to hypothetical increases in salinity conditions in areas where fish in these early life history stages are known to occur.

We developed a stochastic model composed of environmental factors (river discharge, tidal phase, and

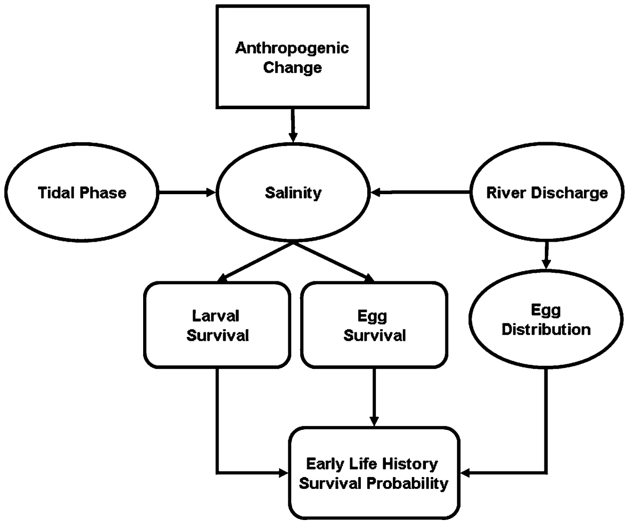

Fig. 2 Influence diagram representing how potential anthropogenic changes in the Savannah River estuary that affect salinity may also affect early life history survival probability. The decision node is square, probabilistic variables are ovals, and objective functions are represented as rounded rectangles (Varis and Kuikka 1999). Directional arrows indicate a functional dependence (e.g., salinity is dependent on tidal phase and river discharge)

salinity), striped bass egg distribution, egg and prolarval survival, and hypothetical salinity shifts (Fig. 2). The model is spatially explicit and operates on a daily step during a striped bass spawning season (typically April in Georgia). The model begins with a specified number of eggs spawned at traditional spawning areas in the upper estuary between rkm 42 and 50. Fertilized eggs are then transported downstream, and their distribution in the river at hatching (approximately 44 hours after spawning) is estimated as a function of river discharge. Egg hatching and surviving into prolarvae is modeled as a function of river salinity. The prolarvae then are transported downstream as a function of river discharge where they transform into larvae (i.e., actively swimming) in approximately six days (Setzler and others 1980). The survival of prolarvae to larvae is modeled as a function of salinity. Surface-salinity gradients are modeled as a function of river discharge and tidal phase (spring, neap, or mixed). Stochasticity is imposed by randomly generating values for discharge and tidal phase during striped bass spawning. We impose additional stochasticity by randomly generating errors for the salinity, egg distribution, and survival models.

Egg Distribution

In the Savannah River, striped bass egg distribution is primarily influenced by river discharge, although other factors may have minor influences as well. River discharge is regulated by upstream dams and rainfall events in the lower basin. Striped bass eggs tend to be found in the middle and upper reaches of the estuary (rkm 35 to 45), although extreme discharges may shift egg distribution downstream (e.g., in 1998 when average April discharge was 922 m^3/s; Fig. 3A). The river is relatively narrow (average width over study area is approximately 260 m) and channelized, unlike larger, more open systems, such as the Chesapeake Bay, and episodic weather events (e.g., wind mixing, etc.) are unlikely to have a significant influence on egg position (e.g., North and others 2005). In addition, the location of an estuarine turbidity maximum has not been identified for the estuary. Like many small southeastern rivers, the lower Savannah River likely has too many heterogeneous sources contributing to the overall estuarine signature to create a defined turbidity maximum (J. Blanton, Skidaway Institute of Oceanography, personal communication, August 2003). In this system, a detectable salt wedge only occurs during neap tides, reducing the formation of a "sediment trap," further decreasing the strength or likelihood of an identifiable estuarine turbidity maximum (Schubel 1968). Because behavioral compensation by adult fish in response to changing downstream conditions (e.g., changes in downstream salinity) is unlikely in striped bass (Ulanowicz and Polgar 1980), we assumed that the relative location of spawning aggregations remained unchanged (although actual spawning location may be influenced by conditions at the spawning grounds). Hence, we used the same egg-distribution model across evaluations. Therefore, the proportion of eggs (π) occurring at river location j (sampling station) was modeled as a multinomial function of river discharge as

$$\pi_j = \frac{\exp(\beta_{0j} + \beta_{1j} * \text{discharge})}{\sum_{k=1}^{7} \exp(\beta_{0k} + \beta_{1k} * \text{discharge})}, \quad (1)$$

where β_0 and β_1 are the location-specific estimated intercept and slope. Model parameters were estimated by fitting a multinomial logistic regression model (Agresti 2002) to egg captures by station and discharge data using furthest upstream sample station as the baseline response category. The overall model was statistically significant ($p < 0.0001$) and indicated that downstream egg distribution was positively related to discharge (Table 1 and Fig. 3B).

Hatching and Survival

The probability of hatching success and larval survival was modeled as a function of salinity using data from Winger and Lasier (1994). In their study, Savannah River striped bass eggs and larvae were exposed to serial dilutions of saltwater (range 0‰ to 33‰) to calculate postfertilization egg mortality (i.e., hatching success) and early larval mortality (up to 10 days old). We fit separate logistic

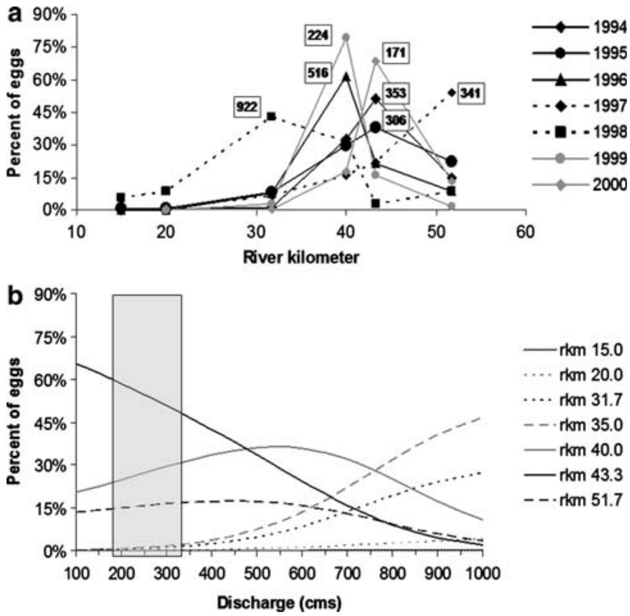

Fig. 3 Measured and predicted effects of discharge on striped bass egg distribution in the Savannah River estuary. (A) Percent of striped bass eggs captured per rkm in the Front River from 1994 through 2000. Numbers in boxes are the average April discharge (m^3/s) during sampling as reported at the USGS gauging station near Clyo, GA. The grey lines represent 1999 (circles) and 2000 (diamonds) when egg sampling did not occur at the most downstream station (rkm 15). Data are from Reinert and others (1996, 1998) and Will and others (2000, 2001). (B) Percent occurrence of striped bass eggs by location (rkm) as predicted by the egg-distribution model (Equation 1). Grey bar indicates range of discharges observed during salinity measurements and used in the overall model

regression models relating egg-hatching success and prolarval survival to salinity using the data in Winger and Lasier (1994). Both logistic regression models were statistically significant ($p < 0.0001$) in predicting egg-hatching success and larval survival, respectively (Table 2).

Salinity Conditions

Salinity at a given location in the estuary is influenced by river discharge and varies with tidal phase and amplitude (Alber and Sheldon 1999). Because striped bass eggs and prolarvae are planktonic and experience net-downstream advection during development, they may experience a temporally and spatially variable range of salinity. Conditions in the upper-estuary spawning grounds may remain suitable even as conditions in the lower estuary (where eggs eventually are distributed) deteriorate. To approximate estuarine salinity conditions, we first divided discharge into two categories: low (<225 m^3/s) and average (225 to 326 m^3/s), which corresponded to conditions experienced during ATM's 1997 and 1999 salinity sampling periods (July through October) and was relative to long-term trends in Savannah River discharge. Dividing discharge into the aforementioned categories of "average" and "low" also captured fairly common (average) and relatively uncommon (low) flows during the typical striped bass spawning period (March through May), although we were unable to evaluate higher flows during this study (such flows were not experienced during the collection of the salinity data). Each sampling day during the ATM salinity study also was assigned a tidal phase category based on mean tidal range for that day. Days when tidal range exceeded 1 SD of the monthly mean were considered "spring" tides, and those days when tidal range was <1 SD of the monthly mean were considered "neap" tides. All

Table 1 Parameter estimates (i.e., intercepts and slopes), SEs, and upper and lower 95% CIs for the multinomial logit model of striped bass egg distribution in the Savannah River estuary during sampling seasons 1990 through 1991 and 1994 through 2000[a]

Sampling location	Model parameter	Estimated coefficient	SE	Upper 95% CI	Lower 95% CI
rkm 15.0	Intercept	−8.8784	1.3980	−6.1383	−11.6185
	Discharge	0.0094	0.0022	0.0136	0.0051
rkm 20.0	Intercept	−6.6660	0.9325	−4.8383	−8.4937
	Discharge	0.0068	0.0018	0.0103	0.0032
rkm 31.7	Intercept	−4.6338	0.3969	−3.8559	−5.4117
	Discharge	0.0067	0.0008	0.0084	0.0051
rkm 35.0	Intercept	−4.2953	0.3478	−3.6136	−4.9770
	Discharge	0.0069	0.0008	0.0084	0.0054
rkm 40.0	Intercept	0.3415	0.1652	0.6653	0.0177
	Discharge	0.0008	0.0005	0.0017	−0.0001
rkm 43.3	Intercept	1.8138	0.1505	2.1088	1.5188
	Discharge	−0.0023	0.0004	−0.0014	−0.0031

CI = confidence interval

[a] Estimated coefficients should be interpreted relative to upstream station at rkm 51.7 (the baseline). Components of this model were used to predict egg distribution in the estuary

Table 2 Parameter estimates, SEs, and upper and lower 95% CIs for the logistic regression model of striped bass egg and larval survival in the Savannah River estuary based on data presented in Winger and Lasier (1994)

Life stage	Model parameter	Estimated coefficient	SE	Upper 95% CI	Lower 95% CI
Egg	Intercept	0.6664	0.0167	0.6992	0.6336
	Salinity	−0.0969	0.0013	−0.0944	−0.0994
Larvae	Intercept	0.5068	0.1315	0.7646	0.2491
	Salinity	−0.1193	0.0111	−0.0976	−0.1410

other days were assigned to the "average" category. Assignment of tidal phase also was cross-validated with lunar phase for each day. Spring tides occur during full and new moons, whereas neap tides occur during first and last quarter phases (Pond and Pickard 1983).

Only one salinity-monitoring site corresponded exactly to an egg and larval sampling station (rkm 30; Fig. 1). Hence, salinity conditions at the rkm 30 station were modeled using the corresponding salinity data. For the remaining stations, salinity was linearly extrapolated using the salinity data for the nearest up and downstream salinity stations as

$$c_k = (l_u - l_k) \cdot \frac{c_d - c_u}{l_u - l_d} + c_u, \quad (2)$$

where l is the location (rkm) and c is the salinity at the egg sampling station (k), upstream (u) and downstream (d) salinity sampling stations.

Salinity measurements from each station were grouped by discharge and tidal phase for a total of six groups/station: (1) average discharge, average tide; (2) average discharge, neap tide; (3) average discharge, spring tide; (4) low discharge, average tide; (5) low discharge, neap tide; and (6) low discharge, spring tide. Salinity data for each station and group were fit to three statistical distributions (normal, log-normal, and gamma) using SAS Proc Capability (SAS, Cary, NC). We selected the optimal statistical distribution for each grouping based on lowest χ^2 score. The best-fitting statistical distribution and associated fit parameters (e.g., mean and variance) were used to characterize the salinity regime associated with each station under each discharge and tidal phase.

We modeled five scenarios of upstream shifts in the salinity regime: 1.67, 3.33, 5.00, 6.67, and 8.33 km. The baseline salinity regime for the portion of the estuary where salinity had been empirically measured was modeled and those conditions were progressively shifted upstream in 1.67-km increments (Fig. 4). The choice of 1.67-km increments corresponds with river mile, which is commonly used by local resource managers and others for location and orientation. The furthest downstream location

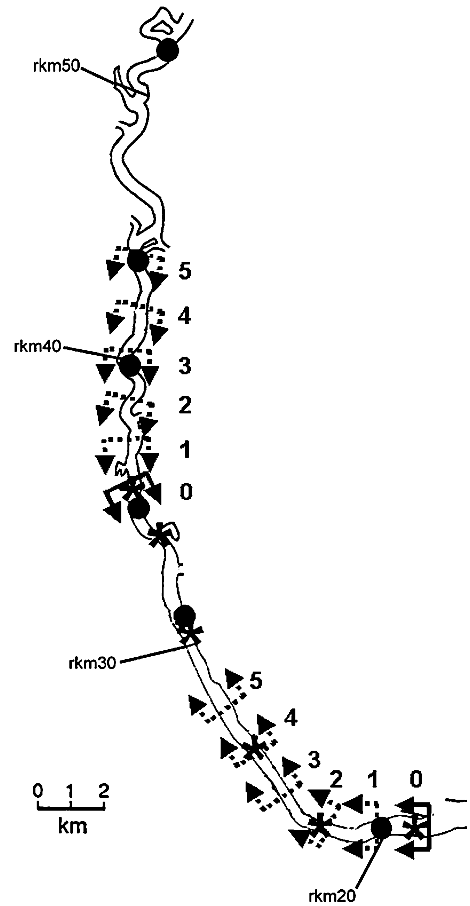

Fig. 4 Map of the Front River portion of the Savannah River estuary with graphic representation of modeled salinity shifts. Baseline salinity conditions specific to discharge and tidal phase were modeled in the area depicted between solid arrow brackets and denoted by "0." Progressive 1.67-km upstream shifts in the modeled salinity distribution are denoted by dashed-arrow brackets and labeled 1 through 5. *Salinity-measurement stations. •Egg-sampling stations

(rkm 18.3) remained at baseline (no change) conditions across all simulations because we could not estimate salinity downstream of that location. Similarly, the location at rkm 20 changed with the initial 1.67-km shift (adopting the baseline conditions of rkm 18.3) and then remained constant for the next four shifts. For the three egg-sampling stations located upstream of the range of the salinity model, baseline salinity conditions were estimated from historic egg-sampling and salinity-monitoring data (Wallin and Van Den Avyle 1995a, Reinert and others 1996, 1998, Will and others 2000, 2001). For modeling purposes, the salinity regime remained at baseline until a projected shift reached the respective station. Therefore, the station at rkm 40 was affected only by shifts ≥5 km (when the baseline conditions of rkm 35, the furthest upstream salinity station, reached rkm 40), and the station at rkm 43.3 was affected only by the 8.33-km shift (when the baseline conditions of rkm 35 reached rkm 43.3). The uppermost station (rkm

Table 3 Model parameters and unconditional probabilities used in model process, observed range during salinity monitoring, and source or rationale of how each state was assigned for root nodes in the BBN used to evaluate harbor-management decisions on early life history survival probability in the Savannah River estuary

Parameter	State	Unconditional probability	Range (observed)	Source or rationale
Tidal phase	Average	0.67	1.89–2.71 m	Based on April tidal phase frequency, 1999 through 2003 (NOAA 2003)
	Neap	0.16	1.58–1.89 m	
	Spring	0.17	2.71–3.32 m	
Discharge	Average	0.91	225–326 m^3/s	Based on mean April river discharge 1999 through 2003 (USGS 2003)
	Low	0.09	171–225 m^3/s	

51.7) was not affected by salinity shifts and remained at baseline conditions under all scenarios.

Objective Value

Our objective value (ELHS) was estimated as

$$ELHS = 100 * \sum_{j=1}^{7} \pi_j \cdot s_{ej} \cdot s_{lj}, \qquad (3)$$

where π_j is the proportion of eggs, s_{ej} is egg hatching success at sample station j, and s_{lj} is larval survival at sample station j.

Model Parameterization

To examine changes in ELHS in response to upstream shifts in salinity, we modeled the relation between components using a Bayesian belief network (BBN; Charniak 1991). BBN model relations among components using probabilistic dependencies. This format allowed us to integrate the model into user-friendly software (in this case, Netica 1.12; Norsys, Vancouver, BC, http://www.norsys.com) that facilitated computation and allowed us to recast the model in a form that was readily accessible to decision makers. This format and software also allows users with limited quantitative skills the ability to directly test model assumptions and evaluate model sensitivity by simply clicking on model components. This format facilitates communication between biologists, decision makers, and the public during evaluations of proposed policy charges (Peterson and Evans 2003). In addition, BBNs can be readily updated and improved as additional data become available (Lee and Rieman 1997, Marcot and others 2001).

We used a two-step process similar to that described by Lee and Rieman (1997) and Peterson and Evans (2003) to parameterize the BBN. During this process, egg and larval distribution and survival were simulated using the stochastic model described previously, and the model output was used to parameterize the probabilistic network. We computed 100,000 simulations for baseline conditions and the five salinity-shift scenarios with six discharge and tidal phase combinations (n = 36 total) using random combinations of model parameters. Egg distribution among stations was randomly assigned assuming a multinomial distribution with probabilities calculated using the randomly selected discharge and Equation 1. Salinity was randomly selected for each station from the scenario-specific distribution, and egg hatching and prolarval survival were estimated using the empirical models (Table 2). Discharge and tidal phase were included as state-specific probabilities based on typical April conditions (Table 3). ELHS then was estimated by way of Equation 3. We then estimated conditional probabilities for each combination of parameters using the frequency distributions. We incorporated the uncertainty associated with model components (e.g., egg distribution, salinity, mortality) by assigning probability distributions for each based on empirical estimates (Table 4) and the outcomes from the 100,000 simulations described previously. After BBN parameterization, we conducted one-way sensitivity analyses (Clemen 1996) to identify which components had the greatest impact on ELHS.

Results and Discussion

Modeled salinity distributions for the estuary varied by location, discharge, and tidal combinations. For example, at station rkm 18.3, a gamma distribution best described spring tides regardless of discharge, and a normal distribution best described the neap tide regardless of discharge. The average discharge/average tide was best described by a normal distribution, whereas the low discharge/average tide was best described by a lognormal distribution. Overall, gamma distributions described the majority of situations (n = 23 of 36), including all but one of the spring tide scenarios (Table 4).

Predicted upstream shifts in salinity had a marked effect on estimated egg-hatching success and prolarval survival, the main components of our ELHS metric. As the salinity shift progressed upriver (by rkm), hatching success and

Table 4 Selected distribution and associated scale and shape[a] parameters for each station, discharge, and tidal phase combination. Salinity data for each station, denoted by rkm, were fit with all three distributions, and the best-fitting model (based on lowest χ^2 score) was selected. Discharge: average = 225 to 326 m^3/s; low = <225 m^3/s

Location (rkm)	Discharge	Tidal phase	Distribution	Scale	Shape
18.3	Average	Average	N	10.8	3.5
		Neap	N	9.8	1.6
		Spring	G	1.4	7.4
	Low	Average	LN	2.5	0.3
		Neap	N	11.8	2.5
		Spring	G	1.0	12.9
23.3	Average	Average	G	0.5	14.4
		Neap	LN	1.9	0.2
		Spring	G	0.7	10.2
	Low	Average	LN	2.0	0.4
		Neap	N	8.8	2.5
		Spring	G	1.2	7.5
26.7	Average	Average	N	5.5	2.4
		Neap	G	0.4	12.0
		Spring	N	4.1	2.2
	Low	Average	LN	1.8	0.5
		Neap	LN	1.8	0.3
		Spring	G	1.2	5.2
30.8	Average	Average	G	1.3	1.9
		Neap	G	1.6	2.1
		Spring	G	1.4	1.5
	Low	Average	G	2.1	1.5
		Neap	N	4.6	2.5
		Spring	G	1.5	2.1
33.3	Average	Average	G	2.4	0.6
		Neap	LN	−1.1	1.5
		Spring	G	1.3	0.7
	Low	Average	G	3.5	0.7
		Neap	G	6.0	0.5
		Spring	G	1.8	0.9
35.8	Average	Average	G	2.9	0.6
		Neap	G	4.1	0.6
		Spring	G	1.7	0.6
35.8	Low	Average	G	3.8	0.5
		Neap	G	5.0	0.6
		Spring	G	2.6	0.7

N = normal; LN = log-normal; G = gamma

[a] Mean and SD for N distributions; scale and shape for LN and G distributions

prolarval survival probabilities both decreased relative to baseline levels (Fig. 5). Overall, we estimate that a 1.67-km shift would result in a 6% decrease in ELHS, whereas shifts of 6.67 km and 8.33 km would result in decreases of 23% and 28%, respectively (Fig. 6). Previously, operation of the tide gate shifted the salinity gradient upstream, on average, 3.8 km in the Front River and 5 km in the Back River (Pearlstine and others 1993). The CPUE of adult fish that were spawned after installation of the tide gate decreased, on average, 30% per year (range 10% to 53%) from 1980 through 1990 until the tide gate was removed and stocking initiated in 1991 (Reinert and others 2005). This suggests that our model may underestimate the effect the salinity gradient changes had on Savannah River striped bass populations, presumably caused by model assumptions. Upstream shifts in salinity may have other effects on early life history survival that the model in its current form does not address. Changes in the location of adequate nursery habitats may further influence survival of eggs and larvae. Quality of nursery habitats also may decrease, decreasing available resources and further reducing survival probability. As an example, salinity changes may impact prey resources, by either shifting their location or reducing biomass, therefore negatively affecting striped bass early life history survival. Therefore, we believe that our estimates of the effects of salinity shifts may be conservative.

However, one mechanism that has been observed in other estuaries (but not fully investigated in the Savannah) is that of a retention component resulting from a salinity gradient or estuarine turbidity maximum (Jassby and others 1995, Secor and Houde 1995, Rulifson and Tull 1999, North and Houde 2001). Such a feature could increase survival by retaining eggs in low-salinity waters and, hypothetically, would move upstream with any concomitant shifts in the salinity regime downstream. In the Savannah system, eggs tended to be captured in roughly the same location (approximately rkm 40) regardless of flow (with the exception of 1998 and exceptionally high flows; see Fig. 3). This might suggest some sort of retention mechanism in that area, but because location of peak egg abundance was largely independent of freshwater flow, the notion of a salt wedge or estuarine turbidity maximum acting as the causative factor in retention cannot sufficiently explain the phenomenon because the location of such a retention feature is tightly coupled to freshwater inflow. Some other mechanism must be operating here, at least in part. Striped bass may shift spawning locations in response to freshwater flow (e.g., Dovel and Edmunds 1971), resulting in eggs winding up in roughly the same location year after year, regardless of flow (in most cases). Striped bass adults are more likely to choose spawning locations based on freshwater flow (something they can sense) compared with salinity conditions at a point further down the estuary (e.g., Ulanowicz and Polger 1980).

As described earlier, an estuarine turbidity maximum is unlikely in the Savannah (or unlikely to be very strong), and effects of such phenomenon can vary greatly between

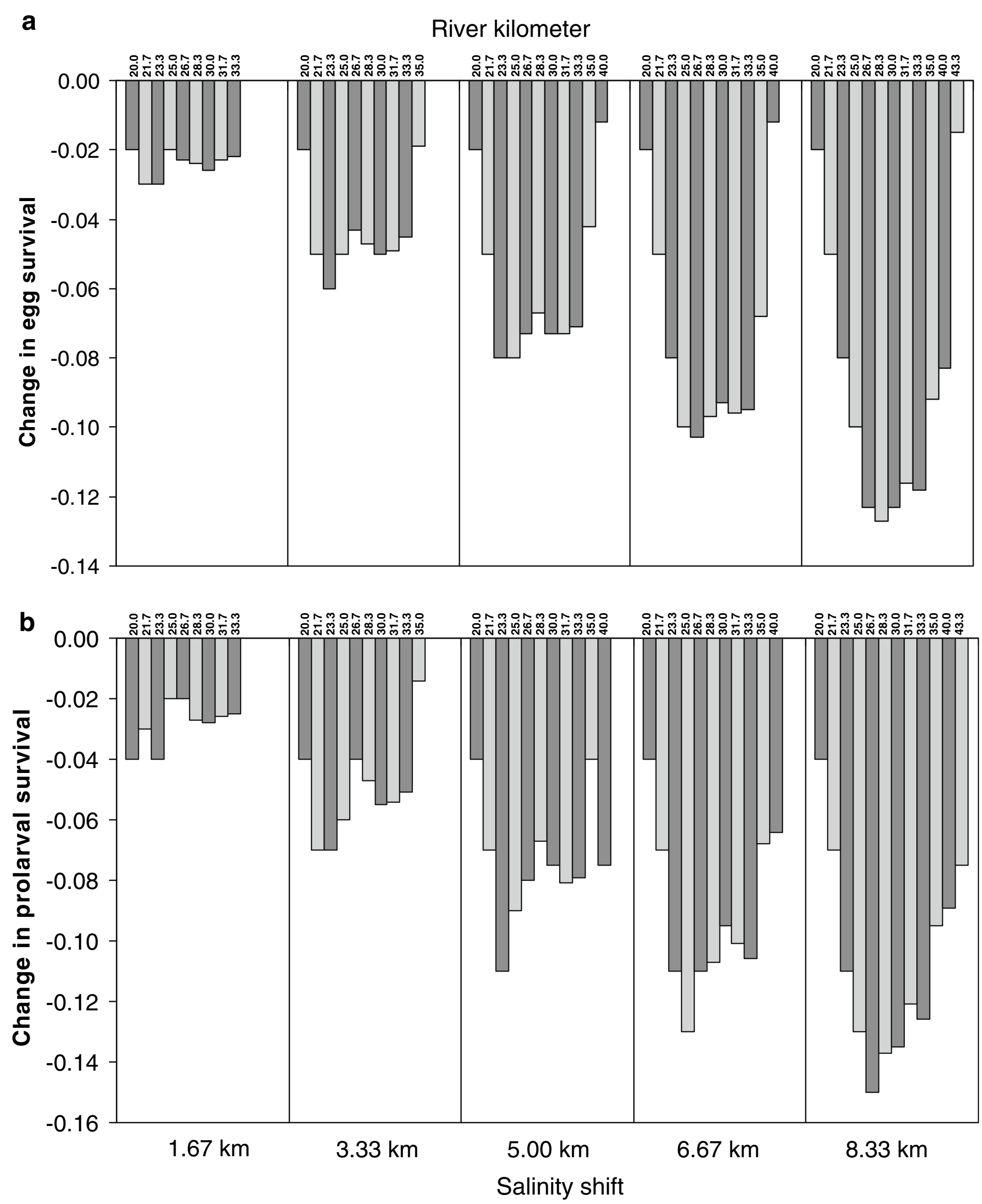

Fig. 5 Changes in predicted striped bass (**A**) egg and (**B**) prolarval survival probabilities for each location modeled in the Savannah River estuary (by rkm). Modeled salinity shifts did not affect survival probabilities at stations rkm 18.3 and rkm 51.7 and are not depicted

estuaries and temporally within an estuary (Sanford and others 2001), making application of results from other systems (e.g., the Chesapeake Bay) to the Savannah inappropriate. In addition, striped bass eggs were captured in areas below the salt front (albeit a small percentage of eggs overall), and transport to areas of high salinity was concluded to be the primary mechanism of the original population decrease (Van Den Avyle and Maynard 1994). A retention mechanism did not appear to be operating at that time, and we cannot presume one to be acting currently without additional observation; therefore we did not account for retention in our model. If further research determines that such a mechanism is in place and a rate of retention can be estimated, the model could be updated to reflect this phenomenon.

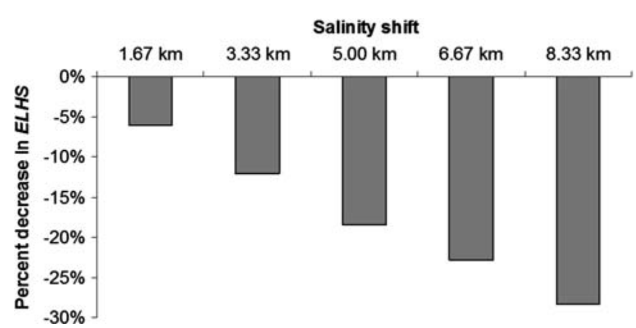

Fig. 6 Estimated relative change in striped bass ELHS for 1.67-km upstream shifts in the prevailing salinity conditions in the Savannah River estuary. Percentage decreases are relative to unchanged salinity

Sensitivity analyses indicated that the egg-distribution component of our model had the greatest influence on

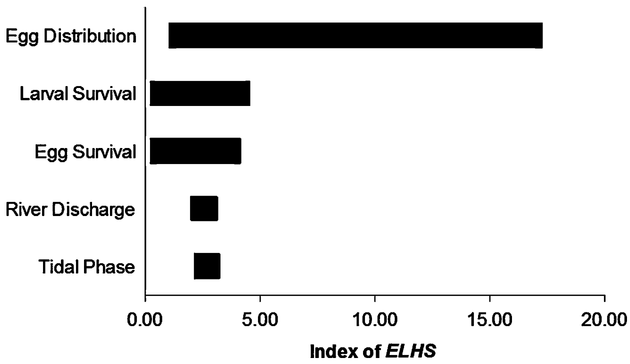

Fig. 7 Tornado diagram for one-way sensitivity analysis with model components listed from greatest (top) to least influential for potential changes in the Savannah River estuary resulting in shifts in prevailing salinity conditions. For each component, bar length represents the extent to which ELHS varies in response to changes in the value of that component, with all other components held at base values

ELHS, whereas river discharge had the least influence (Fig. 7). We estimate that, on average, 74% of eggs are located at the two stations between rkm 40 and 43 of the Front River (see Figs. 1 and 3). Egg survival at these stations is equal and the highest among the stations modeled. However, egg survival during baseline (no change) conditions decreases progressively downstream on average 3%/rkm. Therefore, relatively small changes (or error) in estimated egg distribution produce relatively large changes in ELHS. Much of the error in our egg distribution estimates is caused by the difficulty in sampling striped bass eggs. Striped bass spawn in the Savannah River in brief pulses of short duration. To capture these pulses, daily egg sampling is required. These sampling efforts are labor intensive and not without difficulties. The river is hazardous at night, and the semidiurnal tides create a constantly changing window of sampling opportunity. During the striped bass spawning season, rain storms are common, resulting in difficult sampling conditions and sudden changes in river flow. These difficulties result in extremely low sampling efficiencies (i.e., overall estimated average probability of capturing spawned eggs 0.0007%; see Reinert and others 2004) and therefore high sampling error (Thompson and Seber 1994). Consequently, we suggest that future efforts at model improvement focus on obtaining better estimates of egg distribution.

Perhaps surprisingly, river discharge had little relative influence on ELHS; however, the actual range of flows we included in the model was limited to those flows measured during salinity-sampling efforts. Because we did not want to extrapolate beyond the bounds of the observed data, we limited our model projections to the range of flows during which the salinity measurements were collected (154 to 326 m^3/s) Consequently, we modeled average flows (225 to 326 m^3/s) as occurring with a 91.3% probability. In reality, this range only represents approximately 23% of flows that historically occur in April. Typically, flows are higher than this and may have a stronger effect than predicted here by decreasing salinity and altering egg distribution. However, only very high discharge periods appear to affect the distribution of eggs in the estuary (Fig. 3A). Eggs were generally collected in the same area (typically rkm 35 to 45) during discharges ranging from 171 to 516 m^3/s. Because these areas are immediately upstream of existing shipping and urban centers, they would be particularly vulnerable to upstream shifts in salinity, should such shifts occur after harbor deepening or any other anthropogenic modification of the lower estuary.

Although the salinity conditions that existed in the Back River before tide-gate operation have been mostly restored (Reinert and others 2005), anthropogenic modifications to the harbor (e.g., deepening) or freshwater input could increase salinity intrusion into the Front River and again affect the striped bass population. Based on our estimates, salinity increases in spawning and nursery grounds could result in a perpetual reduction in the number of eggs and larvae available for recruitment. Adult striped bass in the Savannah River estuary produce between 0.4 and 1.0 million eggs/female (Will and others 2002). A 20% reduction in the number of adults potentially could mean a loss of tens or hundreds of millions of eggs. Currently, an adequate population estimate does not exist for Savannah River striped bass; therefore, projections into the future based on known fecundity and predicted early life history survival differences were not possible.

If salinity shifts do occur and cause any level of recruitment failure in the estuarine spawning stock of striped bass, could the population adapt to these altered salinity conditions? As previously discussed, adult striped bass are unlikely to alter spawning locations because of downstream changes to nursery areas if traditional spawning areas remain largely unaffected. Indeed, no such shift was detected during the previous upstream shift in salinity regime and concomitant population decrease. Trace amounts of spawning have been detected in upstream reaches, primarily between rkm 144 and 253, although egg densities were 1 order of magnitude lower than estuarine samples collected at approximately the same time (Paller and others 1986, Van Den Avyle and Maynard 1994). In 1990, additional upstream sampling yielded even lower egg densities (Wallin and Van Den Avyle 1995a). Therefore, there always may have been some upstream spawning of eggs, but the preferred location appears to be the upper estuary. Spawning in these upstream areas was unable to mitigate the precipitous population decrease that occurred in the 1980s because of increased salinity in the estuary. Potential upstream shifts in spawning naturally could occur with time through natural selection (if most estuarine-spawned progeny fail to recruit), and although such shifts were not detected during the previous population decrease and recruitment failure, too little time had passed to detect such life history shifts, which likely would take decades to occur.

Conclusion

Our model provides an example of how biologic and environmental data may be used to evaluate effects of management decisions; however, similar to all models, the structure of our model was limited in scope. We did not consider other environmental factors that may have contributed to or limited egg and larval survival. In this system, such variables as dissolved oxygen and current velocity also are likely to be affected by anthropogenic alterations and may have significant effects on survival of striped bass in early life history stages. The aforementioned phenomenon of egg and larval retention because of salinity or the presence of an estuarine turbidity maximum also could influence survival and the outcome of our modeling efforts. In addition, we have not considered survival of fish in later life stages, such as YOY, that may be important to recruitment. Although striped bass year–class strength in some systems primarily is structured by density-independent mechanisms occurring during fish early life history periods (e.g., Chesapeake Bay: Polgar 1982, Rutherford and Houde 1995, Secor and Houde 1995, North and Houde 2001), density-dependent mechanisms may predominate in other systems (e.g., San Francisco Bay: Kimmerer and others 2000, 2001). Such relations have not been conclusively investigated in the Savannah River estuary.

Currently, little is known about striped bass YOY survival in the Savannah River estuary. Survival studies of stocked individuals in the estuary suggest that survival is higher for larger (150 to 250 mm total length) than for smaller individuals (15 to 90 mm; Wallin and Van Den Avyle 1995b). Recent captures of known wild juvenile striped bass suggest that natural recruitment currently is taking place (Collins and others 2003), but whether there is a survival bottleneck for wild-spawned YOY remains to be investigated. Incorporating additional environmental variables and expanding the ELHS metric to include YOY survival likely would create a more robust model. However, this would require additional data, such as survival of YOY, that currently are not available. Despite this, we believe that we have provided a “first-order” model that incorporates an environmental variable of demonstrated importance (salinity) and life history stages (eggs and early larvae) that have been shown to be crucial to establishment of year–class strength in other systems (Ulanowicz and Polgar 1980, Polgar 1982, North and Houde 2001).

An area of concern for the utility of our model may be that the salinity and egg distribution data sets had poor temporal overlap. We used our own historic egg-sampling data combined with a unique data set of salinity measurements originally obtained for creation and calibration of a complex three-dimensional hydrodynamic model. These salinity data, although taken during summer months, allowed us to create an empirical model relating discharge and tidal amplitude in the estuary to salinity. We have little reservation that the relation would hold true for similar conditions during the striped bass spawning season. In addition, these relations were developed under relatively low flows (compared with average spawning season conditions) and should be considered as such. Recently, Georgia and the southeastern United States suffered a 4-year drought (1997 to 2001) when low water levels were common during the striped bass spawning season. Therefore, our model is effective at evaluating potential impacts of the combined effects of lower discharges (through either drought or increased upstream water demand) and increased salinity (primarily through anthropogenic alterations to channel configuration in the lower estuary).

Coastal Georgia and Savannah in particular are burgeoning areas of population and economic growth. A growing population and economic sector will place higher demands on area resources, particularly water resources. The states of South Carolina and Georgia have capped groundwater withdrawals from the underlying Floridian aquifer, and future water needs in the Savannah area must be met by increasing surface-water withdrawals from the Savannah River (LeRoy Crosby, United States Army Corps of Engineers, personal communication, June 2000). In addition, economic growth may increase demands for a deeper harbor. Future harbor modifications may once again increase saltwater intrusion into the estuary.

Decision makers are increasingly relying on tools that can address the concerns of multiple-user groups and that can integrate research and management goals across disciplines. The most useful decision-making tools should be explicit and transparent so that assumptions about how the system works and the nature of the relation among components then can be examined and quantitatively tested. In addition, useful decision tools should be user friendly so managers and decision makers are comfortable with their use. In this case, the use of a BBN allowed us to develop an explicit predictive model that incorporated uncertainty and natural variability in a user-friendly format that is readily accessible to managers and decision makers. In addition, models such as the one developed here can incorporate new information to reduce uncertainty and improve decision making in an adaptive context (Williams and others 2002). Therefore, we believe that explicit, quantitative decision models are necessary for developing effective and efficient conservation and restoration strategies for estuarine-dependent species and encourage natural resource managers and decision makers to incorporate them into future efforts evaluating potential impacts of anthropogenic modifications to the environment.

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