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Author: Robinson, Kelly F.

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ARTICLE

Maximizing Age-0 Spot Export from a South Carolina Estuary: An Evaluation of Coastal Impoundment Management Alternatives via Structured Decision Making

Kelly F. Robinson[1]
Georgia Cooperative Fish and Wildlife Research Unit,
D. B. Warnell School of Forestry and Natural Resources, University of Georgia, 180 East Green Street,
Athens, Georgia 30602, USA

Cecil A. Jennings*
U.S. Geological Survey, Georgia Cooperative Fish and Wildlife Research Unit,
D. B. Warnell School of Forestry and Natural Resources, University of Georgia, 180 East Green Street,
Athens, Georgia 30602, USA

Abstract

Estuaries are among the most productive of all ecosystems and provide critical nursery habitat for many young-of-the-year (age-0) marine fish. Along the South Carolina coast, former rice field impoundments in some estuarine areas are now managed to provide habitat for waterfowl. Marine fish that enter these structures during water level manipulation become trapped and suffer high mortality rates. Because these fish cannot emigrate back to coastal waters to complete their life cycles, these impoundments appear to act as sinks for marine-transient species. Our goal was to identify which of a set of management options would maximize export of age-0 spot *Leiostomus xanthurus* from the Combahee River, South Carolina, to the coastal population. We used a structured decision-making approach to evaluate four decision alternatives: to maintain status quo, to close all impoundments while age-0 spot are most abundant in the river, to change the water level manipulation strategy to improve fish passage from impoundments, or to breach all impoundments. We also wanted to evaluate how impoundments and natural mortality influence the export of age-0 spot. The optimal management decision was to change the water level manipulation strategy to increase fish passage from the impoundments. Spot export was most sensitive to juvenile settlement in the estuary and natural mortality. The results of this model can be used adaptively for impoundment management along the Combahee River and can be modified for other estuarine areas or other fish species.

Estuaries are among the most productive ecosystems on the planet and provide critical nursery habitat for larval and juvenile marine fish (Mitsch and Gosselink 2000). The young of many recreationally and commercially important marine fish species enter estuaries throughout the year to take advantage of abundant food resources and for protection from predators (Weinstein 1979; Haedrich 1983; Boesch and Turner 1984). The importance of marsh habitat to coastal fish populations is evident through the observed positive relationship between the ratio of marsh area to open water and commercial landings of

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*Corresponding author: jennings@uga.edu
[1]Present address: New York Cooperative Fish and Wildlife Research Unit, Department of Natural Resources, Cornell University, B02 Bruckner Hall, Ithaca, New York 14853, USA.
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estuarine-dependent species in coastal waters of the western North Atlantic (Nixon 1980). Although this relationship does not predict how removal of marsh habitat (e.g., through the impoundment of large tracts of coastal marsh) in a single system will affect overall marine-transient population dynamics, it does indicate that habitat removal could be detrimental to estuarine-dependent fish populations.

In South Carolina, about 28,000 ha of coastal marsh (approximately 14% of total marsh area) are currently impounded, with an additional 30,000 ha of abandoned impoundments now subject to tidal inundation (Tiner 1977; DeVoe et al. 1987; Kelley 1999). Most of these impoundments are managed to provide food and habitat for migratory waterfowl (DeVoe et al. 1987; McGovern and Wenner 1990). Impoundment water levels are manipulated through wooden frames (known as rice field trunks) in the dikes. Flap gates and flashboard risers on these trunks regulate water levels to stimulate the growth of plants that are eaten by migratory waterfowl (McGovern and Wenner 1990). Management decisions for individual impoundments, including flooding and draining, are made according to the needs of the individual impoundment as deemed necessary by impoundment managers. These management decisions are largely designed to benefit waterfowl, and estuarine fish communities typically are not considered.

Numerous studies conducted along U.S. coastlines have indicated that fish and invertebrate communities are adversely affected by estuarine impoundments (McGovern and Wenner 1990; Rey et al. 1990; Rozas and Minello 1999; Swamy et al. 2002). For most of the year, impounded wetlands in South Carolina occupy habitat that age-0 fish would otherwise use for feeding and refuge from predators (Wenner et al. 1986; Rozas and Minello 1999). Additionally, marine-transient species enter impoundments during water level manipulation (Wenner et al. 1986; McGovern and Wenner 1990; Rozas and Minello 1999) and when water tops the dikes during extreme high tides (E. Mills, Nemours Wildlife Foundation, personal communication). Because very few fish leave the impoundments when the water level is drawn down, the marine transients that enter these structures are effectively trapped and unable to complete their life cycles (Wenner et al. 1986; McGovern and Wenner 1990; our unpublished data). Many transient species, including the spot *Leiostomus xanthurus*, Atlantic croaker *Micropogonias undulatus*, southern flounder *Paralichthys lethostigma*, tarpon *Megalops atlanticus*, and ladyfish *Elops saurus*, have been observed in South Carolina impoundments (Wenner et al. 1986; Robinson 2011).

Once fish enter impoundments, there are some detriments to survival. Dissolved oxygen (DO) levels are often very low during the early hours of summer mornings, which subsequently may kill transient species that are not adapted to surface breathing (Portnoy 1991) and may reduce the total number of transients that can emigrate successfully from these structures. If hypoxic stress causes individuals to move into the more oxygenated surface water, they also may experience higher predation rates by water birds (Wenner et al. 1986). If transients are unable to escape an impoundment because of physical entrapment or because of mortality (e.g., physiological stress or predation), then the impoundment is acting as a sink for these taxa. Sinks are defined as areas where immigration exceeds emigration and mortality rates exceed birth rates, such that the population within is sustained only through continued influx from a source population (Pulliam 1988).

In addition to impounded wetlands, other stressors may influence the dynamics of marine-transient fish in estuaries. Many factors that affect the size of coastal transient populations are unknown, and scientific investigations on the magnitudes of the influences of known factors are either incomplete or nonexistent. Those studies that have investigated factors contributing to mortality of age-0 transients in estuarine nurseries rarely have explored the interaction of factors. Additionally, uncertainty in adult population sizes, juvenile densities, and how these two affect each other further complicates our ability to fully understand coastal transient population dynamics. Because of these uncertainties, we used an approach that allows for the incorporation of various sources of uncertainty to model marine-transient population dynamics in a South Carolina estuary with impounded wetlands. These sources include structural uncertainty about how the system works, uncertainty about the probabilities of particular outcomes, and stochasticity in the environment (terminology follows Williams et al. 2002). Accordingly, we used a Bayesian belief network (BBN) to model marine-transient population dynamics. Bayesian belief networks are useful in ecological analyses because they graphically depict the influences of factors on the parameter of interest in a clear fashion, allow for the use of both categorical and continuous data, use empirical data and expert opinions, and express the outcome as likelihoods that are easy to use in risk management (Marcot et al. 2001).

We developed two primary goals for our study. Our first goal was to determine the optimal management strategy to maximize export of spot, a model transient species, from the Combahee River, South Carolina. We used a decision-theoretic approach—structured decision making (SDM)—to determine the optimal strategy. This method allowed us to decouple scientific issues from stakeholder objectives and account for uncertainty in decision outcomes (Conroy et al. 2008). Unlike the current method of decision making for impounded wetlands, SDM provides a quantitative model, a BBN, which combines preferences and uncertainty to organize a decision problem and possible alternatives. Through SDM, these preferences and uncertainty, as well as decision–outcome combinations, can be quantified to provide an objective optimal decision (Peterson and Evans 2003). This same framework was used to attain our second goal: to estimate how sink habitat and other anthropogenic and natural stressors affect the export of age-0 spot. The coastal spot population may be adversely affected by impoundments because they remove nursery habitat. We hypothesized that factors such as marsh impoundment would greatly decrease export of age-0 marine transients from the

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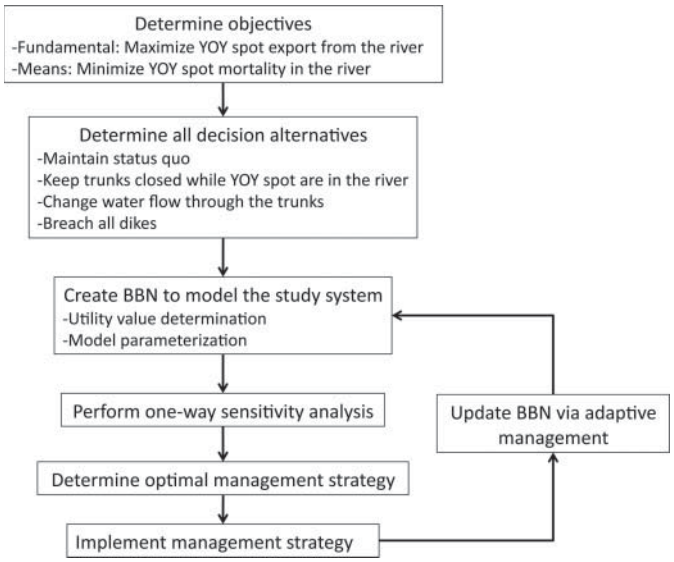


FIGURE 1. Flowchart showing the steps of the structured decision-making process, including the use of a Bayesian belief network (BBN), for young-of-the-year (YOY; i.e., age-0) spot in the Combahee River.

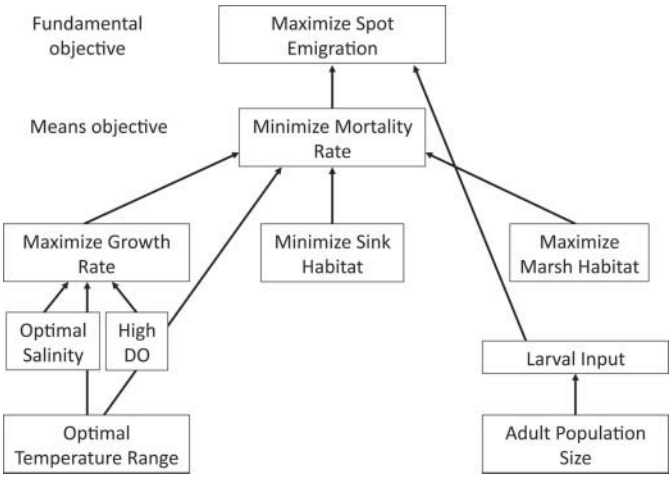


FIGURE 2. Objective network depicting the fundamental and means objectives for age-0 spot in the Combahee River (DO = dissolved oxygen concentration). Arrows connect the means objective (middle level) and methods (bottom level) to the fundamental objective (top level).

Combahee River. Because impoundments are not just eliminating suitable habitat but also are acting as sinks by facilitating the direct removal of individuals from the population, we hypothesized that impounded marsh in a wetland complex would have a greater negative influence on export levels than other stressors in the system (e.g., drought or extreme temperatures).

METHODS

Our methodological steps (Figure 1) began with the determination of fundamental and means objectives for the decision analysis. Fundamental objectives are the main objectives of the decision makers (i.e., those things that the decision makers value most), whereas means objectives are met to achieve the fundamental objective (Peterson and Evans 2003; Figure 2). The fundamental objective in our SDM framework was also the first goal of our study: to maximize age-0 spot export from the Combahee River. We determined four management alternatives that would achieve the fundamental objective and assigned utility values to each combination of decision alternative and outcome. We then created a BBN to model the study system and populated its components with data from previously published research, expert opinion, and data from simulations. This framework was input into Netica software (Norsys Software, Vancouver, British Columbia), which was used to determine the optimal strategy for impoundment management and to conduct a one-way sensitivity analysis. The one-way sensitivity analysis allowed us to meet our second goal: to determine the relative influences of multiple environmental and anthropogenic factors on spot export.

Study site and focal species.—This study was part of a larger investigation to evaluate the ecological value of waterfowl impoundments for fish inhabiting the Combahee River region in Beaufort County, South Carolina. The Combahee River is part of the Ashepoo–Combahee–Edisto River (ACE) basin watershed, so named because it includes the coastal areas of those rivers. Much of the ACE basin is protected through private and public land stewardships; as such, this study system has fewer anthropogenic influences than other estuarine areas in coastal South Carolina.

Our analysis of age-0 fish export from nurseries focused on spot, a marine migrant that commonly shows initial recruitment in the lower-salinity stretches of the Combahee River. This species is one of the better-studied members of the estuarine community, is widespread in its distribution, and is a dominant member of the marine-transient guild in South Carolina (Weinstein and Walters 1981; Weinstein 1983; Beckman and Dean 1984; Currin et al. 1984; Rogers et al. 1984; Flores-Coto and Warlen 1993; Ross 2003; McNatt and Rice 2004; Peterson et al. 2004). The wealth of data on mortality and growth rates in nurseries throughout the southeastern coast of the United States, as well as factors that influence these rates, make spot a particularly suitable species for this analysis. For example, spot reside in the upper and middle reaches of an estuary for an average of about 90 d (Weinstein 1983). This information was incorporated into our model to more accurately describe spot mortality throughout their residence in the estuary. Additionally, spot have a maximum life span of 4 years (Piner and Jones 2004), which allows for a simpler model than would be possible for a longer-lived species. However, the spot is a relatively hardy species (Hales and Van Den Avyle 1989) and may be less responsive to some factors than other marine-transient species.

Management objectives and decision alternatives.—In the SDM process, fundamental and means objectives must be identified. We chose a fundamental objective of maximizing export of age-0 spot, a model marine-transient species, from the Combahee River. The fundamental objective of maximizing

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spot export could not be quantified a priori (Peterson and Evans 2003) because researchers have not focused on quantifying the densities of age-0 spot leaving the estuary. We assumed that higher age-0 spot survival in the estuary would translate to higher densities of age-0 spot upon export from the Combahee River. Based on this assumption, our means objective was to minimize age-0 spot mortality in the Combahee River (Figure 2). Within our objective network, we assumed that larval input would have a direct effect on the fundamental objective of maximizing spot export (Figure 2).

Four impoundment management alternatives were identified that would meet our goal of maximizing age-0 spot export from the Combahee River. The first alternative was to maintain status quo, allowing impoundment managers to manage as they see fit, typically without regard to the estuarine fish community. Two of the alternatives were hypothesized to minimize the influence of impoundments as sink habitats. These decision alternatives were to either (1) keep impoundment trunks closed when age-0 spot are most abundant in the river or (2) manipulate water levels to minimize the number of fish that enter the impoundments and maximize the number of fish exiting the impoundments. This second strategy would involve drawing river water in from the top of the water column (minimizing impoundment immigration) and releasing water from the bottom of the water column (maximizing emigration from impoundments; DeVoe et al. 1986; McGovern and Wenner 1990). The last alternative was to breach all impoundment dikes along the river to maximize the amount of marsh habitat available to age-0 spot.

Assignment of utility values.—Structured decision making requires quantification of the outcomes of each decision alternative, termed utilities (Conroy et al. 2008). These utilities represent the value placed on each combination of a decision and an outcome and were calculated as functions of decision outcomes (e.g., number of age-0 spot surviving; Conroy et al. 2008). Stakeholder meetings were held to determine the best decisions for the management of a system of breached and impounded wetlands along the Cooper River, South Carolina (Consensus Solutions 2004), which is similar to the Combahee River system. This group included developers, land and timber managers, representatives of industry and the federal government, landowners, environmental advocates, community leaders, local government officials, and state agency staff. These stakeholders decided that impoundments were important in the estuarine landscape but that these structures must allow for animals to move freely between impounded and natural marsh. They suggested replacing flap gates and flashboard risers with structures that allowed for more water movement and subsequently more animal movement between impounded and unimpounded areas of the marsh (Consensus Solutions 2004). The results of these stakeholder meetings, specifically the value that these stakeholders put on impounded wetlands and fish migration, were used to parameterize our model.

Given the stakeholders' interests in the Cooper River (Consensus Solutions 2004), we assigned decision costs of 0.00, 0.00, 0.25, and 0.75 to our four decision alternatives of maintaining status quo, changing water manipulation practices, closing the impoundments during high age-0 river density months, and breaching impoundments, respectively. The outcomes were given values of 1.00 (high spot export), 0.75 (medium spot export), and 0.50 (low spot export). The decision costs were subtracted from the value of the outcome to provide the utility values. Additionally, when the outcomes were less than optimal (high density upon export), 0.25 was subtracted from the utility value for maintaining status quo because we assumed that stakeholders value a decrease in spot export with no action lower than the same decrease in export coupled with management actions (Table 1).

TABLE 1. Utility values assigned to each combination of decision utility and outcome of the three ranges of age-0 spot density (fish/m^2) upon export from the Combahee River. The impoundment management strategies were to maintain status quo in the system (None), to breach all impoundment dikes within the Combahee River (Breach), to close all impoundment trunks while spot are in the estuary (Closed), or to change the way that impoundment water levels are manipulated (Top in, bottom out). Highest and lowest utility values are in bold italics.

	Age-0 spot density upon export		
Impoundment management	<0.302 fish/m^2	0.302–0.563 fish/m^2	>0.563 fish/m^2
None	0.25	0.50	***1.00***
Breach	***0.00***	***0.00***	0.25
Closed	0.25	0.50	0.75
Top in, bottom out	0.50	0.75	***1.00***

The ideal outcomes for this model, based on the utility values, were to achieve the highest level of age-0 spot export from the Combahee River while maintaining status quo or changing the water manipulation strategy (Table 1). The outcome that was considered the least desirable involved achieving either medium or low spot export while breaching the dikes. All other decision–outcome combinations fell in between these extremes. The sensitivity of the optimal strategy to this scheme was evaluated by decreasing the change from high to medium export and from medium to low export to 0.15 (0.30 for a change from high to medium export under the strategy of maintaining status quo). Likewise, the change from high to medium export and from medium to low export was also increased to 0.50 (1.00 for maintaining status quo with a change from high to medium export). The optimal strategy was determined under each scheme. These utility values populated the utility component of the decision BBN, where they were used to calculate the expected utility value of each decision alternative (Figure 3).

Bayesian belief network parameterization and sensitivity analysis.—The factors that we believed were most likely to influence age-0 spot export, through the means objective, were used to populate the components of the decision BBN that was constructed and modeled with Netica software (Figure 3). Netica analyzes BBNs via a user-friendly graphical interface. Our decision BBN followed 4 years of spot population dynamics,

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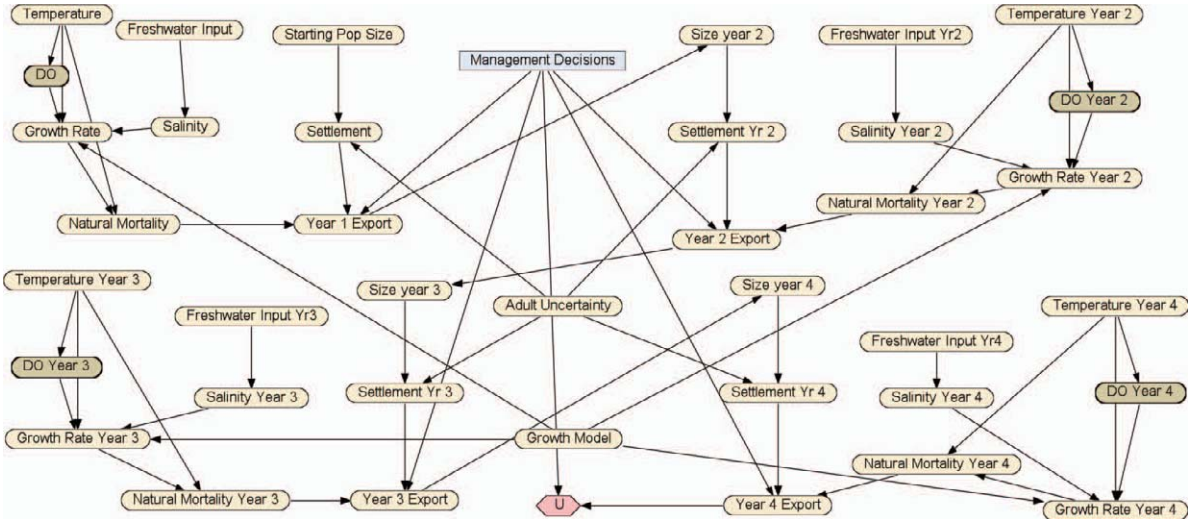


FIGURE 3. Decision Bayesian belief network used to predict the optimal impoundment management decision for maximizing age-0 spot export from the Combahee River (DO = dissolved oxygen concentration; Yr = year; Pop = population; U = utility).

with the export of age-0 spot from each year influencing the adult population size in the following year. The factors in the decision model included those deemed to be sources of environmental uncertainty in the system; these included the possibility of drought conditions, water temperature fluctuations, and natural mortality levels, as well as factors that are influenced by impoundment management strategies. The data to parameterize our components were obtained from previous studies on spot populations (see Table 2 for component descriptions). Two groups of alternative models also were considered to account for structural uncertainty in the decision model. The first group of two alternative models dealt with uncertainty as to the extent of the influence of adult population size on age-0 settlement in the estuary (Myers and Barrowman 1996; Houde 2008). One model allowed for complete dependence of the magnitude of juvenile settlement on the size of the coastal adult population (density dependent), and the other assumed that adult population size did not influence settlement (density independent). The second group of two alternative models addressed our uncertainty of how multiple factors that depress growth rate in age-0 spot interact to affect overall growth. The first model assumed that each addition of a growth-rate-reducing factor would result in a linear increase in the probability of low age-0 spot growth. The second model assumed that the addition of more detrimental factors would increase the probability of low growth in an exponential fashion. We used the monomolecular growth function (Figure 4; France and Thornley 1984; López et al. 2000) to describe this increase in the probability of low growth. For both sets of models, the optimal management decision was determined under three scenarios: equal belief in both and 100% belief in each of the two competing models in each set; this approach yielded a total of nine different model combinations.

The conditional probability tables (CPTs) in the decision model are a representation of our understanding of the probability of a given component being in a particular state based on the information from the influencing components (Peterson et al. 2008). The CPTs associated with each of the components of the network were estimated based on previous studies of spot, unpublished data, output from simulation models, personal experience, and expert judgment (CPTs are provided in Appendix Tables A.1–A.7).

Previous studies have not described total densities of spot upon export from estuarine habitat. To populate the age-0 export CPT for each year of the model, we simulated the density of

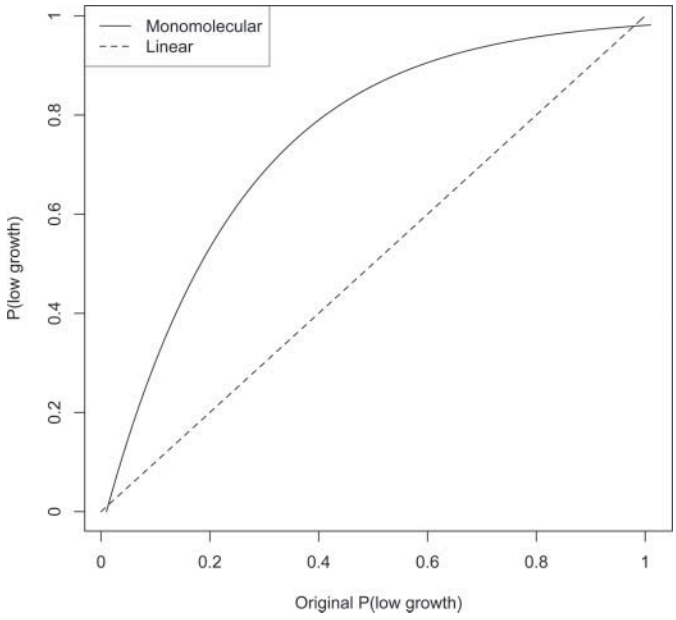


FIGURE 4. Linear and monomolecular growth curves used to determine how the probability (P) of low growth would increase with the addition of variables that reduce the growth rate of spot in the Combahee River.

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age-0 spot after 90 d in the estuary for each combination of the two natural mortality states, four impoundment management strategies, and three juvenile settlement density states, for a total of 24 simulated scenarios. We used 1,000 simulations of each combination of the above components. The model operated on a 1-d time step, encompassing a total of 90 d, and began with the density of age-0 spot upon settlement in the river. The density of fish was converted to the abundance of fish based on the amount of available marsh habitat (26,461 ha). The amount of available habitat was calculated as the amount of marshland available to age-0 spot within a 5-km buffer of the tidally influenced portion of the Combahee River (Geographical Information Systems Data Clearinghouse, South Carolina Department of Natural Resources, personal communication; ArcGIS, Environmental Systems Research Institute, Redlands, California). Upon immigration into the estuary, spot either settled in the river marsh or settled in impoundments based on the probabilities of impoundment ingress from our research and previous studies (Table 3). Spot in natural marsh habitat were subjected to natural mortality, with the daily mortality rate randomly drawn each day for 90 d from a uniform distribution based on the state of the component (Table 3). The bounds of these uniform distributions were chosen using previously estimated rates of natural mortality for age-0 spot in the southeastern United States. Our observations of spot within two study impoundments along the Combahee River indicated that approximately 80–100% of the age-0 spot that immigrate into these structures die over the course of a year (our unpublished data). Therefore, in our model, spot that entered the impoundments were subjected to a one-time mortality event resulting in the death of 80–100% of those impounded fish because daily mortality rates for impounded spot have not been estimated. Upon completion of the 90-d residence time, remaining spot within the impoundments exited the structures based on a predefined impoundment emigration rate (Table 3), and the density of all surviving fish within the river was calculated and assumed to be the density upon export. The predefined ranges of all parameter values are based on previous studies of age-0 spot, our observations within impounded wetlands, and our expert opinion. The parameter values were randomly selected from a uniform distribution for each simulation and the simulations were performed in R software (R Development Core Team 2010).

The final densities simulated in our study (0.042–0.843 spot/m^2) were separated into three intervals of density upon export with equal ranges (similar to Peterson and Evans 2003): densities less than 0.302 spot/m^2, between 0.302 and 0.563 spot/m^2, and greater than 0.563 spot/m^2. The proportions of the 1,000 replicate simulations that resulted in final densities in each of these ranges were used to populate the CPTs for the 4 years of age-0 spot export (Table A.7).

Before including the decision and utility components of the BBN, a one-way sensitivity analysis was performed to identify the factors that had the greatest influence on juvenile export (Clemen 1996). A one-way sensitivity analysis systematically varies the values of each component to determine how it affects the component of interest. The results were restricted to the influence of the components on obtaining high age-0 spot export in year 4. Based on this sensitivity analysis, we determined which variable or set of variables contributed most to observing export densities greater than 0.563 spot/m^2.

The decision and utility components then were added to the network such that the four decision alternatives replaced the impoundment component and influenced age-0 spot export in each of the 4 years of the model (Figure 3). The expected utility values for each decision alternative were calculated as the weighted average (using the probabilities of each outcome as the weights) of the utilities over the possible outcomes from a decision. The decision with the highest expected utility value was determined to be the optimal decision (Peterson and Evans 2003). We then evaluated the sensitivity of the optimal decision to the variables in the model. We chose the two variables to which age-0 export was most sensitive based on the results of the one-way sensitivity analysis, and we determined the optimal decision for each state of those two components. This method allowed us to determine how sensitive our optimal decision was to uncertainty in the most influential components of the model. All calculations were performed with Netica software.

In addition to the above calculations, we evaluated our decision BBN with greater proportions of age-0 spot entering impoundments. In our simulations, we assumed that 0.3–3.4% of spot that enter the Combahee River estuary immigrate into impoundments (Wenner et al. 1986). We determined the optimal management strategy and performed a sensitivity analysis under two other scenarios: (1) an order-of-magnitude greater percentage of spot entering the impoundments (3–34% of total age-0 spot) and (2) 50% of total age-0 spot entering the impoundments.

RESULTS

The optimal management strategy for maximizing age-0 spot export from the Combahee River was to change the water manipulation strategy so water is pulled into the impoundments from the top of the water column and drawn out from the bottom of the water column. The second most optimal strategy was to maintain status quo. The optimal management strategy was not affected by structural uncertainty in the effect of adult population size on juvenile settlement and the growth model chosen. Additionally, the optimal strategy was not sensitive to changes in settlement and natural mortality in year 4, the two components that most influenced spot export (Figure 5). Under each state of settlement and natural mortality, the ranks of the expected values of the decision alternatives remained constant with one exception. Under low larval settlement, the second most optimal strategy was impoundment closure (Figure 5). Likewise, the optimal management strategy was not sensitive to changes in the weighting scheme for the utility values. Regardless of how the

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TABLE 2. Component definitions and states for the decision Bayesian belief network (BBN) created to determine the optimal management strategy for maximizing the export of age-0 spot from the Combahee River estuary.

Component	Definition	States
Impoundment management	The four alternative impoundment management decisions (Table 1). This component was used only for the sensitivity analysis and was replaced by the decision component in the decision BBN.	None Breached Closed Top in, bottom out
Freshwater input (years 1–4)	Annual discharge (cm^3/s) in a given year, estimated from U.S. Geological Survey discharge data from the Salkahatchie River flow gauge (1952–2008)[a].	State: probability Drought (<300 cm^3/s): 0.29 Normal (300–450 cm^3/s): 0.53 Wet (>450 cm^3/s): 0.18
Salinity (years 1–4)	Predicted salinity distribution in the Combahee River as influenced by freshwater input. Probability based on expert opinion and salinity data (practical salinity units [psu])[b]. See Table A.1 (in Appendix) for the conditional probability table (CPT).	0.0–18.0 psu 18.1–25.0 psu
Adult population (years 1–4)	Density (fish/ha) of spot collected in South Carolina waters from fishery-independent trawl surveys (1999–2009)[c]. States and year-1 probabilities were determined using 25% and 75% quartiles. Years 2–4 influenced by the previous year's age-0 export as determined by expert opinion. See Table A.2 for the CPT.	Low: <20.6 fish/ha Medium: 20.6–52.9 fish/ha High: 52.9–143.0 fish/ha
Temperature (years 1–4)	Percentage of time that the river water was measured in each temperature increment (February–July 2002–2009)[d]. See Table A.3 for the CPT.	10–29°C in 1°C increments
Dissolved oxygen (years 1–4)	Dissolved oxygen (DO) levels experienced by spot in the Combahee River each year based on linear regression (DO = [–0.2465 × overall temperature] + 10.933) as determined from temperature and DO data collected in the Combahee River (2002–2009)[d]. States were based on "growth-protective" and "survival-protective" cut-offs[e]. The DO in a given year was influenced by that year's temperature component.	0.0–2.3 mg/L 2.3–4.8 mg/L 4.8–10.0 mg/L
Growth rate (years 1–4)	Relative growth rate in terms of weight for age-0 spot while residing in the Combahee River each year[f], as influenced by DO[g], salinity[f], temperature[h], and the growth model. Probabilities were estimated via expert opinion based on growth rates determined from individual factors in previous studies. See Table A.4 for the CPT.	Low: 3.76% per day High: 4.44% per day
Adult model	Effect of the current year's spawning population size on age-0 settlement in the Combahee River. This component addresses structural uncertainty in this relationship[ij], and probabilities were estimated by expert opinion.	Density dependent Density independent
Growth model	This component addresses the structural uncertainty of how multiple factors affect the overall probability of high or low growth of age-0 spot in the Combahee River. The linear model assumes a linear increase in the probability of low growth with each addition of a growth-rate-reducing factor. The monomolecular function $W = W_f - (W_f - W_o)e^{-kt}$ was used to convert the probability of low growth under the linear model to the probability of low growth under the monomolecular model (W = new probability of low growth, $W_f = 100$, $W_o = 0$, t = probability of low growth under the linear model, and $k = 0.04$).	Linear model Monomolecular model

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TABLE 2. Continued.

Component	Definition	States
Settlement (years 1–4)	Density of early juvenile spot settling in the Combahee River as influenced by spawning population size and the adult effect model. Densities were determined from the range of densities reported in previous studies[k–r], and probabilities were estimated via expert opinion. See Table A.5 for the CPT.	Low: 2.0–11.0 fish/m^2 Medium: 11.1–20.0 fish/m^2 High: 20.1–29.0 fish/m^2
Natural mortality	The daily natural mortality rate experienced by age-0 spot in the estuary, as influenced by temperature[h] and growth rate[f]; estimated via expert opinion. See Table A.6 for the CPT.	Low: 3.0–4.4% per day High: 4.4–6.4% per day
Age-0 export (years 1–4)	Total density of age-0 spot upon export from the Combahee River (calculated as if all fish were exported at the same time) as influenced by settlement, natural mortality, and impoundment management. States were the lower, middle, and upper thirds of the total range of densities obtained through simulation; probabilities were the proportion of the 1,000 simulations falling within each of the three states. See Table A.7 for the CPT.	<0.302 fish/m^2 0.302–0.563 fish/m^2 >0.563 fish/m^2

[a] USGS 2009.
[b] Upchurch and Wenner 2008.
[c] SEAMAP-SA 1999–2009.
[d] B. Roumillat, South Carolina Department of Natural Resources, Inshore Fisheries Unit, unpublished data.
[e] USEPA 2000.
[f] Ross 2003.
[g] Stierhoff et al. 2009.
[h] Peterson et al. 2004.
[i] Myers and Barrowman 1996.
[j] Houde 2008.
[k] Turner and Johnson 1974.
[l] Weinstein 1979.
[m] Rogers et al. 1984.
[n] Rozas and Hackney 1984.
[o] Allen and Barker 1990.
[p] Warlen and Burke 1990.
[q] Flores-Coto and Warlen 1993.
[r] Stokesbury and Ross 1997.

utility values were weighted (amount of change between high, medium, and low export of age-0 spot for each decision alternative), the rank of the expected utility values remained constant. Finally, changing the water level manipulation strategy was the optimal management strategy for all three levels of spot immigration into the impoundments (0.3–3.4, 3–34, and 50%).

Under the optimal strategy, the probability of low age-0 spot export (<0.302 spot/m^2) was 0.576–0.644, the probability of

TABLE 3. Estimates of parameters used in the simulation of spot density upon export from the Combahee River for each combination of states representing the three components that influence spot export (i.e., natural mortality, age-0 settlement, and impoundment management strategy); references for parameter values are shown. Impoundment management strategies (none; seasonal closure; and top in, bottom out) are defined in Table 1.

Parameter	Estimate	References
Age-0 settlement density	Low: 2.0–11.0 fish/m^2 Medium: 11.1–20.0 fish/m^2 High: 20.1–29.0 fish/m^2	Turner and Johnson 1974; Weinstein 1979; Rogers et al. 1984; Rozas and Hackney 1984; Allen and Barker 1990; Warlen and Burke 1990; Flores-Coto and Warlen 1993; Stokesbury and Ross 1997
Impoundment immigration rate (one-time event)	None: 0.30–3.40% Seasonal closure: 0.00–0.10% Top in, bottom out: 0.15–1.70%	Wenner et al. 1986; expert opinion
Impoundment emigration rate (one-time event)	None or seasonal closure: 2.50–7.50% Top in, bottom out: 12.50–17.50%	Wenner et al. 1986; expert opinion
Natural mortality rate	Low: 3.0–4.4% per day High: 4.5–6.4% per day	Weinstein and Walters 1981; Ross 2003

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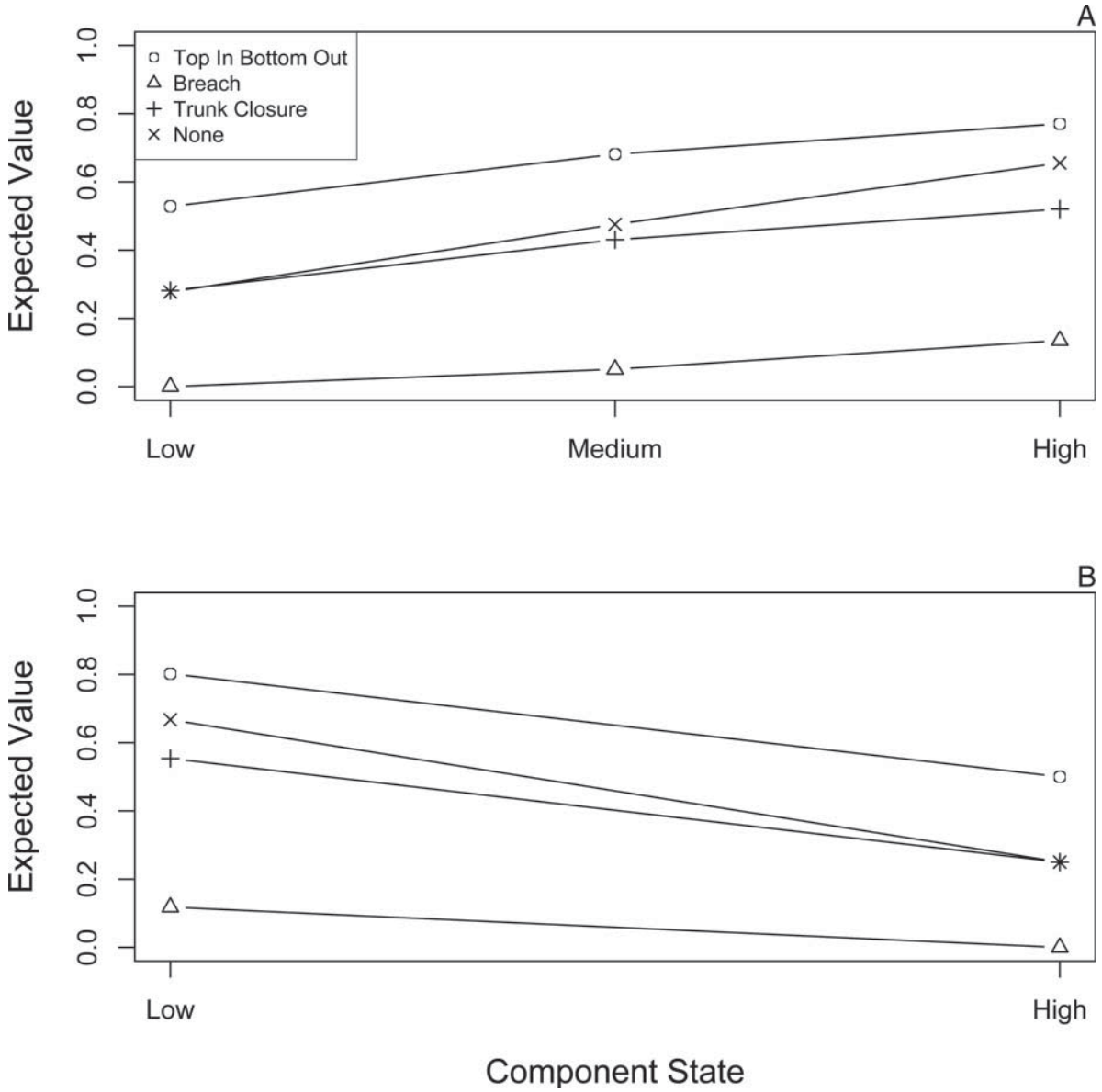


FIGURE 5. Expected utility values of the four decision alternatives for each state of **(A)** larval spot settlement in year 4 and **(B)** spot natural mortality in year 4 for the decision Bayesian belief network for age-0 spot export from the Combahee River. The four impoundment management strategies (represented by symbols) are defined in Table 1; component states are defined in Table 2.

medium export (0.302–0.563 spot/m^2) was 0.133–0.168, and the probability of high export (>0.563 spot/m^2) was 0.223–0.256. The combination of the density-dependent adult effect model and the monomolecular growth model produced the highest probability of low export. The density-independent adult effect model and linear growth model combination yielded the highest probabilities of medium and high spot export; this combination also yielded the lowest probability of low export. The monomolecular growth model consistently produced the highest probabilities of low spot export, whereas the linear growth model was the most optimistic, yielding the lowest probabilities of low spot export. Under all models of uncertainty, the most probable state of the juvenile export component was less than 0.302 spot/m^2.

In our BBN, age-0 spot export from the Combahee River was most sensitive to settlement in the estuary in year 4, followed by natural mortality in year 4 and adult density in year 4 (Figure 6). The models of uncertainty (effects of multiple stressors on probability of low growth and effects of adult population size on juvenile settlement) had little influence on age-0 spot export. For example, varying the states of models of growth uncertainty only changed the probability of high age-0 spot export by 0.03.

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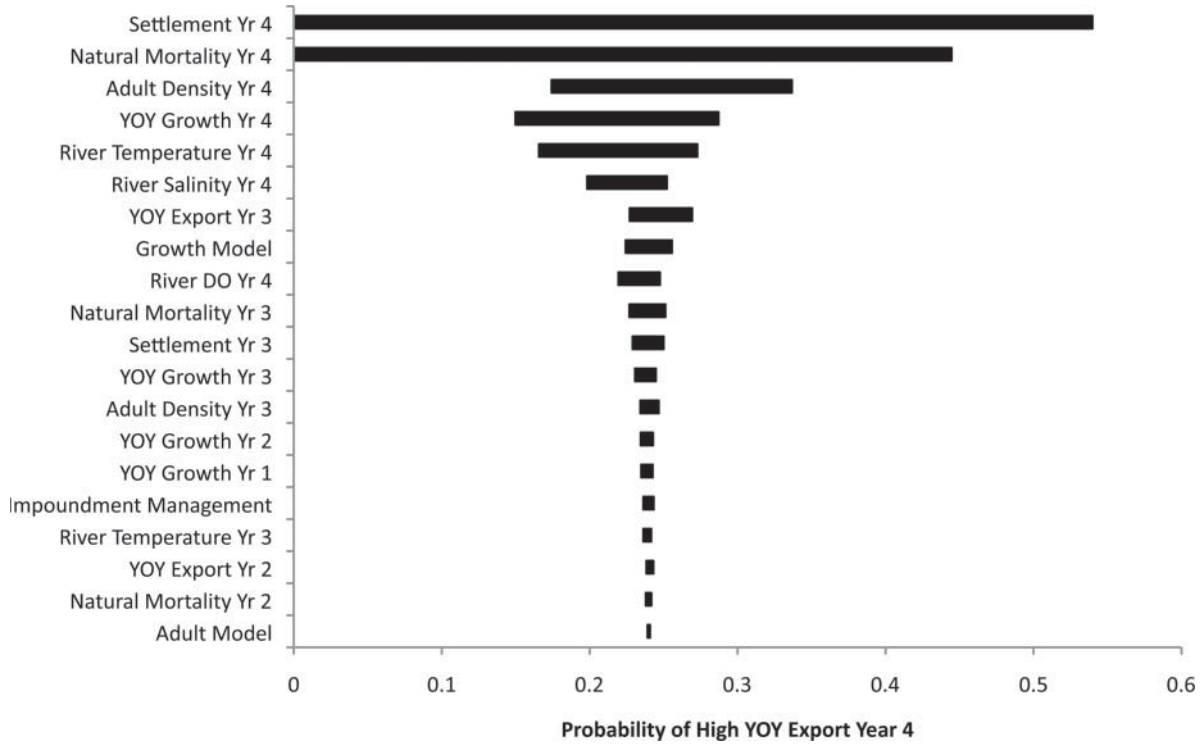


FIGURE 6. Sensitivity of the probability of high juvenile spot export from the Combahee River to changes in the Bayesian belief network components (defined in Table 2). Components (on the *y*-axis) are listed from most to least influential (Yr = Year; YOY = young of the year [i.e., age 0]; DO = dissolved oxygen concentration). The bars show the range of variation observed in the probability of high levels of age-0 spot export in year 4 when values of the states in each component were varied over their entire range while holding all other components constant.

Likewise, the impoundment management strategies had little influence on age-0 spot export because varying the states of this component changed the probability of high export by less than 0.01.

Under higher levels of spot immigration into the impoundments, we found that age-0 spot export was still most sensitive to settlement in year 4 and natural mortality in year 4. However, the relative importance of impoundment management strategies on age-0 export increased (Figure 7). For example, when 50% of spot entering the Combahee River were assumed to enter the impoundments, impoundment management was the third most influential component on age-0 spot export. Varying the states of the impoundment management component in this scenario changed the probability of high age-0 spot export in year 4 by 0.22 (Figure 7B).

DISCUSSION

Our first objective in this study was to determine the optimal management strategy to allow for the greatest possible levels of age-0 spot export from the Combahee River estuary while taking into account stakeholder values. The optimal strategy in this BBN—to change the way that water flows through the impoundment trunks—is a reflection of the stakeholders' ideals. Stakeholders that were asked to come to a consensus about management of impoundments on the Cooper River, South Carolina, valued impounded wetlands in the landscape but wanted to allow for better flow of organisms into and out of the impoundments (Consensus Solutions 2004). Because of the influence of stakeholder ideals on model utility values, the optimal management decision is not always the most ecologically beneficial decision, as economic and societal values also are considered (Conroy et al. 2008). In the Combahee River, however, the optimal decision satisfied conservation interests as well as economic and social interests because this decision preserves impoundments in the estuarine landscape while providing increased fish emigration from these structures. Under all scenarios in this decision model, however, low age-0 spot export densities were predicted with the highest probability.

Under the optimal decision, densities less than 0.302 spot/m^2 are available for export from the Combahee River, with probabilities ranging from 0.58 to 0.64. The range of probabilities for this level of export underscores the predictive uncertainty inherent in natural systems as well as the incomplete knowledge of these systems (Borsuk et al. 2002). A benefit of BBNs is that they allow the user to pinpoint research areas that are data poor (Renken and Mumby 2009). In the case of age-0 spot, estimates of spot density upon export are lacking in the literature and this information would help us evaluate whether the densities predicted by our model represent low, medium, or high levels

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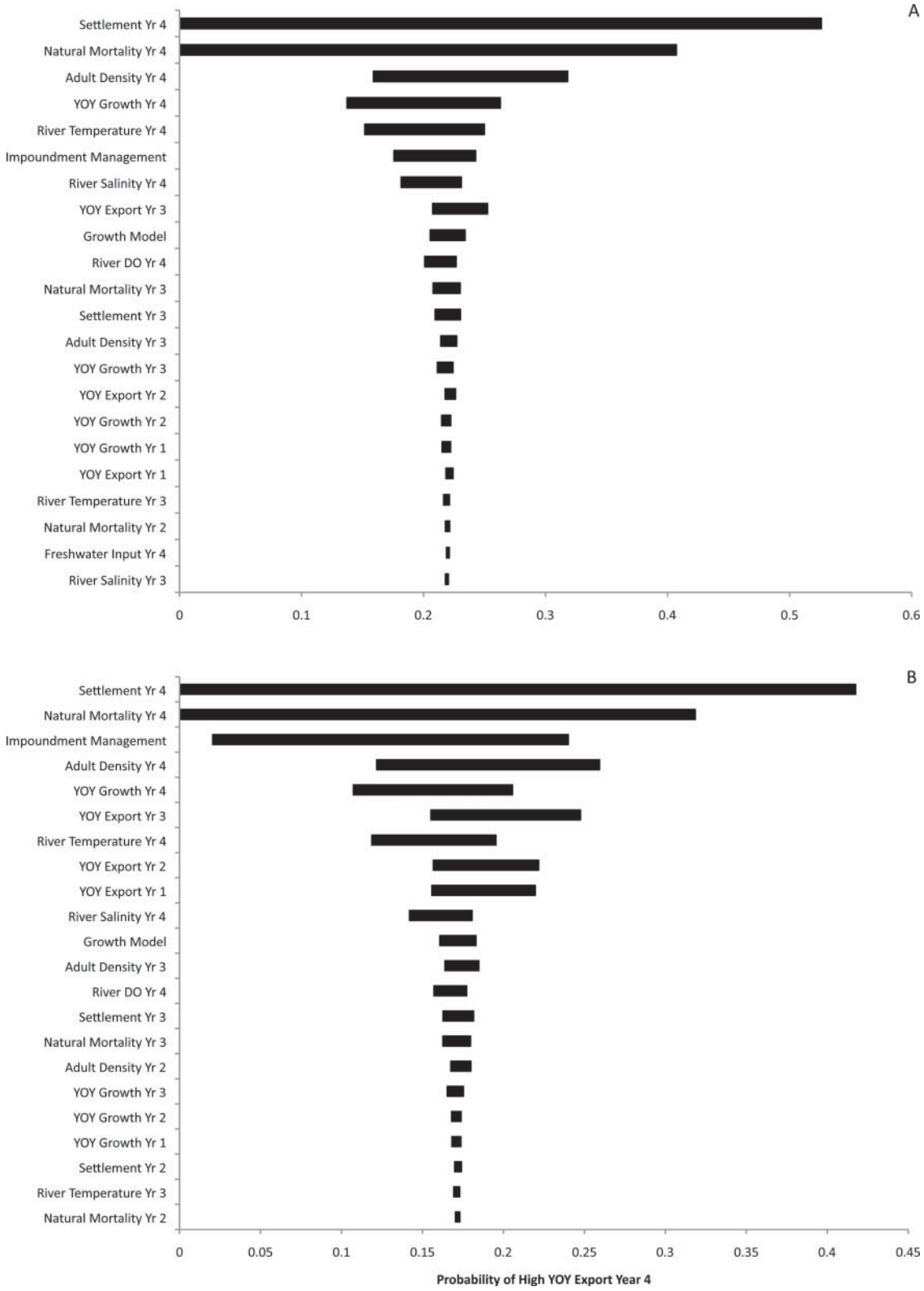


FIGURE 7. Sensitivity of the probability of high juvenile spot export from the Combahee River to changes in the Bayesian belief network components (defined in Table 2) when the percentage of total age-0 spot immigrating into impoundments is **(A)** 3.0–34.0% or **(B)** 50%. Components (on the *y*-axis) are listed from most to least influential (Yr = Year; YOY = young of the year [i.e., age 0]; DO = dissolved oxygen concentration). The bars show the range of variation observed in the probability of high levels of age-0 spot export in year 4 when values of the states in each component were varied over their entire range while holding all other components constant.

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of export. Additional information also is needed about how different factors interact to affect juvenile spot growth throughout estuarine residency and how adult spawning size dictates larval input.

Our optimal strategy remained the same regardless of the degree of structural uncertainty in these variables, indicating that we observed stochastic dominance in our system. This pattern also indicated that the expected value of perfect information in the present case is zero (Williams et al. 2002). When the expected value of perfect information is zero, this suggests that efforts to identify appropriate models of growth and influence of adult populations would not be justified in the context of impoundment management (Williams et al. 2002). However, because understanding the population dynamics of coastal marine-transient species is important for more than establishing policies for managing waterfowl impoundments, an investigation of the factors that influence growth rates and juvenile settlement densities definitely would be helpful. In addition to field and laboratory studies to better understand the process of export and the interaction of factors affecting age-0 spot, decision BBN models provide an avenue for updating information through adaptive resource management (ARM; Borsuk et al. 2002; Conroy et al. 2008).

Adaptive resource management allows researchers to learn from management decisions and incorporate this new understanding into management actions via a technique known as sequential decision making (Walters and Holling 1990; Conroy et al. 2008). Sequential decision making with ARM can help reduce uncertainty in a system through feedback of information (Borsuk et al. 2002; Conroy et al. 2008). This technique requires monitoring of the system after the implementation of a management decision and updating the model based on the outcome of that decision (Conroy et al. 2008; Figure 1). In this way, initial weights in CPTs that were populated based on incomplete information or expert judgment can be refined to reduce uncertainty in the model (Conroy et al. 2008). The model can be updated easily through Bayesian updating in Netica. For example, coupling ARM with monitoring would enable us to update the incomplete information for spot densities upon export. Updating the model via a monitoring program in conjunction with ARM also would decrease the structural uncertainty in our competing models regarding spot growth rates and the influence of adult population size (Conroy et al. 2008). Adaptive management of impoundments on the Combahee River under the optimal decision would reduce the uncertainty associated with the migration of transient fishes into and out of the impoundments under new water flow strategies and would strengthen the model and allow for better prediction of age-0 spot export. Finally, our model could be used to apply sequential decision making with ARM to other sites along the South Carolina coast. The optimal decision of changing the water level manipulation strategy for impoundments could be implemented in some of these sites and the monitoring efforts would provide feedback for decision implementation in other areas (Conroy et al. 2008).

Our second objective was to understand the relative effects of multiple factors on age-0 spot export. We hypothesized that juvenile spot would be most affected by factors associated with impoundment management activities. Our results suggest, however, that age-0 spot export is most sensitive to the influences of juvenile settlement in the estuary and natural mortality in the current year and is insensitive to impoundment factors. The Combahee River watershed is sparsely populated by humans. Most of the marshland in the ACE basin is undeveloped, and much of the land in this watershed is protected through private and public land stewardship. Because of these factors, only a small proportion of marsh habitat (about 10%) is impounded. The results of the sensitivity analysis suggest that this proportion of impounded marsh does not adversely affect age-0 spot survival and export. In heavily developed watersheds with managed impoundments, such as those around Georgetown, South Carolina, the impoundments may occupy a larger proportion of the marsh landscape and therefore may exert a larger influence on age-0 spot population dynamics than we observed in the relatively pristine ACE basin. For example, we found that when 50% of spot enter impoundments in the estuarine landscape, impoundment management strategies have a greater influence on spot export from the Combahee River. This result suggests that if greater proportions of spot are entering impoundments because less natural marsh is available, the impounded wetlands will have a much greater influence on spot population dynamics within that estuarine system. Additionally, the results of the sensitivity analysis are dependent on the factors that were modeled in this study. The use of sequential decision making with ARM would reduce uncertainty in these factors. Adaptive management also would help identify other factors that should be included in the model and that might influence age-0 spot export.

In our study, juvenile spot export was most sensitive to age-0 spot settlement in the Combahee River. Ross (2003) hypothesized that most age-0 marine transients, including spot, are recruitment limited and that mortality experienced in the estuary is less important than presettlement mortality in determining year-class strength. The results of our sensitivity analysis support this hypothesis. Additionally, a recent study in a North Carolina estuarine system showed a positive correlation between larval spot abundance in coastal waters during ingress and spring juvenile abundance (Taylor et al. 2009). According to our model, the number of juveniles that settle in the river most strongly drives the number of spot that exit the estuary in the spring. Additional information on presettlement mortality rates would strengthen the hypothesis that this input is the strongest predictor of year-class strength (Ross 2003).

In addition to juvenile settlement in the estuary, age-0 spot export also was sensitive to natural mortality during residence in the river. In our model, growth rate, temperature, and salinity all influenced natural mortality rates. We acknowledge that these are not the only variables that influence natural mortality, and this is reflected by the high degree of uncertainty in our CPTs for the 4 years of natural mortality. Other studies have suggested that

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the bulk of juvenile marine-transient mortality in nursery areas is the direct result of predation (Miller et al. 1984; Rice et al. 1993; Ross 2003). In our sensitivity analysis, natural mortality was the second most influential factor; other factors (e.g., growth rate, which influences predation) also greatly influenced spot export in our analysis. Prey species typically grow faster than their predators (Olson 1996; Persson et al. 1996); as such, the growth rate while in nursery areas will affect how long spot are most vulnerable to piscine predators (Craig et al. 2006).

The factors to which age-0 spot export was most sensitive are not necessarily subject to much anthropogenic influence, especially in the ACE basin. Human influence on factors that affect juvenile growth rates could serve to increase natural mortality experienced by spot, but because the ACE basin is a relatively pristine area, these effects probably are nominal. In densely populated watersheds, such as around Charleston County, South Carolina, the effects of human activities (e.g., eutrophication) could negatively influence age-0 spot growth.

The results of our decision analysis indicate that spot are relatively unaffected by anthropogenic influence in the Combahee River and probably throughout the ACE basin watershed because of its pristine nature. These results may not be similar for the other marine-transient species that use the ACE basin as nursery habitat. Spot are relatively hardy and ubiquitous in southeastern United States estuaries (Weinstein 1983; Hales and Van Den Avyle 1989; Ross 2003). As such, they may be less susceptible to adverse conditions than some other age-0 marine transients. Although this decision BBN was created specifically for age-0 spot in the Combahee River, it can be modified easily for other marine-transient species in the Combahee River or in other intertidal wetland systems located along the coasts of the southeastern United States.

A decision model, such as our model of spot dynamics, for marine-transient fish in nursery habitats is a useful tool for management and conservation. Estuaries constitute essential fish habitat (EFH) for marine transients, and efforts to conserve EFH are mandated under the 1996 revision of the Fishery Conservation and Management Act of 1976 (Minello 1999). Conservation of EFH necessitates an understanding of the habitat requirements of age-0 marine transients and how different management practices will affect these species. This decision model combines these types of information, promotes adaptive management, and provides a framework for protecting and enhancing estuarine nursery habitat for marine-transient fish.

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APPENDIX: CONDITIONAL PROBABILITY TABLES

Conditional probability tables for salinity, adult population (years 2–4), temperature, growth rate, settlement, natural mortality, and age-0 export components of the decision Bayesian belief network created to determine the optimal management strategy for maximizing the export of age-0 spot from the Combahee River estuary.

TABLE A.1. Conditional probability table of the salinity components for all years of the decision Bayesian belief network (BBN). States of the salinity component are in practical salinity units (psu).

	States of the salinity component	
Parent component: freshwater input	0–18 psu	18–25 psu
Drought	0.750	0.250
Normal	0.775	0.225
Wet	0.800	0.200

TABLE A.2. Conditional probability table for the adult spot population (density [fish/ha], years 2–4) components of the decision Bayesian belief network. States of the parent component are defined in Table 2.

	States of the adult population component		
Parent component: age-0 export from previous year	0.0–20.6 fish/ha	20.6–52.9 fish/ha	52.9–143.0 fish/ha
Low	0.450	0.350	0.200
Medium	0.250	0.500	0.250
High	0.200	0.350	0.450

TABLE A.3. Conditional probability table for the temperature components for all years of the decision Bayesian belief network.

Temperature (°C)	Probability
10	0.024
11	0.010
12	0.039
13	0.068
14	0.068
15	0.010
16	0.024
17	0.073
18	0.024
19	0.049
20	0.112
21	0.010
22	0.049
23	0.073
24	0.024
25	0.073
26	0.073
27	0.098
28	0.024
29	0.073

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TABLE A.4. Conditional probability table for the age-0 spot growth rate components for all years of the decision Bayesian belief network (DO = dissolved oxygen concentration; psu = practical salinity units). Parent components and the states of the growth rate component are further defined in Table 2.

Parent component				States of the growth rate component	
DO (mg/L)	Salinity (psu)	Growth model	Temperature (°C)	Low	High
0.0–2.3	0–18	Monomolecular	10–16	0.929	0.071
			17–27	0.733	0.267
			28–29	0.929	0.071
		Linear	10–16	0.660	0.340
			17–27	0.330	0.670
			28–29	0.660	0.340
	18–25	Monomolecular	10–16	0.981	0.019
			17–27	0.929	0.071
			28–29	0.981	0.019
		Linear	10–16	0.990	0.010
			17–27	0.660	0.340
			28–29	0.990	0.010
2.3–4.8	0–18	Monomolecular	10–16	0.862	0.138
			17–27	0.483	0.517
			28–29	0.862	0.138
		Linear	10–16	0.495	0.505
			17–27	0.165	0.835
			28–29	0.495	0.505
	18–25	Monomolecular	10–16	0.963	0.037
			17–27	0.862	0.138
			28–29	0.963	0.037
		Linear	10–16	0.825	0.175
			17–27	0.495	0.505
			28–29	0.825	0.175
4.8–10.0	0–18	Monomolecular	10–16	0.733	0.267
			17–27	0.000	1.000
			28–29	0.733	0.267
		Linear	10–16	0.330	0.670
			17–27	0.000	1.000
			28–29	0.330	0.670
	18–25	Monomolecular	10–16	0.929	0.071
			17–27	0.733	0.267
			28–29	0.929	0.071
		Linear	10–16	0.660	0.340
			17–27	0.330	0.670
			28–29	0.660	0.340

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TABLE A.5. Conditional probability table for the early juvenile spot settlement components for all years of the decision Bayesian belief network. Parent components and the states of the settlement component are further defined in Table 2.

Parent component		States of the settlement component		
Adult population (fish/ha)	Adult effect model	Low	Medium	High
0–20.6	Density independent	0.330	0.340	0.330
	Density dependent	0.700	0.150	0.150
20.6–52.9	Density independent	0.330	0.340	0.330
	Density dependent	0.250	0.500	0.250
52.9–143.0	Density independent	0.330	0.340	0.330
	Density dependent	0.100	0.150	0.750

TABLE A.6. Conditional probability table for the age-0 spot natural mortality components for all years of the decision Bayesian belief network. Parent components and the states of the natural mortality component are further defined in Table 2.

Parent component		States of the natural mortality component	
Growth rate	Temperature (°C)	Low	High
Low	10–12	0.250	0.750
	13–29	0.350	0.650
High	10–12	0.550	0.450
	13–29	0.650	0.350

TABLE A.7. Conditional probability table for the age-0 spot export components for each year of the decision Bayesian belief network. Impoundment management strategies are defined in Table 1; states of the parent components are defined in Table 2.

Parent component			States of the export component		
Impoundment management	Settlement	Natural mortality	<0.302 fish/m^2	0.302–0.563 fish/m^2	>0.563 fish/m^2
Closed	Low	Low	0.781	0.219	0.000
		High	1.000	0.000	0.000
	Medium	Low	0.000	0.639	0.361
		High	1.000	0.000	0.000
	High	Low	0.000	0.000	1.000
		High	1.000	0.000	0.000
Breached	Low	Low	0.782	0.218	0.000
		High	1.000	0.000	0.000
	Medium	Low	0.000	0.640	0.360
		High	1.000	0.000	0.000
	High	Low	0.000	0.000	1.000
		High	1.000	0.000	0.000
Top in, bottom out	Low	Low	0.767	0.233	0.000
		High	1.000	0.000	0.000
	Medium	Low	0.000	0.681	0.319
		High	1.000	0.000	0.000
	High	Low	0.000	0.000	1.000
		High	1.000	0.000	0.000
None	Low	Low	0.824	0.176	0.000
		High	1.000	0.000	0.000
	Medium	Low	0.000	0.674	0.326
		High	1.000	0.000	0.000
	High	Low	0.000	0.000	1.000
		High	1.000	0.000	0.000

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