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ARTICLE

Using Ecopath with Ecosim to Explore Nekton Community Response to Freshwater Diversion into a Louisiana Estuary

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Abstract

Current methods to restore Louisiana's estuaries include the reintroduction of Mississippi River water through freshwater diversions to wetlands that are hydrologically isolated from the main channel. The reduced salinities associated with freshwater input are likely affecting estuarine nekton, but these effects are poorly described. Ecopath with Ecosim was used to simulate the effects of salinity changes caused by the Caernarvon freshwater diversion on species biomass distributions of estuarine nekton. A base model was first created in Ecopath from 5 years of monitoring data collected prior to the opening of the diversion (1986–1990). The effects of freshwater discharge on food web dynamics and community composition were simulated using a novel application of Ecosim that allows the input of salinity as a forcing function coupled with user-specified salinity tolerance ranges for each biomass pool. The salinity function in Ecosim not only reveals the direct effects of salinity (i.e., increases in species biomass at their optimum salinity and decreases outside the optimal range) but also the indirect effects resulting from trophic interactions. Through multivariate analyses we determined that the simulated species biomass distributions in the estuary change significantly with distance from the diversion. However, the simulations do not show a significant difference estuarywide between the modeled distributions (with pooling of the data from different distances) before and after the opening of the diversion. This indicates a redistribution of species in the estuary rather than the replacement of species within the estuarine nekton community. The salinity function is a useful addition to the Ecopath with Ecosim software for estuarine ecologists and fisheries managers.

Fisheries scientists are more frequently turning to ecosystem-based approaches when studying coastal fisheries to advise natural resource managers. The complexity of estuarine ecosystems necessitates a holistic approach; ecosystem-based modeling explicitly accounts for ecological interactions that can reveal unexpected indirect effects (Walters et al. 1997, 2008). In this study the ecosystem-based modeling software Ecopath with Ecosim (EwE; www.ecopath.org) was used to simulate the effects of a coastal restoration effort on estuarine nekton communities and species biomass distributions (SBDs) in a Louisiana estuary.

A current method to restore Louisiana's estuaries includes reintroducing freshwater and sediments to wetlands that are hydrologically isolated from the Mississippi River because of the construction of levees. The Caernarvon freshwater diversion (CFD) is the second-largest Mississippi River diversion in Louisiana and affects the Breton Sound estuary by redirecting

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freshwater, sediments, and nutrients (Mossa 1996; Lane et al. 1999) from the river into the estuary through a water control structure. The CFD has been operational since 1991 with the purpose of stabilizing salinities in the estuary to optimize commercial shellfish production (USACE 1984). In addition, the introduced sediments may counteract coastal erosion (Wheelock 2003; Snedden et al. 2007).

The use of diversions as a restoration tool remains controversial because of their perceived negative impacts on fisheries (Turner and Rabalais 1991; Turner 2006). By lowering salinity, freshwater diversions are presumed to negatively affect fisheries resources that favor the prediversion regimes; notable nekton examples are penaeid shrimp (brown shrimp *Farfantepenaeus aztecus*, white shrimp *Litopenaeus setiferus*, and pink shrimp *Farfantepenaeus duorarum*) and spotted seatrout *Cynoscion nebulosus* (Chesney et al. 2000; Reed et al. 2007; Rozas and Minello 2011). The reduction in salinity associated with freshwater input likely affects the estuarine nekton community; different, species-specific salinity tolerance ranges within the community will lead to changes in community structure. However, there is little information as to which salinity regimes will be tolerated by fisheries species in the field and the points at which they will disappear from an estuary (Rozas et al. 2005a; Day et al. 2009; Kimmerer et al. 2009; Rozas and Minello 2011).

The purpose of this study was to determine how changes in salinity in the Breton Sound estuary as a result of the diversion of freshwater have altered estuarine nekton communities and SBDs and how this has affected fisheries species. To this end, an ecosystem model of Breton Sound was built based on 5 years of fisheries-independent monitoring data before the opening of the CFD. This model was then used to test different freshwater flow scenarios by entering different monthly salinity time series and simulating the response of the nekton community through time with a new version of Ecosim that allows the user to specify an empirically derived salinity function for each biomass pool. Ecopath provided a static, mass-balanced snapshot of data on the biomass pools and trophic flows in the Breton Sound estuary, while Ecosim was used to create dynamic simulations for exploration of the different scenarios (Christensen et al. 2004). The addition of the new function in Ecosim, specifically developed for this study, makes this approach especially useful in testing the effects of freshwater input on nekton in estuaries. Salinity data can now be entered as a forcing variable, along with user-specified salinity optima and tolerance ranges for each species or species group (i.e., biomass pool) in the model. This allows for simulation of species-specific responses to salinity changes in addition to the trophic interactions that are simulated in Ecosim. This study is the first use of this new application of the EwE software.

We hypothesized that within the estuarine nekton community some species with a preference for higher salinity would be displaced by species with a preference for lower salinity at sites closest to the CFD. In addition, predator–prey relationships would influence this simple response (Walters et al. 2008). Trophic interactions can lead to indirect salinity effects; for example, a change in the biomass of a predator due to a change in salinity can affect the biomass of its prey.

This study also resulted in a descriptive ecosystem model of the Breton Sound estuary that describes species relationships by visualizing energy transfers, trophic fluxes, and assimilation efficiency (Villanueva et al. 2006), which can be used to study the nekton community response in a variety of additional scenarios. The added salinity function in Ecosim described here provides resource managers tools with which to assess the state and trophic-interaction dynamics of nekton populations in ecosystems with variable salinities.

METHODS

Study area.—The 1,100-km^2 Breton Sound estuary is located 20 km south of New Orleans, Louisiana. It is bounded by the levee of the Mississippi River on the west side, and the levee of the Mississippi River Gulf Outlet on the east side. The CFD is a water control structure located in a bend of the Mississippi River at the north end of the estuary. From there, Mississippi River water flows directly into the estuary with a mean discharge of 45 m^3/s and a maximum flow of 226 m^3/s. The Louisiana Department of Wildlife and Fisheries (LDWF) has sampled nekton and measured salinity monthly at several fixed stations in Breton Sound since 1986. The six stations chosen for this study are located in a salinity gradient along the main flow path of the diverted freshwater flow (Snedden et al. 2007; Figure 1).

Analyses.—The modeling software used for this study, EwE, was created to estimate the biomass and food consumption of the modeled groups through trophic flows or food web interactions and to simulate the effects of these estimates on the fisheries. The Ecopath model was originally designed by Polovina (1984a, 1984b) to create steady-state trophic models of ecosystems; researchers at the University of British Columbia's Fisheries Centre then combined it with theoretical ecology concepts, mainly the network models proposed by Ulanowicz (1986, 1995). The Ecopath approach was expanded for use in fisheries management, and for addressing environmental questions, by including a temporal component (Ecosim) and a spatiotemporal component (Ecospace) (Walters et al. 1997, 1999, 2000; Pauly et al. 2000). A detailed explanation of EwE can be found in the user guides (Christensen et al. 2004, 2009), which are available online at www.ecopath.org.

Ecopath.—A balanced ecosystem model of the Breton Sound estuary before the opening of the diversion was built starting with EwE version 5.1 and continued in version 6, both of which are downloadable free of charge at www.ecopath.org. This Ecopath model of Breton Sound simulates the biomass dynamics of 39 groups. Ecopath as used here requires the following input variables for each group: biomass and, where applicable, the production : biomass and consumption : biomass ratios, stanza age breaks (split between juveniles and adults [months]), the growth parameter (k) from the von Bertalanffy growth function

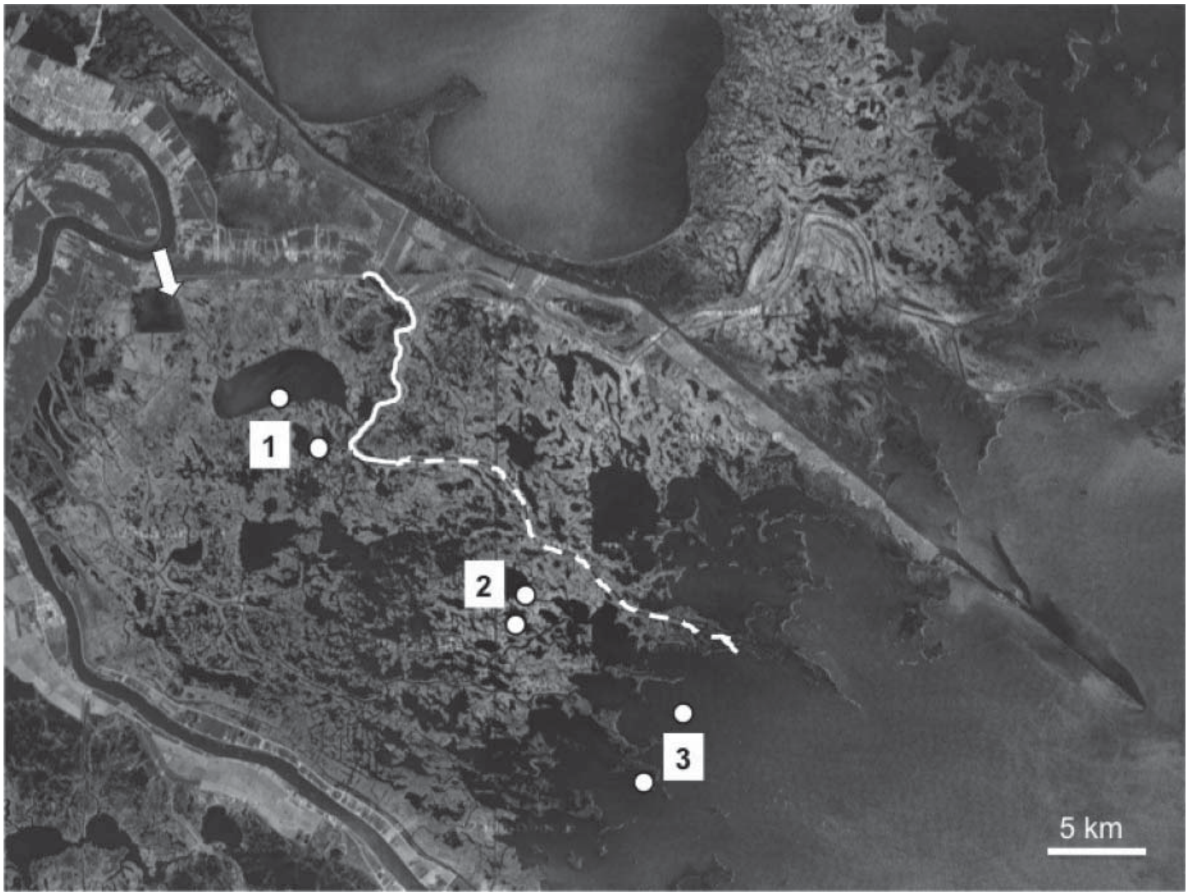

FIGURE 1. Arial photograph of the research area. The Caernarvon freshwater diversion discharge is indicated with an arrow. The white line indicates a natural levee banking Bayou Terre aux Boeufs, which blocks most freshwater flow. Because of this, the main flow path is through the three sets of sampling sites. The circles indicate the sites at which the nekton collections and salinity measurements were made monthly from 1986 to 2007. The numbers refer to the three Ecosim scenarios, indicating the sites from which the salinity data (as forcing functions) and the nekton data (as comparative time series) were used to create each Ecosim scenario. To create the Ecopath model, nekton data from all sites from 1986 to 1990 were used.

(von Bertalanffy 1928), optimum salinity, and the standard deviation of the salinity tolerance range of the group (Table 1). With this information and information on each group's diet, a working model of the Breton Sound ecosystem was developed in Ecopath. There are two master equations at the basis of Ecopath, plus the assumption of mass balance over an arbitrary period, here (and usually) a year. These equations and other terms and equations on the functioning of EwE have been presented in various papers on the development of this tool (Christensen and Pauly 1992, 1993b; Walters et al. 2000; Christensen et al. 2004, 2009; Christensen and Walters 2004).

The choice of which nekton species and biomass to use for the groups in the Breton Sound Ecopath model was based on 5 years of fisheries-independent data collected monthly by the LDWF. Five years is enough time for most of the species to reproduce at least once, which means that two or more generations were represented in the data on which the Ecopath model was based. The Ecopath model represents an "average year" before the opening of the CFD. Nekton was collected using 15.24-m bag seines with 6-mm mesh deployed from a boat by setting and anchoring one end of the seine and circling that point with the boat three times with the seine extended. Fish and crustaceans were identified to the lowest possible taxonomic level, counted, and weighed to the nearest 0.1 g wet weight.

The 5-year mean biomass (g/m^2) of all species collected at the study sites in the estuary from 1986 to 1990 was calculated. These were the 5 years just prior to the opening of the CFD in 1991. To control for between-year differences in effort, total biomass (g) per year was first divided by the number of net tows (units of effort) in that year and subsequently by the area (m) swept in one unit of effort to obtain grams per square meter.

Based on these data, species were selected for inclusion in the ecosystem model. First, species selection was based on dominance in the estuary (the species that together comprised 75% of the nekton biomass in the estuary were modeled as species-scale biomass groups). Second, species with low biomass that were expected to experience an increase in biomass with the inflow of freshwater were included in the model (e.g., largemouth bass and sunfish). Third, a large enough forage base for the predators had to be present in the model to achieve mass balance, so some adjustments were made to the biomass of important forage groups in the system. Bay anchovy is the dominant forage fish, but their total biomass was initially not sufficient to sustain all predators (partly because other forage fishes like Gulf killifish *Fundulus grandis* and inland silversides *Menidia beryllina* are part of predator diets and partly because the biomass of these fishes was probably underestimated based on the seine catches used for the initial biomass estimation; Allen et al. 1992; Rozas and Minello 1997). The underrepresentation of small forage fishes in particular may be due to the method of seining; circling one end of the net with a boat samples mainly open water, while small forage fishes could be concentrated on the marsh surface, at the edge of the marsh, or within shallow patches of submerged aquatic vegetation. The biomass of all small forage fishes collected was pooled with that of bay anchovy, and the biomass of this pool was increased (i.e., we increased the biomass of bay anchovy to represent a generic "forage base" group with the properties of bay anchovy; as a result, enough forage biomass was included in the model to support higher trophic level species).

For the same reason, the biomass of all penaeid shrimp present in the system was combined and increased, creating a penaeid shrimp group consisting of brown shrimp, white shrimp, and pink shrimp. Brown shrimp was the predominant of the three species, representing 98% of the penaeid shrimp biomass in the LDWF collections. Altogether, the nekton groups in the Ecopath base model represented 98% of the yearly mean nekton biomass present in the system as reported in the LDWF collections.

In addition to the nekton groups, a zoobenthos group was added consisting of zoobenthos biomass derived from an Ecopath model of Weeks Bay, a shallow subestuary of Mobile Bay, Alabama (Althauser 2003), plus the biomass of grass shrimp *Palaemonetes* spp. estimated from LDWF data in Breton Sound. Zooplankton, phytoplankton, benthic algae and detritus groups were added to the model with biomasses borrowed directly from the Weeks Bay model. An SAV group was added for which the biomass was determined from collections made from 2006 to 2008 in an area in Breton Sound that does not receive freshwater flow from the diversion (a proxy for the "before" conditions). Altogether, a base model was formed consisting of consumer groups including fish (several species as individual biomass pools), crustaceans, zooplankton, and zoobenthos; producer groups including phytoplankton, SAV, and benthic algae; and a detritus group. Birds, reptiles, and mammals were not included, and interpretation of the results should be restricted to the groups included in this model.

Each fish group (except bay anchovy, which was a pool of multiple species) was split into adults and juveniles with the multistanza feature in EwE (Walters et al. 2008, 2010). Adults and juveniles of the same species often have different functions in a food web and are therefore best split into separate groups with separate diets, predators, and salinity ranges. This separation also allows for cannibalism by adults on juveniles in the model. For each juvenile–adult combination, species-specific von Bertalanffy growth function parameters (von Bertalanffy 1928), total mortality rates, and the ages (months) at stanza breaks were entered (Table 1). These values were based on FishBase (www.fishbase.org). When more values were available, the value obtained nearest to our estuary, or in a system most similar to our estuary, was chosen. When no values for a species were available, the value from a similar species was chosen. Some information from FishBase was slightly adjusted to fit our system (Table 1).

Each consumer group has a diet consisting of one or more of the other groups. Each prey item was entered as a proportion of the consumer's diet. The diet of each species or consumer group was based on local stomach content analysis when available (T. Pasco, Louisiana State University, unpublished data), otherwise on information obtained from FishBase. Diets were adjusted to create a model of one possible working, balanced ecosystem. Within realistic boundaries, the exact relative proportions of the prey items that a predator eats are a function of availability. Diets were adjusted until the Ecopath-generated ecotrophic efficiency of each group was between 0 and 1, where 0 indicates that the group is not being consumed and 1 indicates the group is being heavily preyed upon (Christensen et al. 2004). When a balanced model of the ecosystem is established, Ecopath calculates the trophic level of each group based on its diet. These values were used to determine whether the diet matrix represented a food web with a valid trophic structure.

Ecosim.—Ecosim allows time-dynamic simulations of the initial parameters from the Ecopath base model through a series of coupled differential equations representing changes in the mass flux rates with changes in the biomass and behavior of the interacting biomass groups (see Christensen et al. 2004, 2009). When no time-forcing data are entered as part of an Ecosim scenario, the model predicts no change from the initial Ecopath base model, but only if the Ecopath base model is indeed balanced and no biomass accumulation rate is entered.

In the Ecosim scenarios described here for investigating the effects of salinity, fishing and other forcing and mediation functions were not included. Three Ecosim scenarios were created to test the effects of different salinity regimes on the nekton community structure and SBD in the Breton Sound estuary. Monthly salinity measurements, made by the LDWF from 1986 to 2007 at three different distances from the CFD along a salinity gradient within the main flow path of the diversion (Figure 1), were used for the three flow scenarios. Discreet salinity measurements made prior to the seine samples were used for this purpose. Measurements at approximately 10, 25, and 35 km from the opening of the CFD were used, creating low (scenario 1), medium (scenario 2), and high (scenario 3) salinity (as a correlate of flow) scenarios based on empirical data (Figure 2). These monthly mean salinities were entered as forcing functions in the model, together with species-specific salinity tolerance ranges.

TABLE 1. Biomass groups included in the Breton Sound Ecopath model. The table reports the biomass (g/m^2), production-to-biomass ratio (*P*/*B*), consumption-to-biomass ratio (*Q*/*B*), the age (months) at which an individual becomes an adult (stanza break), the *k* parameter used in the von Bertalanffy growth function, and the optimum value and SD of the salinity tolerance range of each species Asterisks denote values generated by Ecopath; superscripted numerals denote values from other sources, as follows: 1 = collected in this system, 2 = the Weeks Bay Ecopath model (Althauser 2003), 3 = the Gulf of Mexico Ecopath model (Walters et al. 2008), 4 = C. Walters (personal observation), and 5 = FishBase.

Group	Biomass (g/m^2)	*P*/*B*	*Q*/*B*	Stanza break (m)	*k*	Optimum salinity (‰)	SD of salinity
Alligator gar *Atractosteus spatula*						3	4
Juveniles	0.0000531*	2[4]	9.649*		0.2[4]		
Adults	0.0376[1]	0.193[2]	1.490[2]	12[4]		7	5.6
Spotted seatrout *Cynoscion nebulosus*							
Juveniles	0.527*	3.7[3]	6.442*		0.2[5]	15.6	8.3
Adults	1.88[1]	0.7[3]	1.6[3]	18[3]		14.6	9.3
Red drum *Sciaenops ocellatus*							
Juveniles	0.280*	2.2[3]	4.870*		0.4[5]	26.5	13.5
Adults	1.526[1]	0.62[3]	1.86[3]	18[3]		9.2	6.8
Largemouth bass *Micropterus salmoides*							
Juveniles	0.000210*	2[4]	9.011*		0.4[4]	0.1	1.5
Adults	0.0063[1]	0.6[4]	2.814[2]	12[4]		2.9	2
Sheepshead *Archosargus probatocephalus*							
Juveniles	0.00357*	2[4]	28.9*		0.25[4]	12.5	7.1
Adults	0.396[1]	0.417[2]	6.359[2]	12[4]		12.5	7.1
Sunfishes *Lepomis* spp.							
Juveniles	0.0000361*	2[4]	12.280*		0.6[4]	3.1	2
Adults	0.0004[1]	0.8[4]	4.966[2]	12[4]		1.5	2.5
Ladyfish *Elops saurus*							
Juveniles	0.00984*	2.8[3]	18.147*		0.26[5]	15	5.2
Adults	0.0932[1]	1.6[3]	6[3]	10[3]		15	5.2
Atlantic croaker *Micropogonias undulatus*							
Juveniles	0.0136*	2[4]	20.035*		0.75[4]	17	7
Adults	0.0454[1]	1.5[3]	10[3]	12[4]		17	7
Spot *Leiostomus xanthurus*							
Juveniles	0.00510*	2[4]	25.452*		0.75[4]	13.9	8.5
Adults	0.0268[1]	1.1[3]	12[3]	12[4]		15.5	5.5
Hardhead catfish *Ariopsis felis*							
Juveniles	0.00878*	2[4]	22.403*		0.4[4]	13.1	8.4
Adults	0.156[1]	0.8[3]	7.6[3]	12[4]		15	7
Black drum *Pogonias cromis*							
Juveniles	0.00209*	2[4]	34.129*		0.15[4]	8.9	6.7
Adults	0.274[1]	0.5[4]	6.359[2]	12[4]		8.9	6.7
Southern flounder *Paralichthys lethostigma*							
Juveniles	0.000278*	2[4]	26.189*		0.3[4]	7	5
Adults	0.0241[1]	0.417[2]	6.359[2]	12[4]		14	5
Gulf menhaden *Brevoortia patronus*							
Juveniles	0.0113*	2.3[3]	11.536*		0.8[4]	14.2	6.4
Adults	0.023[1]	1.9[3]	6[3]	12[3]		15.2	5.4
Striped mullet *Mugil cephalus*							
Juveniles	0.741*	2.4[3]	22.417*		0.3[4]	9.4	7.3
Adults	3.167[1]	0.8[3]	8[3]	18[3]		9.4	7.3
Bay anchovy *Anchoa mitchilli*	1.750[1]	2.530[3]	14[3]			15	8
Brue crab *Callinectes sapidus*							
Juveniles	0.0551*	3[4]	17.037*		0.7[4]	11.5	6.4
Adults	0.07[1]	2.4[3]	8.5[3]	12[4]		7.6	7.4

TABLE 1. Continued

Group	Biomass (g/m²)	*P*/*B*	*Q*/*B*	Stanza break (m)	*k*	Optimum salinity (‰)	SD of salinity
Penaeid shrimp							
Juveniles	0.00991*	3[4]	66.651*		1.5[4]	17	6.6
Adults	0.750[1]	2.4[3]	19.2[3]	3[4]		9.8	6.6
Zooplankton	0.609[2]	28.772[2]	84.87[2]			15	40
Zoobenthos	3.22[2]	4.5[3]	22[3]			15	40
Phytoplankton	1.946[2]	101.702[2]				1	15
Macroalgae, submerged aquatic vegetation	60.24[1]	9.014[3]				5	40
Benthic algae	12.876[2]	3.909[2]				15	40
Detritus	4[2]						

The tolerance range of each species was based on extensive LDWF data from monthly collections from 1966 to 2007 in all of coastal Louisiana. Using the collected nekton and salinity data, the catch frequency of each nekton species in the model was plotted against the salinity measured at the time of collection. For this the mean catch frequency per unit effort was grouped into salinity bins with 0.5‰ increments (Figure 3). This created roughly dome-shaped curves, from which an optimum and a standard deviation (SD) could be derived. For most species, there was considerably more variability in abundance at the optima of the curve, with decreasing variability at the tails. Variability in abundance at the optima is inferred to occur in response to salinity as well as other factors, whereas at the tails of the curve salinity is believed to have a greater limiting effect on abundance.

This function was then used in the model to modify the feeding rate, with a multiplier between 0 and 1. The maximum feeding rate occurs at the optimum salinity (feeding rate multiplied by 1), with feeding rate declining as salinity deviates from the optimum at a rate determined by the SD (feeding rate multiplied by a number between 0 and 1 determined by the species-specific salinity tolerance curve). Examples of this function are shown for spotted seatrout and largemouth bass (Figure 3); the salinity optima and standard deviations of all groups are listed in Table 1. Suboptimal feeding rates affect performance in the ecosystem, thus leading to reductions in biomass.

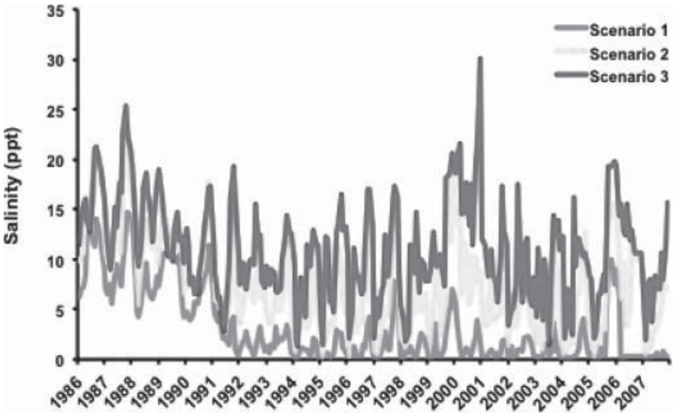

FIGURE 2. Salinity time series for the three Ecosim scenarios.

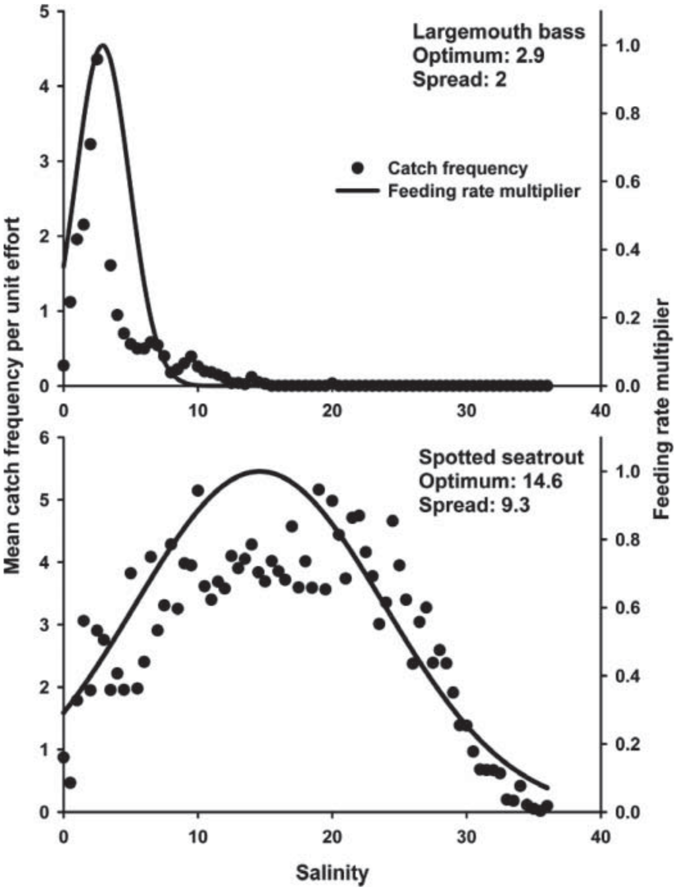

FIGURE 3. Salinity response curves for largemouth bass and spotted seatrout. The feeding rate multiplier (right *y*-axis) is 1 at optimum salinity and declines from the optimum at a rate determined by the standard deviation (the "spread"). The response curves are based on mean catch frequency per unit effort (left *y*-axis) by salinity plots created with data collected by LDWF in the entire Louisiana coastal area from 1966 to 2007.

Because the feeding rate–salinity response curve is dome shaped, moving away from optimum salinity imposes little penalty on the feeding rate up to 0.50 SD from the optimum, after which the feeding rate declines rapidly until it trails off asymptotically. Thus, species can recover if salinities return to favorable levels, and the responses to slight deviations in salinity from the optimum are moderate.

Model runs to evaluate the simulation scenarios began in 1986 with the community composition and SBD described in the Ecopath base model and continued until 2007. The combination of salinity and species-specific salinity ranges, together with trophic interactions following foraging arena theory (Walters and Martell 2004), determined the resulting SBDs for each scenario. Foraging arena theory is based on the principle that prey fish moderate predation risk by hiding and moving (Walters and Juanes 1993). In the model, prey was present in two states: vulnerable and invulnerable to predation. Prey groups became vulnerable to predation when they entered the "foraging arena," where feeding and predation rates are concentrated (Walters and Martell 2004).

Validation.—Nekton data were collected from 1986 to 2007 as part of ongoing fisheries-independent monitoring by the LDWF. These samples were collected at the same times and locations as the salinity measurements on which the flow scenarios were based (Figure 1). The 5-year mean biomass per species averaged over all sites in the estuary (two sites per scenario) from 1986 to 1990 was used as a basis for the Ecopath model; the yearly biomass per species at each location from 1986 to 2007 was used to validate the Ecosim runs as follows: the simulated biomass per species of flow scenario 1 was compared with the yearly mean biomass per species at location 1 (consisting of two LDWF sampling sites), the simulated biomass from scenario 2 was compared with the yearly biomass per species at location 2, and so forth. For each flow scenario, the sum of squared deviations between the observed and simulated biomasses of all fish groups was calculated, resulting in one such sum per scenario.

Statistical analysis.—To test whether the salinities used in the scenarios were indeed significantly different from one another, an analysis of variance (ANOVA; $\alpha = 0.05$) followed by a Tukey's test was performed in SAS 9.1.3 (SAS 2005). The data met all of the conditions for parametric statistical testing, so no transformations were performed.

The Monte Carlo routine in Ecosim was used to perform sensitivity analyses for both Ecopath and Ecosim. This routine tests the sensitivity of Ecosim's output to Ecopath input parameters by drawing input parameters from a uniform distribution centered on the base Ecopath value with the coefficient of variation set to 0.1 (Christensen et al. 2009). Because each Monte Carlo run creates a different Ecosim output, these outputs can be used as samples in statistical analyses. We ran the Monte Carlo application five times for each scenario with 10 iterations each and retained the best outcome (the trial with the lowest weighted sum of squared deviations) of each application run. These five best outcomes were treated as samples in the statistical software PRIMER 6 (Clarke and Warwick 2001). Five samples of the Ecopath SBD (run start), along with five samples of each Ecosim salinity scenario SBD output, were used in an analysis of similarity (ANOSIM). The ANOSIM procedure was used to test whether the nekton SBDs at the end of the salinity scenario runs differed significantly from one another and from those used in the Ecopath base model. The ANOSIM analysis was performed on a Bray–Curtis similarity matrix of square-root-transformed biomass data. The data were square root transformed to equalize the significance of large (heavy) and small (light) animals in the analyses; the transformation reduces the differences between the weights of the variables. The number of permutations was set at 9,999 and fell between 126 and 9,999 in practice, depending on the number of possible permutations. The α level was set at 1.0% for the ANOSIM (equivalent to 0.01 in a parametric test); it was lower than the conventional 5.0% to reduce the chance of a type II error in pairwise comparisons (Sokal and Rohlf 1994). Two final analyses were done: one one-way analysis with four factor levels (start, scenario 1, scenario 2, and scenario 3) and one one-way analysis with two factor levels (before [start] and after [pool of the three scenario outcomes]). The second analysis tested the diversion's effect on species biomass and community composition at the scale of the entire estuary. The level "start" or "before" refers to the nekton SBDs of the Ecopath model, which were derived from Monte Carlo runs as described above. The level "after" refers to the pooled SBDs at the end of each run; all five samples of all three scenarios are "after" samples in this analysis.

Following the ANOSIM, a similarity percentages (SIMPER) routine was performed to determine which species contributed the most to the dissimilarities between the nekton SBDs at the end of each scenario run and that in the base model. Only nekton species were included in the ANOSIM and SIMPER analyses; the detritus, plant, plankton, and zoobenthic groups were excluded. This was not only because these lower trophic groups can obscure information on the nekton SBDs owing to their high biomass but also because they are not part of the nekton community structure. The results were based on model runs with all groups, but only those for nekton were tested to determine whether the salinity scenarios created significantly different nekton communities.

RESULTS

Ecopath

The main adjustment required to achieve a balanced Ecopath model was to increase the biomass of small forage fishes and penaeid shrimp; as noted above, these two groups were probably underrepresented in the seine tows that provided the biomass-per-species information for the Ecopath model (Rozas and Minello 1997). After adjusting those two biomass pools and diet data (Kavanagh et al. 2004), a balanced Ecopath model was achieved. The main diet adjustments required were in the proportions of small forage fishes. During the balancing process,

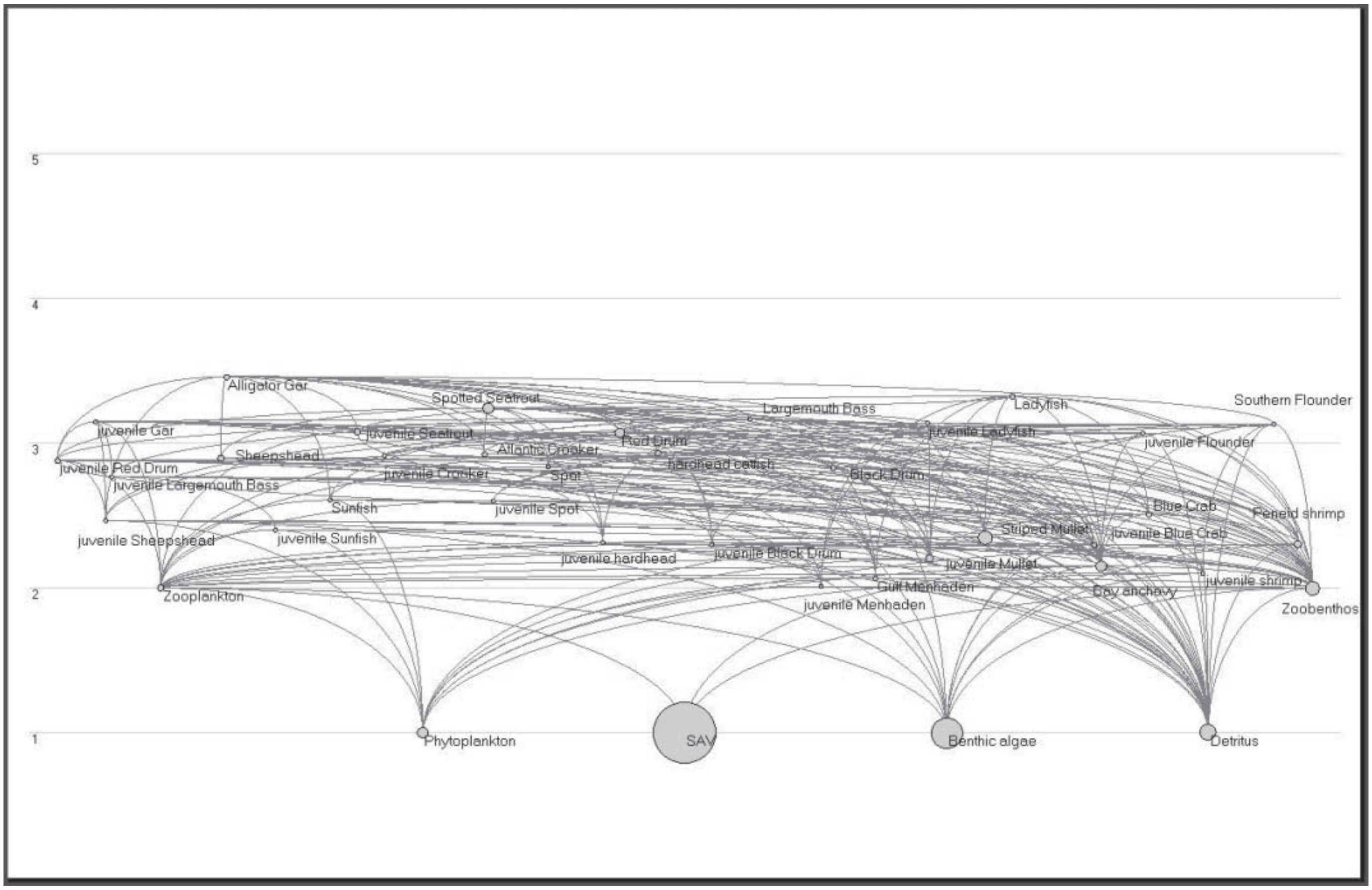

FIGURE 4. Flow diagram of all biomass pools and flows in the Breton Sound Ecopath model. The sizes of the dots indicate the sizes of the biomass pools, and the *y*-axis indicates the model-generated trophic levels of the pools based on the diets entered into the model.

Ecopath generates missing parameter values to complete a functioning ecosystem (Table 1).

A graphical representation of all trophic flows and biomasses shows that the highest trophic level in the ecosystem model was 3.46, while the mean (of the nekton species) was 2.67 (Figure 4). The proportion of total flow originating from detritus was 0.45. The mean transfer efficiencies from primary producers and detritus were 8.5% and 6.4% respectively.

Ecosim and Statistical Analyses

The differences between outcomes in Ecosim scenario runs are solely a function of the differences between salinity forcing values and their effect on trophic interactions. When no salinity scenario was selected during an Ecosim run, the biomass pools remained constant over time; this confirms that the Ecopath model is balanced and that the initial Ecosim state is not unstable (a saddle point). When fitted to real time series, the lowest sums of squared deviations were 752 for scenario 1, 296.7 for scenario 2, and 398.1 for scenario 3.

There were significant differences among the three salinity scenarios ($F_{786} = 330.04$, $P < 0.0001$); all scenarios differed from one another according to Tukey's test ($P < 0.05$; Figure 2). The mean ± SD salinities after the opening of the diversion were 1.4 ± 3.6‰ in scenario 1, 6.0 ± 4.6‰ in scenario 2, and 10.3 ± 3.6‰ in scenario 3. The mean salinity before the opening of the diversion also differed significantly from that after the opening ($F_{786} = 312.73$, $P < 0.0001$). The salinity of the whole estuary was 11.9 ± 3.6‰ before the opening of the CFD and 5.9 ± 5.1‰ after the opening.

The Monte Carlo routine created a balanced model for each trial when varying the input parameters with 10% standard deviations around the Ecopath base value. The total biomass in the Ecopath base model was 11.51 g/m^2. The total predicted mean ± SD biomass of nekton at the end of each run was highest for the low-salinity scenario (12.32 ± 1.85 g/m^2), intermediate at the medium-salinity scenario (9.77 ± 0.31 g/m^2), and lowest at the high-salinity scenario (7.86 ± 0.51 g/m^2).

The ANOSIM analysis performed on the SBD samples derived from the Monte Carlo runs reveals that there were significant differences in SBD among the three scenarios after accounting for uncertainty in the parameter values entered for the Ecopath base model ($R = 0.805$, $P = 0.0001$). Pairwise comparisons indicate significant differences among the SBDs of the three scenarios and between each scenario and the SBD

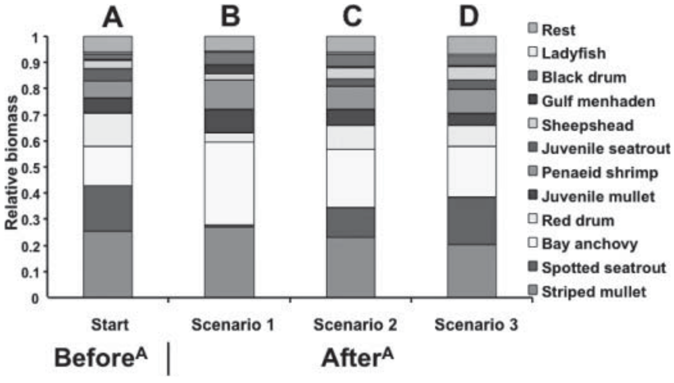

FIGURE 5. Species biomass distributions (SBDs) from the Ecopath base model and the three Ecosim scenarios in Breton Sound. The distinct letters above the bars indicate that the individual scenarios differed significantly from each other; the superscript A with the designations "Before" and "After" indicates that there was no significant difference before (Ecopath model) and after (the three end scenarios) the opening of the Caernarvon freshwater diversion. The species are listed from bottom to top in the order of their contribution to the dissimilarity between the four SBDs. The "Rest" category consists of species that together contributed less than 10% to the dissimilarities between the distributions.

of the Ecopath model (which is at the start of each scenario). All *R*-values were 0.78 or more, with *P* in each comparison being 0.008. However, when all SBD scenario outcomes were pooled and compared with the Ecopath base model, the SBD before the opening of the CFD did not differ significantly from that after the opening ($R = 0.101$, $P = 0.189$; Figure 5).

The species most responsible for the significant differences among the SBDs of the scenarios and between those of the scenarios and the Ecopath base model are striped mullet, spotted seatrout, bay anchovy, and red drum. The biomass differences of these species together are responsible for around 50% of the differences in each pairwise comparison. Striped mullet and bay anchovy had their highest simulated biomass in the low-salinity scenario (3.35 and 3.66 g/m^2, respectively), lower biomass in the intermediate-salinity scenario (2.78 and 2.48 g/m^2), and their lowest in the high-salinity scenario (2.25 and 1.81 g/m^2). Spotted seatrout had their lowest biomass in the low-salinity scenario (0.53 g/m^2), higher biomass in the intermediate-salinity scenario (1.21 g/m^2), and their highest biomass in the high-salinity scenario (1.70 g/m^2). Red drum had their highest biomass in the intermediate-salinity scenario (1.05 g/m^2), lower biomass in the high-salinity scenario (0.87 g/m^2) and their lowest biomass in the low-salinity scenario (0.73 g/m^2). The biomass of each species in the Ecopath base model is listed in Table 1; the proportional biomasses of the species responsible for 90% of the differences among scenarios are shown in Figure 5.

DISCUSSION

The results of the present model reveal that the low-, medium-, and high-salinity scenarios result in significantly different nekton SBDs. The SBD at the end of each scenario can be interpreted as the one that is expected to occur when each salinity scenario is played out estuarywide. However, when all scenario results were pooled and compared with that in the base model, there was no significant difference. Since each salinity scenario is based on empirical salinity data measured at three different distances from the diversion, the salinity changes due to the CFD with its current flow regime have probably not significantly altered the nekton community composition in the Breton Sound estuary, although the more localized spatial distributions of the biomass within the estuary may have changed. A separate modeling effort in Barataria Bay, which is adjacent to Breton Sound, also produced no significant reductions in the populations of fisheries species due to salinity changes beginning there in 1990 (Reed et al. 2007).

Using the Monte Carlo routine in Ecosim as a sensitivity analysis, the Ecopath base model was shown to be robust to at least modest (10% SD) variation in input parameter estimates, since each Monte Carlo trial balanced and there was little variation among the five best trials for each scenario. This indicates that small errors in Ecopath input values would probably not significantly affect Ecosim outcomes.

The flows, more than the size of the biomass pools, represent the contribution of each biomass pool to the estuarine food web; ecosystem functioning can be viewed in terms of biomass fluxes between trophic levels (Villanueva et al. 2006). The mean transfer efficiencies (the energy transferred to the next trophic level) from primary producers and detritus (8.5% and 6.4%, respectively) are low compared with Lindeman's suggested transfer efficiency of 10% in freshwater lakes (Lindeman 1942). Christensen and Pauly (1993a) found the mean of 41 systems to be 9.2%, but the range was very large, with mean trophic transfer efficiencies as low as 3.2% and as high as 17.6%. Therefore, the transfer efficiencies in the model of Breton Sound seem plausible.

The sums of squared deviations of the best fit between the Ecosim scenario runs and their respective time series data are high and probably could be lowered if other factors influencing nekton biomass (e.g., fishing) were added as forcing or mediation functions in Ecosim. Still, comparing the total biomass predicted for 2007 at the end of each Ecosim simulation with field collections performed at the same sites in 2007 (De Mutsert 2010) revealed similar biomass patterns. Converting the seine collections of De Mutsert (2010) to grams per square meter, the total biomass at the low, medium and high sites was 9.61 ± 1.56 g/m^2, 8.68 ± 1.90 g/m^2, and 8.35 ± 1.27 g/m^2, respectively, compared with predicted values of 12.32 ± 1.85 g/m^2, 9.77 ± 0.31 g/m^2, and 7.86 ± 0.51 g/m^2. The empirical values are without a correction for the underrepresentation of small forage species, as was done in the Ecopath model (see Methods), which is probably the reason for the lower biomass in the field observations. The field observations confirm the trend predicted by the model of lower total biomass with higher salinity.

While salinity is often the major factor influencing nekton distribution in estuaries (Bulger et al. 1993; Wagner 1999), other factors, including temperature, SAV, dissolved oxygen, turbidity, physical habitat, nutrient input, and fishing influence observed SBDs (Neill and Magnuson 1974; Cushing 1975; Rozas and Odum 1988; Pihl et al. 1991; Benfield and Minello 1996; Chesney et al. 2000; Thomas and Connolly 2001; Piazza and La Peyre 2007). Modifications to improve fit will be made during future Ecosim runs aimed at simulating more than the effects of salinity on nekton biomass (e.g., by including mediation factors). One example of a mediation factor that would improve this model is that of SAV on several predator–prey relationships; the fact that SAV alleviates predation pressure on forage species that use it as habitat will then be featured in the model.

Nonetheless, obtaining a perfect fit to empirical data by adding numerous mediation and forcing functions might not result in the best model. An additional reason for the high sums of squared deviations is the high variability in the empirical time series; the model runs are compared with highly variable fisheries-independent data collected at two sites per scenario.

Because the purpose of this modeling effort was to study the effects of salinity changes on estuarine nekton, and because no more causes or forces should be assumed than are necessary to account for the facts, a parsimonious model is appropriate. The advantage of this model is that the effects of salinity are explicit and separated from other factors that confound the relationship between salinity and estuarine nekton community structure.

It is interesting that in the Breton Sound Ecosim scenario runs small forage fishes (represented by the dominant bay anchovy) achieve their highest biomass in the lowest-salinity scenario (Figure 5). This is especially interesting because this group has an optimum salinity of 15.0 ± 8.0‰ in the model (Table 1), indicating that this SBD is caused by trophic interactions and thus not directly driven by the salinity forcing function. This indicates that predation pressure on some biomass pools can be lowered by low salinities that displace more stenohaline predators, many of which are marine transients. This mechanism may indirectly enhance the nursery function of the estuary, as these areas serve as refuge for forage fishes and, especially juveniles of estuary-dependent nekton species (Gunter 1967; McHugh 1984; Houde and Rutherford 1993). A similar result was demonstrated in a field study with a before-after-control-impact (BACI) design in the same estuary (de Mutsert 2010), in which more small individuals were present in the inflow area of the CFD than in the higher-salinity control area.

Although Reed et al. (2007) predicted a positive relationship between bay anchovy biomass and salinity in Barataria Bay, they pointed out that this was a result of a positive correlation between bay anchovy biomass and the ratio of open water. Open water was found more in saline marshes than freshwater marshes because more marsh reverts to open water at higher salinities. In both cases, salinity is only indirectly responsible for the distribution of bay anchovy but may drive other mechanisms (a decrease in predation pressure at lower salinities or an increase in open water at higher salinities) to which bay anchovy respond. What adds to the differences between the two estuaries is that Barataria Bay has more uniform and higher salinities than Breton Sound; there are no areas with salinities low enough to deter marine predators from using the entire estuary. MacRae (2006) showed that based on the LDWF metadata, bay anchovy have decreased in Barataria Bay over time, perhaps owing to rebuilding stocks of predators such as spotted seatrout and red drum (due to changes in fishing regulations). These results highlight the importance of trophic interactions and the need for a holistic ecosystem-scale approach to studying the nekton response to environmental changes (Cowan et al. 2008). In future modeling efforts in Breton Sound, both salinity and landscape patterns will be included explicitly by using the temporally and spatially dynamic Ecospace.

The results in Breton Sound further suggest that under the current flow regime total nekton biomass is positively related to freshwater input from the CFD, as the highest total nekton biomass was predicted for the low-salinity scenario while the highest-salinity scenario produced the lowest biomass. In our model, the main reason for this result is probably that the forage base with high biomass prefers the lower-salinity area due to the lower predation pressure there. In general, the fact that a freshwater diversion can increase secondary production is not surprising (Cushing 1975; Iverson 1990; Nixon and Buckley 2002; Day et al. 2009). The effect of the Mississippi River on estuarine and coastal ecosystems is probably the basis for the high Louisiana fishery productivity (Chesney et al. 2000; Cowan et al. 2008). A study conducted closer to the CFD in Breton Sound also documented higher nekton densities and biomass in the CFD inflow area than in a control area (Piazza and La Peyre 2007). Because Piazza and La Peyre (2007) studied Breton Sound during a freshwater flood pulse event, they could link higher nekton densities to river input (Piazza and La Peyre 2007). In future improvements of this model, river nutrient inputs will be added explicitly, which will probably result in higher biomass production than currently estimated by the model.

The species of nekton that were expected to be negatively affected by the CFD are spotted seatrout and brown shrimp (Gunter et al. 1964; Serafy et al. 1997; USACE 2004; Rozas et al. 2005b; Rozas and Minello 2011). The biomass of spotted seatrout was indeed predicted to have an inverse relationship with salinity, but it is still predicted to occur at its before-diversion level at the high-salinity end of the estuary. The biomass of brown shrimp, which in the model represents 98% of the biomass of the penaeid shrimp group, actually shows a slight positive relationship with lower salinities in the simulations (flow scenario 1), which might be due to a reduction in predation pressure as described above. With empirically derived optimum salinities of 9.8 ± 6.6‰ for adults and 17.0 ± 6.6‰ for juveniles, compared with the mean salinity in flow scenario 1 of 1.4 ± 3.6‰, penaeid shrimp were not expected to prefer low salinities a priori. However, because shrimp tolerate a large range of salinities, the limiting factor in simulations is predation pressure, which is predicted to be lower at the low-salinity sites. With more information, a more complex response curve could be created for each penaeid shrimp species individually, increasing the accuracy of shrimp biomass and distribution predictions.

Currently, the empirical relationship between the distribution of brown shrimp and freshwater inflow is somewhat unclear. Rozas et al. (2005b) concluded from their study in Breton Sound that the evidence for an effect of freshwater inflow from the CFD on brown shrimp distributions was inconclusive and that the response of brown shrimp to salinity patterns in estuaries is still a matter of debate. They suggested a BACI study and a modeling approach to answer this question. The results of such a study in this estuary (de Mutsert 2010) suggest that brown shrimp were not negatively affected by the current flow regime of the CFD. That study reveals that reported brown shrimp biomass declines actually began before the opening of the diversion and that biomass appears to have increased in the inflow area since 1996 (de Mutsert 2010).

While total biomass was highest in the low-salinity area, some fisheries species preferred the high-salinity area (e.g., spotted seatrout and sheepshead) or the medium-salinity area (e.g., red drum). The biomass of largemouth bass was highest in the lowest-salinity scenario (data not shown), but the species was predicted to be present at such low biomass overall that it did not contribute to the significant differences among the community compositions of the different scenarios. These results indicate that it would be prudent to maintain a salinity gradient in the estuary when management decisions are made concerning flow regime through the CFD.

The descriptive model presented in this paper demonstrates that the new salinity function in Ecosim is useful in detecting the direct as well as indirect effects of salinity changes within the nekton community. This is a useful addition when modeling ecosystems with dynamic salinities, and it can be applied to any other coastal ecosystem; the salinity function is currently included in the freely downloadable EwE software package.

Our current descriptive model can be used as a predictive model once other factors affecting nekton biomass (discussed above) are included. Future research will include testing different hypothetical freshwater flow rate scenarios; the current simulations were based on empirical data collected in the estuary. Such numerical experiments will be possible by coupling a hydrodynamic model that can simulate salinity distribution based on CFD flow rates to Ecosim and Ecospace, which can then be used to simulate nekton distributions based on the salinity output as well as changes in habitat (Ma et al. 2010). In this way, it may be possible to evaluate which flow regime is optimal for wetland restoration without losing nekton biomass and species of interest that prefer higher salinities. The results of the combined models could then be used as a flexible gaming tool (Walters et al. 2008) with which to provide advice to resource managers about flow regimes in this and other planned diversion projects in coastal Louisiana (USACE 2008). The tools and approach presented here can be used in any other fisheries ecosystem in which salinity or other environmental factors may be affecting nekton biomass. The results of this and other studies (e.g., Reed et al. 2007; Day et al. 2009; Kim et al. 2009) appear to indicate that freshwater diversions can benefit wetlands and promote land building without negatively affecting the nekton populations in Louisiana's estuarine ecosystems.

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