



Employing ecosystem models and geographic information systems (GIS) to investigate the response of changing marsh edge on historical biomass of estuarine nekton in Barataria Bay, Louisiana, USA



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ABSTRACT

Louisiana's coastal ecosystem has a long historical record of productive fisheries. Even in light of the multiple perturbations experienced in this region, fish and shellfish landings have remained stable or increasing. These disturbances have resulted in many unforeseen ecological consequences; one such consequence is the loss of marsh vegetation in southern Louisiana (LA). Marsh habitats are thought to function as nursery habitats for post-larval and juvenile fishes, providing both refuge from predation and increased foraging opportunities. As the loss of marsh appeared to have a null effect on fish and shellfish yields, there evolved a hypothesis that described a positive effect on nekton production; increasing marsh edge distance during marsh degradation provides a potential short-term increase in marsh access for organisms. Here we used Geographic Information System (GIS) data to determine the patterns of marsh loss over a 10 year period and to create marsh edge maps for further analysis in an ecosystem model. We used the ecosystem model Ecopath with Ecosim and Ecospace (EwE) to determine if a suitable response mechanism between estuarine organisms and marsh edge distance could be developed. The scenario analysis of multiple theoretical response functions showed Ecospace's ability to model changing habitat and environmental variables over time and space. More specifically, while the results of this modeling effort revealed species-specific responses to marsh edge, the association between nekton and marsh edge may not be as tightly coupled as once thought in coastal LA.

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1. Introduction

For almost 40 years, scientists have hypothesized that Louisiana fisheries could be in danger of collapse due to considerable loss of marsh (Turner, 1977; Browder et al., 1989; Nance et al., 1989; Chambers, 1992; Zimmerman et al., 2002; Haas et al., 2004; Valiela et al., 2004). Coastal Louisiana (LA) accounts for 60–80% of the nation's annual wetland loss (Boesch et al., 1994) and fishes that inhabit these estuaries are not only important to recreational and commercial anglers, but are important as indicators of estuarine health (Whitfield and Elliott, 2002). Researchers have long recognized the importance of estuaries as nurseries for species that live in estuary and continental shelf ecosystems (Gunter, 1967;

Nixon, 1980; Boesch and Turner, 1984; Baltz et al., 1993). In fact, one highly cited study directly related the area of intertidal marsh in LA to the amount of penaeid shrimp yield (Turner, 1977). But as fisheries landings in LA remained stable or increasing in the face of marsh loss over the last 50–70 years, studies emerged to find mechanisms for this resiliency (Browder et al., 1985, 1989; Rozas and Reed, 1993; Zimmerman et al., 2002). These studies, and many others, infer that as marsh degradation continues through time, the linear distance of marsh edge will increase to an optimum, thereby increasing the availability of marsh use by estuarine nekton. This increased marsh edge, is hypothesized to mitigate the consequences of overall loss of marsh habitat (i.e. offering increased access to the marsh–water interface for foraging and protection from predation). But as marsh degradation continues, the fragmented marsh begins to wash away, along with marsh edge (Fig. 1). So over the short term, it is thought that species that utilize estuaries would most likely benefit from increased edge, but at the point where marsh becomes more than 50% open water, fish production (and therefore yields) would decrease (Browder et al., 1989).

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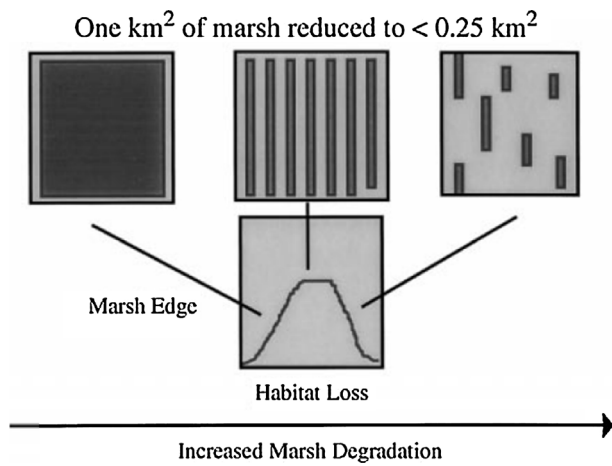


Fig. 1. Marsh degradation contributes to the “edge effect,” where the linear distance of marsh edge initially increases to a maximum, then decreases with continued land loss (from Chesney et al., 2000).

Most of the studies investigating what we call the edge effect, operated at small spatial scales, using drop or lift samplers, and found that organism densities were higher for decapod species nearer to the marsh edge (Rozas and Reed, 1993; Zimmerman et al., 2002; Minello and Rozas, 2002; Rozas et al., 2007). While investigations at this scale are valuable to understanding important ecological interactions, from a management perspective, it is also important to assess the effect of marsh loss on the food web as a whole and at larger spatial scales. In dynamic ecosystems, such as deltaic estuaries, a complex array of perturbations impacts species and food webs simultaneously. To that end, ecosystem models are well suited to capture these complex processes.

The purpose of this study is to determine if an empirical relationship exists between marsh edge distance (hereafter edge) and

estuarine nekton. To accomplish this goal, we first evaluate the patterns of marsh loss within Barataria Bay, LA over a 10 year period by creating a marsh degradation curve as described by Browder et al. (1989). Understanding trends in habitat loss are important in determining if patterns of historical species biomass are driven by these changes. We then developed an ecosystem model using the new spatial-temporal data framework within the Ecopath with Ecosim and Ecospace (EwE) suite of software (Steenbeek et al., 2013) with and without various edge response curves for specific species and life stages. By using a scenario evaluation approach to ecosystem modeling, we are able to compare the fit of each model run to determine which curve (or lack of edge response curve) more precisely hindcasts historical biomass of estuarine organisms. Moreover, this type of modeling application enables the use of multiple drivers within the ecosystem (habitat, salinity, and fishing pressure, for instance), and can later be used to make more reliable predictions about future trends in ecosystems undergoing rapid environmental change (Chesney et al., 2000).

2. Methodology

2.1. Barataria Bay, LA, USA

This study uses data obtained in Barataria Bay, LA, a 6280 km² sub-region of the Barataria-Terrebonne estuary system and member of the National Estuary Program (Nelson et al., 2002). Barataria Bay (Fig. 2), isolated from the Mississippi River since the 1940s, gets the majority of its freshwater input from rainfall and contains freshwater, brackish, and marine coastal marshes. The basin is bounded on the west by Bayou LaFourche and on the east by the Mississippi River. In addition to rainfall, the Davis Pond Freshwater Diversion provides a relatively slow and controlled flow of freshwater (~28 m³/s) into the upper reaches of the estuary.

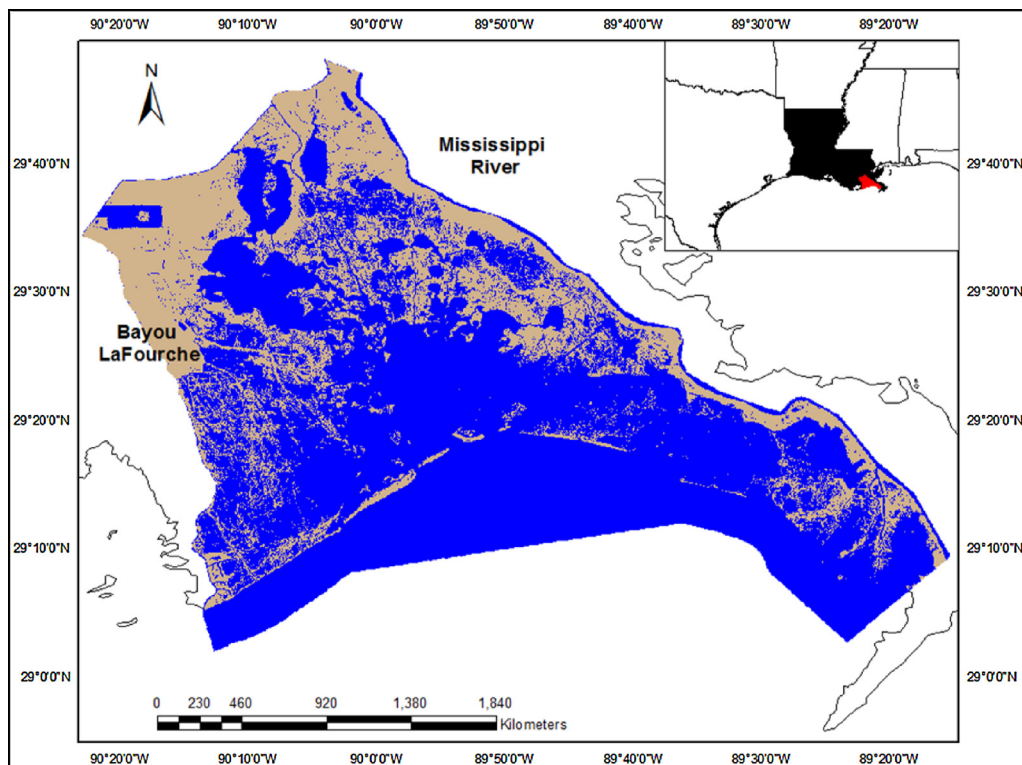


Fig. 2. Barataria Bay, LA, USA, bordered on the east by the Mississippi River and on the west by Bayou LaFourche (Couvillion et al., 2011).

Table 1
Data sources used for vectorization and Ecospace grid cell development (Couvillion et al., 2011).

Year	Data source
1932	Historical survey data
1956	National Wetlands Inventory aerial photography
1973	Landsat Multi-Spectral Scanner (MSS)
1975	Landsat Multi-Spectral Scanner (MSS)
1977	Landsat Multi-Spectral Scanner (MSS)
1985	Landsat Thematic Mapper
1987	Landsat Thematic Mapper
1990	Landsat Thematic Mapper
1995	Landsat Thematic Mapper
1998	Landsat Thematic Mapper
1999	Landsat Thematic Mapper
2002	Landsat Thematic Mapper
2004	Landsat Thematic Mapper
2006	Landsat Thematic Mapper
2008	Landsat Thematic Mapper
2009	Landsat Thematic Mapper
2010	Landsat Thematic Mapper

2.2. Vectorization

In order to evaluate the results of the ecosystem model scenarios, there was a need to empirically determine the marsh loss trends occurring during the time period of the model run in Barataria Bay. Therefore, we developed time series data of linear distance of edge and total marsh area within Barataria Bay to calculate a marsh degradation continuum over the period 2000–2010. The full suite of land-water datasets were obtained from Couvillion et al. (2011) spanning the years 1932–2010 (Table 1). The linear distance of marsh edge was calculated in Barataria Bay using batch vectorization in ArcGIS® software. To complete the vectorization, all datasets were imported into ArcGIS® as raster images, then clipped to include only the extent of Barataria Basin (using the Intracoastal Waterway as the northern boundary), and finally each dataset was vectorized into polylines (Fig. 4, Panel 1). Once vectorized, edge distance was determined for Barataria Bay by outputting summary statistics within the software. Marsh area was calculated with the Spatial Analyst toolbox within ArcGIS®. Since not every year from 1932 to 2010 was represented by a dataset, we performed a linear interpolation for missing data points with PROC TRANSREG using the SPLINE transformation to create the time series of edge (SAS, 2013). This procedure provides a complete time series of predicted measurements using all available data for edge and area of marsh. Using these data, a marsh degradation curve was plotted using a subset of the full time series (2000–2010) with the LOWESS function in R (v. 3.1.0).

2.3. Ecosystem model data preparation

Biomass data used to develop the Ecopath model initial biomasses and the biomass time series data in Ecosim were derived from data collected by the Louisiana Department of Wildlife and Fisheries (LDWF) Fishery Independent Shrimp/Finfish/Oyster Monitoring Programs (FIMP). For a detailed description of how fishery independent data were collected, please refer to the Marine Fisheries Division Field Procedures Sample Design and Data Collection Manual (LDWF, 2002).

Abundance and length data are the most consistently reported variables in the LDWF fisheries independent monitoring database. Since EwE requires biomass values in $\text{g m}^{-2} \text{yr}^{-1}$ for initial biomass and time series data, LDWF abundance data per unit effort were converted to g m^{-2} for each species in the model by using L-W relationships and estimating the area sampled with each gear (see Appendix A). The species and species groups used in this analysis accounted for over 76% of the total catch in trawl gear samples

(6 taxa), and over 20% of the total catch in gillnet samples (3 taxa; Appendix A).

A diet matrix is included in the development of every Ecopath model to represent the predator–prey interactions occurring in the ecosystem. The diets of juveniles and adults of each species were determined using published literature and Fishbase (www.fishbase.org). The total biomass of any prey item within a system determines its availability for predation. Ecopath generates an ecotrophic efficiency parameter (EE) that ensures a prey item is being consumed within realistic bounds of its overall biomass.

Three types of fisheries data were used in our model: commercial landings data, commercial effort data (number of trips per fishery/month/year) and recreational effort data (trips/year). Landings data were used as initial inputs in the Ecopath base model to represent biomass removal from the ecosystem via fishing and time series landings data were used in Ecosim as a way to assess the fit of model predictions. Fishing effort data were used to drive model dynamics, allowing the model to account for time varying fishing effects on the ecosystem. Landings used as initial inputs in Ecopath were derived from LDWF Trip Ticket data. If these inputs did not meet the mass balance assumption during model balancing procedures, the landings values were iteratively reduced to meet those assumptions. Since the survey data used to create the initial biomasses tend to underestimate total biomass in the system, landings data are often too large to include without small reductions. Low levels of bycatch or discards from the shrimp fisheries were also included in the model. This information is a qualitative assumption based on the knowledge of the primary sources of bycatch in each fleet. Recreational data were only sparsely available and therefore we used recreational data collected by NOAA's MRIP (National Oceanic and Atmospheric Administration's Marine Recreational Information Program) (<http://www.st.nmfs.noaa.gov/recreational-fisheries/index>) to create a relative effort curve that was adjusted to fit fishing mortality per species using a gaming feature in Ecosim, and recreational fishing information from the 2011 spotted seatrout stock assessment report (West et al., 2011).

Until recently, Geographic Information System (GIS) data has been cumbersome to utilize in the Ecospace module of EwE. However, Steenbeek et al.'s (2013) recent innovation that incorporates geo-referenced environmental drivers (i.e. salinity, dissolved oxygen, etc.) has enabled modelers the ability to input spatially and temporally explicit environmental data, and receive output of spatial responses of organisms to these drivers at monthly time steps. Moreover, while many ecosystem-level models have included habitat features in the model, the response of organisms remained relatively simple, as the habitat parameters were fixed, and could not change as the habitat changed over time. The new habitat capacity model (Christensen et al., 2014) in Ecospace directly addresses this issue by allowing a species' foraging capacity to be impacted by multiple factors, such as depth, salinity, temperature, and important to this study, the linear distance of marsh edge. Utilizing the new spatial-temporal data framework along with the development of a smarter habitat capacity model in EwE provides a new perspective to investigating how organisms respond to changes in habitat features and environmental variables over space and time.

The use of the Ecospace spatial-temporal framework requires the definition of maps that describe the ecosystem (e.g. bathymetry and environmental variables) in an Ecospace scenario. The first map that must be developed is the base map, which represents the model area and indicates coastline, the marine boundary, depth, and active (water) and inactive (land) cells. The base map in this study was derived from Couvillion et al.'s (2011) 2010 land/water dataset (Fig. 3). We decided to use 2010 as the base map, since 2010 was determined to have the fewest land cells comparative to

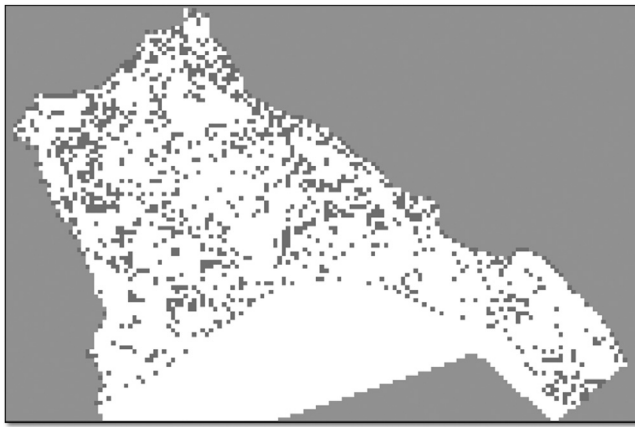


Fig. 3. The Ecospace model base map displaying active water cells (white) and inactive land cells (gray). These data were derived from the 2010 USGS land-water data sets (Couvillion et al., 2011).

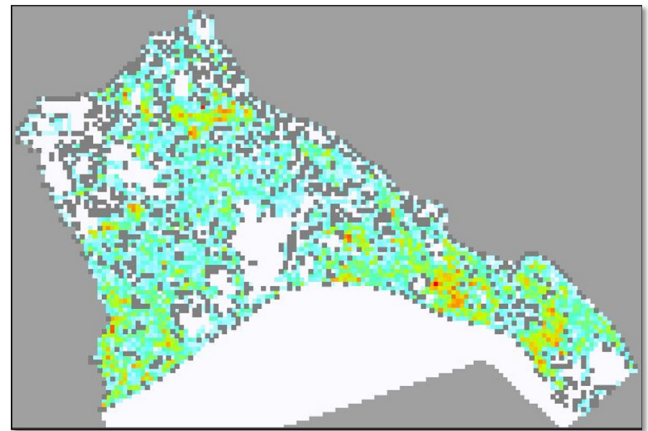


Fig. 5. Marsh edge Ecospace initialization map. Warm colors indicate higher values of marsh edge in the cell. Gray cells indicate inactive (land) cells. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the other datasets, which allowed us to simulate land building during model simulation (Note: currently Ecospace lacks the ability to convert land cells to active water cells, but using the habitat capacity model, Ecospace can add habitat (land) to active water cells). Ecospace accepts the base map (and all environmental and habitat drivers) as ASCII grid files. The Barataria Bay basemap was created in ArcGIS® using the Data Management Toolbox (Create Fishnet), and the size of the grid cells in this base map is 864.95 m × 754.24 m. This cell size is generally smaller than what has been historically utilized in Ecospace, and was decided upon to account for both the spatial variation of water quality drivers and the size of the organisms utilizing the ecosystem.

In addition to the base map, Ecospace requires an initialization map for each environmental and habitat layer in the model. These initial maps provide the baseline for the time dynamic spatial layers and are typically calculated as the spatial mean for that parameter averaged over the first model year. For the purposes of this study, there is an edge initialization map (Fig. 5), a salinity initialization

map (Fig. 6), and a static oyster cultch map (Fig. 7). The cultch map remains unchanged over the entire model run and limits establishment of oysters to where cultch is present. The spatial-temporal salinity data and oyster cultch maps were obtained from the state of Louisiana’s Coastal Protection and Restoration Authority (CPRA) for use in this model.

To develop the time series of edge maps for use in the spatial-temporal data frame work, Couvillion et al.’s (2011) land/water datasets were again processed for this purpose (Fig. 4, Panel 2). First, area was tabulated in each cell in the fishnet grid. Then, for every year in the land/water datasets, a 1-m buffer around the polyline network was created (Fig. 4, Panel 1). After further processing, the buffered polyline shapefile was joined (Toolset: Union) with the fishnet Ecospace grid. Area was calculated for the buffered edge interface in each grid cell, then divided by the total area in each cell to calculate the proportion of marsh edge in each cell. The shapefiles were then converted to raster datasets and finally to ASCII grid

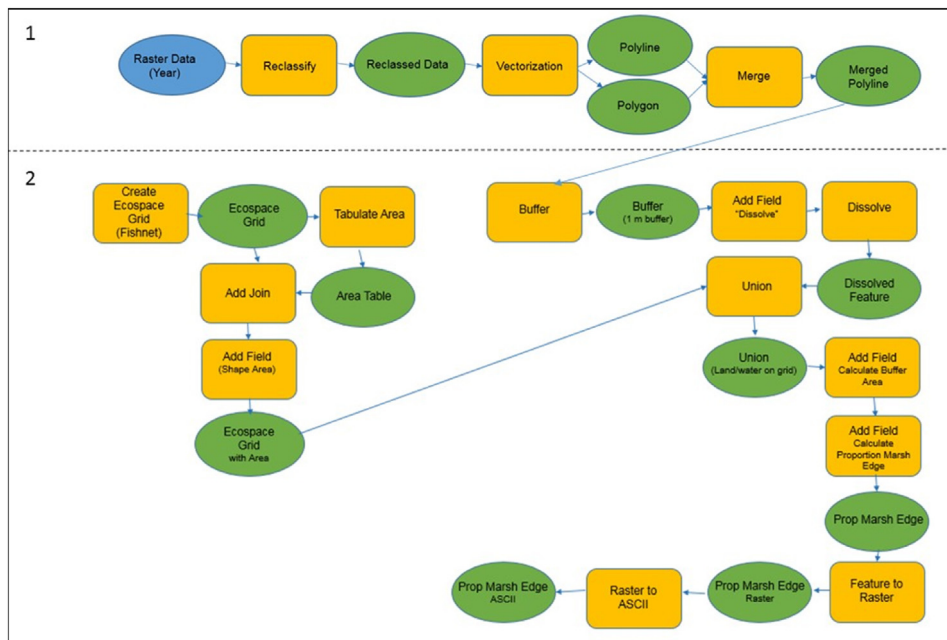


Fig. 4. GIS data processing model to create vectorized land/water datasets (Panel 1) and to create a time series of Ecospace ASCII grids containing the proportional of marsh edge in each grid cell (Panel 2). Blue indicates an input dataset, yellow indicates the tool or process, and green indicates an output dataset, which can also be used as an input dataset. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

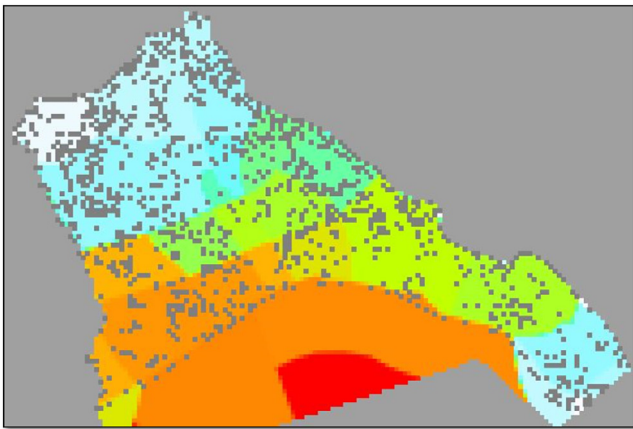


Fig. 6. Salinity Ecospace initialization map. Warm colors indicate higher values of salinity in the cell. Gray cells indicate inactive (land) cells. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

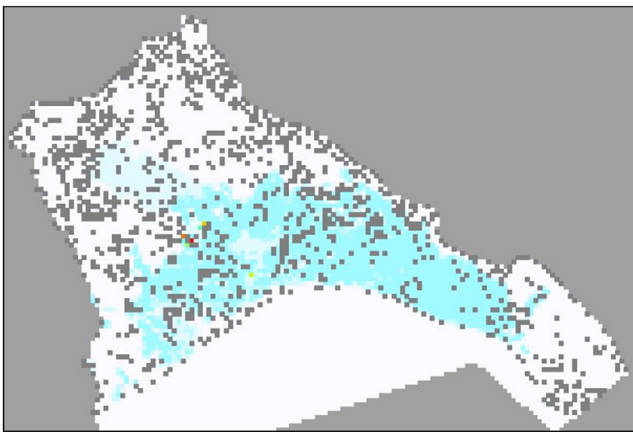


Fig. 7. Oyster cultch Ecospace initialization map. Warm colors indicate higher values of marsh edge in the cell. Gray cells indicate inactive (land) cells. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

files with one value of edge proportion in each cell. This process was carried out for each land/water dataset from Couvillion et al. (2011). The edge ASCII files are represented annually, but not at every time step (see Table 1). Ecospace has the capability of receiving maps that are not equally spaced through time. Since each edge map is time-stamped by year, Ecospace will ‘pick-up’ the edge file in January of the specified year. That edge map will remain in queue until the next map occurs during the model run. In this way, we can utilize available data and do not need to fill in the gaps where data may be lacking, as was done with the linear interpolator for the temporal representation of edge loss.

The salinity ASCII files per month from 2000 to 2009 are geo-referenced, and provide one value of salinity per grid cell over the entire model area. As the model runs, a new set of ASCII files is called into Ecospace by month to create spatial and temporal dynamic environmental driver.

2.4. Response curves in Ecospace

Estuarine species often occur on environmental gradients and the occurrence of species along these gradients can be derived empirically using data collected from the field. This distribution is known as species response curve (Holland, 2014). In the same way,

Table 2

Trapezoid salinity response curves for model species. Data source is indicated in the Source column: FIMP Shrimp represents the LDWF Fisheries Independent monitoring program Shrimp dataset, which uses trawl gear; FIMP Finfish represents the LDWF Fisheries Independent monitoring program Finfish dataset, which uses seine, gillnet and/or trammel gear. The oyster response curve was developed from personal communication (pc) with Scott Milroy at the University of Southern Mississippi.

Species	Salinity curve				Source
	LB	LT	RT	RB	
Adult bay anchovy	0	1	25	40	FIMP Shrimp
Juvenile blue crab	0	1	20	35	FIMP Shrimp
Adult blue crab	0	7	20	35	FIMP Shrimp
Juvenile Atlantic croaker	0	2.7	17.9	43	FIMP Shrimp
Adult Atlantic croaker	0	2	35	40	FIMP Shrimp
Juvenile brown shrimp	0	10	25	35	FIMP Shrimp
Adult brown shrimp	0	10	25	35	FIMP Shrimp
Juvenile Gulf menhaden	0	1	10	25	FIMP Shrimp
Adult Gulf menhaden	0	5	40	40.01	FIMP Shrimp
Juvenile red drum	0	5	20	25	FIMP Finfish
Adult red drum	0	1	15	40	FIMP Finfish
Juvenile spotted seatrout	0	5	20	30	FIMP Finfish
Adult spotted seatrout	0	7.5	20	30	FIMP Finfish
Juvenile white shrimp	0	5	25	35	FIMP Shrimp
Adult white shrimp	0	5	25	40	FIMP Shrimp
Sack oyster	5	10	15	40	S. Milroy, pc

species in the Ecospace model respond to environmental parameters and habitat features with group-specific response curves. Salinity and marsh edge response curves are applied to certain species, which change the effective search rate for these groups. For this modeling effort, salinity data were obtained at the same time that fisheries independent monitoring samples were collected, so species response curves were developed using LDWF FIMP data by calculating optimum (mean) and standard deviation between salinity and the number of species caught per sample. The salinity response curves in our model are applied to all species and age classes using a trapezoid function (Table 2). A species in the model will only respond to an environmental parameter or habitat parameter when a response curve is applied. To that end, not all groups respond to every parameter in the model. For example, the response curves for marsh edge are only applied to the juvenile species in the model as these age classes are thought to benefit from the use of the marsh–water interface in the estuary.

Currently, empirical data are lacking to develop marsh edge response curves for estuarine nekton. Attempts have been made by the authors to create such curves (Lewis, 2014), but the relationship between species and marsh edge was inconsequential at best, using LDWF survey data and the Couvillion et al. (2011) derived edge data. In a theoretical attempt to determine a response curves that could describe the relationship between edge and estuarine nekton, three potential relationships were tested in a series of scenarios. A fourth scenario was also considered in a “no edge response curve” simulation, which consisted of a model run with only salinity response curves applied in the model. The curves defined for this study are deemed linear (more edge is better), asymptotic (more edge is better, to an upper limit) and exponential (more edge is better at an exponential rate) responses (Fig. 8). Applying all four scenarios allowed for evaluation of various response curves for each species, while using the ‘no edge response’ scenario determined if the response curves actually improved the fit of the model.

2.5. Ecospace model development and Ecosim calibration

Prior to conducting the Ecospace scenario evaluations, an Ecospace with Ecosim model was developed. Details on model structure and governing master equations of EwE can be found in Appendix C and Christensen and Pauly (1992), Polovina (1984), Walters et al. (1997), Walters et al. (1999), and Walters et al. (2000). The

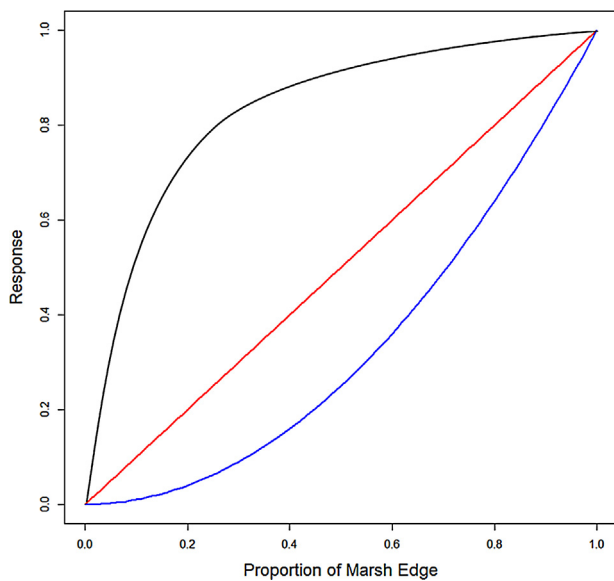


Fig. 8. Linear (red line), asymptotic (black line), and exponential (blue line) marsh edge response curves used in Ecospace model simulations. Values on the x -axis indicate the proportion of marsh edge values found in the marsh edge ASCII grid files. Values on the y -axis range from 0 to 1, where a value a 1 indicates the optimum conditions for that species. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Ecopath model represents the food web in Barataria Bay in the year 2000 using mean biomasses calculated from 1995 to 2000 fishery independent survey data (see Section 2.3; LDWF, 2002). Twenty-five functional groups (species or species guilds) that represent system and biomass dynamics, were defined (Appendix C). Major nekton groups were characterized with a juvenile as well as an adult life stage to better represent the ontogenetic changes through a species' life history (Christensen and Walters, 2004). The consumer groups considered in this study include zoobenthos, zooplankton, crustaceans, and fish. Values for zoobenthos (which includes the biomass of grass shrimp, *Palaemonetes* sp.) and zooplankton were obtained from the Breton Sound EwE model (De Mutsert et al., 2012) while biomass values for all fish and crustaceans were utilized from Barataria Bay specific LDWF fisheries independent data previously discussed. Biomass of producer groups (benthic algae, submerged aquatic vegetation (SAV), and phytoplankton) and detritus were obtained from the Breton Sound EwE model (De Mutsert et al., 2012) and field data collected by K. De Mutsert (SAV).

An important step in using and applying dynamic ecosystem models is to ensure they can reproduce historical patterns of abundance for further use in policy analysis and future predictions (Shannon et al., 2004). Currently, the Ecospace module lacks the ability to calibrate within the model, so for now, calibration occurs in Ecosim. The parameters that are tuned in Ecosim are then utilized by Ecospace during model simulations. A time series of salinity data was included as an environmental driver (in addition to the fishing effort data, mentioned above). The monthly time series data for salinity were obtained from models that supported the 2012 Louisiana Coastal Master Plan provided by CPRA. The salinity data were entered as monthly values over the 10 year period of the Ecosim model.

To calibrate the model, Ecosim was fit to annual relative biomass and landings data and forced with monthly mean salinity and monthly and annual fishing effort data. Calibration was carried out using the Fit-to-Time Series procedure in Ecosim. This procedure was used to find predator–prey interactions that were most sensitive to changes in the vulnerability parameter (v_{ij}) from the nekton

groups for which time series data were available. The model then estimates v_{ij} values that produce a better fit to the observed data. To assess the fit of the model, the sum of squared deviations (SS) of the observed logarithmic (log) biomass values was used (Christensen et al., 2005). Salinity forcing data were applied using procedures from De Mutsert et al. (2012). Detailed calibration procedures can be found in Appendix B.

The SS calculation used in the EwE Fit-to-Time-Series module is a statistical measure of the goodness of fit to currently loaded time series data generated each time Ecosim is initiated. In addition, we calculated the root mean square error (RMSE), a measure of modeled variation to observed variation (Legates and McCabe, 1999), to provide a goodness-of-fit that can be compared with similar ecosystem models. While there is not one value of RMSE that describes a superior model, RMSE is an effective approach to compare various model runs to each other. In general, the smaller the RMSE, the better the model fit to observed data.

2.6. Ecospace simulations

The advantage of moving from Ecosim to Ecospace using the spatial-temporal data framework is that organisms have the opportunity to ‘choose’ which cells to migrate to if conditions in their current cell are not optimal. Here, each edge response scenario was executed for the duration of the model run, 2000–2009, in the Ecospace model. The four scenarios were compared to observed data using RMSE model fit statistics, in addition to assessing the variance (by species and overall model performance). After determining the best fitting response curve for each species, a model run was invoked using the curves that were determined to be most effective at simulating historical trends in biomass (‘best-fit’ model).

3. Results

Marsh edge and marsh area both declined over the time period of the model simulations (Fig. 9). Loss of marsh is a variable process, as noted by the maximum value of edge of 2002. Reversing the x -axis in the marsh degradation curve simulates the temporal component of marsh loss through time.

A balanced Ecopath model for the year 2000 in Barataria Bay was achieved iteratively by first adjusting the diet matrix, as diet compositions represent only snapshots of the feeding habits of individual species and are likely to be relatively variable based on location and time periods of data collection. Other input parameters were also adjusted iteratively, and when a balanced model was achieved, parameters were cross-referenced with other published Ecopath models to ensure the plausibility of each value.

Ecosim calibration using the Fit-to-Time-Series (FTTS) module resulted in an improved fit to data when compared with model runs that did not incorporate the FTTS feature (Table 3). The calibrated Ecosim model adjusted the vulnerabilities in the model to effectively reduce the model SS. Any vulnerabilities that were >10 were iteratively reduced down to a value of 10, with the model fit (SS-calculated internally by Ecosim) being investigated at each step to ensure no large changes in fit occurred during the adjustment (Howell et al., 2013). The final model chosen to move into the Ecospace simulations was fit to the time series biomass data and driven by both salinity and fishing effort (Table 3, Model Run E). Model Run E best captured the observed trends for spotted seatrout (*Cynoscion nebulosus*), brown shrimp (*Farfantepenaeus aztecus*) and bay anchovy (*Anchoa mitchilli*) (Table 4). While the fit statistics for white shrimp (*Litopenaeus setiferus*) appear high compared with other species, the presence of a high observed biomass in year 10 can explain the increased variance from observed to predicted.

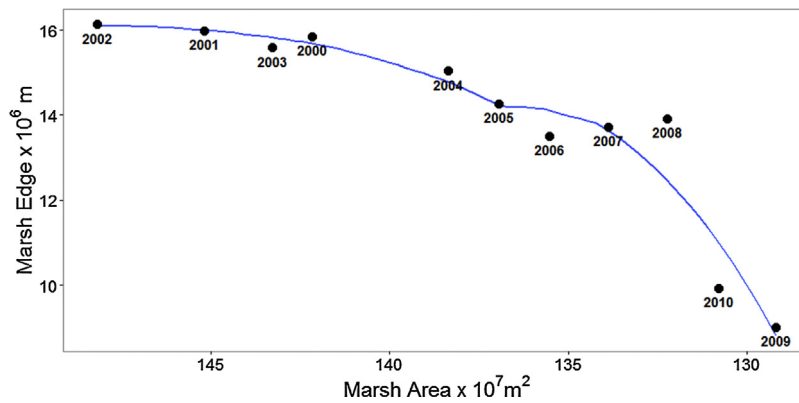


Fig. 9. LOWESS regression of marsh area and edge from Barataria Bay from 2000 to 2009 (blue line). The linear distance of marsh edge decreased over the 10 year model run period. Points indicate values of marsh edge and marsh area derived from Couvillion et al. (2011). (Note the reverse x-axis on the marsh area plots, representing the temporal component of marsh loss.) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3

Results of the Ecosim calibration procedures. The final, accepted model included use of the Fit-to-Time-Series (FTTS) in Ecosim.

Model run	Fitting procedure	Model SS	% Change
A	Time Series	27.15	
B	Effort	41.05	+51.20%
C	Salinity	29.27	+7.80%
D	Effort + Salinity	47.83	+76.17%
E	Effort + Salinity + FTTS	25.46	-6.22%

Table 4

Final calibrated model (Model run E from Table 3) fit statistics calculated from model predicted data and observed field data species for which time series were supplied in the model. Root mean square error (RMSE) and sum of squares (SS) are provided for the model calibrated to fishing effort and salinity data after using the Fit-to-Time-Series module.

Species	RMSE	SS
Spotted seatrout	1.34E-05	0.55
Red drum	4.52E-05	2.97
Black drum	5.00E-04	1.31
Atlantic croaker	3.00E-02	1.26
Blue crab	3.00E-02	3.91
White shrimp	8.00E-03	4.25
Brown shrimp	7.00E-03	0.72
Gulf menhaden	1.00E-03	2.20
Bay anchovy	3.00E-02	0.60
Total	0.1066	17.77

Using the chosen calibrated model in Ecosim, four scenarios of marsh edge response functions (including one scenario without an edge function) were initiated and then compared outside of Ecospace. The results indicated that the best performing model

scenario was the asymptotic curve when summing over all major species in the model (Table 5). However, at closer inspection, the asymptotic curve is not the best fitting edge response function for each species. The asymptotic curve fits best for spotted seatrout, red drum (*Sciaenops ocellatus*) and black drum (*Pogonias cromis*). The linear response curve fits best for blue crab (*Callinectes sapidus*), brown shrimp, and Gulf menhaden (*Brevoortia patronus*). For Atlantic croaker (*Micropogonias undulates*), white shrimp, and bay anchovy, the modeled scenarios indicated a best fit when no edge curve was applied. The exponential edge response curve did not provide a best fit for any species in the model.

Acknowledging that the same response curve applied to all species is most likely not a true depiction of nature, a ‘best-fit’ model was developed using the results of the four scenario runs. The results of this model run showed that model dynamics are quite complex, as the overall RMSE was not superior to the previous four scenarios. However, while the RMSE either stayed the same or in fact increased for some species, the overall and species specific variance decreased considerably (Table 5).

The new Ecospace spatial-temporal framework working in concert with the habitat capacity model, showed the ability of EwE to model species response to changing habitat and environmental variables over time. For instance, Fig. 10 shows example output from the asymptotic edge scenario. The upper panel in this diagram shows the proportion of marsh edge in the year 2009 in each cell, ranging from a value of 0 to a value of 0.038. The bottom panels are the monthly output produced by Ecospace, which displays the species biomass distributed over the model area. The Ecospace output maps clearly show the various juvenile species aggregating to areas where the proportion of marsh edge is greater, a direct result of the governing edge response curve applied in the model.

Table 5

The four Ecospace marsh edge response curve scenarios and the final “best-fit” model results. Values in bold indicate the best goodness of fit statistic (root mean square error, RMSE) all edge scenarios.

Species	Asymptotic		Exponential		Linear		No edge response		Best-fit model	
	RMSE	VAR	RMSE	VAR	RMSE	VAR	RMSE	VAR	RMSE	VAR
Spotted seatrout	0.28	0.007	0.29	0.005	0.3	0.004	0.307	0.009	0.294	0.008
Red drum	0.52	0.01	0.54	0.01	0.56	0.009	0.549	0.005	0.6	0.043
Black drum	0.63	0.09	0.64	0.18	0.65	0.24	1.04	0.19	0.79	0.05
Atlantic croaker	0.56	0.067	0.91	0.29	1.02	0.41	0.48	0.008	0.473	0.004
Blue crab	0.87	0.08	0.87	0.11	0.78	0.04	0.79	0.009	0.825	0.014
White shrimp	0.73	0.02	0.73	0.03	0.76	0.02	0.604	0.042	0.694	0.015
Brown shrimp	0.26	0.08	0.33	0.14	0.22	0.08	0.273	0.019	0.323	0.023
Gulf menhaden	0.41	0.003	0.42	0.005	0.39	0.01	0.466	0.005	0.514	0.047
Bay anchovy	0.25	0.003	0.24	0.002	0.24	0.003	0.234	0.002	0.232	0.001
Total	4.510	0.360	4.970	0.772	4.920	0.816	4.743	0.289	4.745	0.205

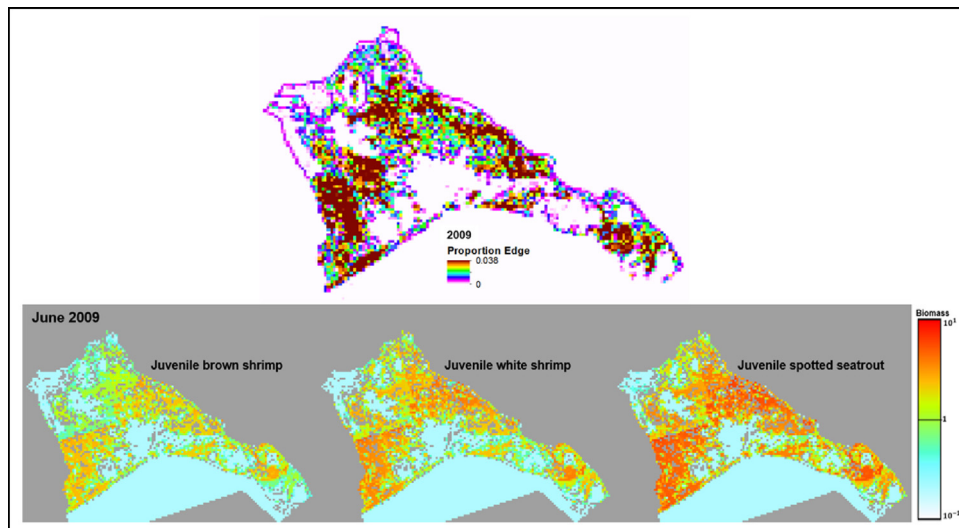


Fig. 10. Example output produced by Ecospace exhibited the ability of the modeled species to respond to changes in marsh edge and salinity using the spatial-temporal data framework and the habitat-capacity model.

Comparison of the observed versus model predicted relative biomass for the asymptotic, linear, ‘no-edge’, and ‘best-fit’ models shows slight variations in model fit depending on scenario (Figs. 11–14). Brown shrimp and spotted seatrout tend to exhibit the best fit to historical data, regardless of the scenario. Red drum, blue crab, Eastern oyster (*Crassostrea virginica*), Gulf menhaden and bay anchovy show little response to changes in the edge response function. It should be noted here that while the edge response function is not applied to oysters directly, their output is provided to evaluate if changes in predator–prey interactions from species that may consume oysters, impacts their overall density in model simulations (e.g. black drum).

4. Discussion and conclusion

In total, five different modeling scenarios were tested in this study in an attempt to empirically derive response curves for marsh edge and estuarine nekton. Comparisons of the overall model performance (Σ RMSE) indicated only small differences in the fit of each model. In other words, applying separate edge response functions, applying different combinations of edge response functions, or not applying any edge functions at all had little impact on the overall fit of the models (Table 5). In the fifth scenario, we constructed the ‘best-fit’ model using the top performing edge response curves for each species. By running the models as a series of scenarios, we allowed the model to inform our decision for inclusion of edge responses in the ‘best-fit’ simulation. While the total RMSE was not the lowest compared to the four previous scenarios, the total variance, was indeed the lowest, since the best fitting curves were applied to each species. RMSE is often more sensitive to other measures of model fit because the squaring process gives more weight to disproportionately large errors.

Looking at species-specific responses, in terms of life history strategies, it was not surprising to see that the asymptotic curve was selected for spotted seatrout, red drum and black drum. Since the response curves are applied to only the juvenile life stages in the model, it stands to reason that species who have little known dependence on vegetated estuary as adults, would reach a maximum amount of benefit from marsh habitat at some point. Considering previous studies on the relationship between marsh edge and decapod crustaceans, it was also not surprising to see model predicted biomasses for brown shrimp and blue crab perform best under the linear edge response function. Various studies

have pointed out that “more is better” when relating marsh edge to the production of these two species (Rozas et al., 2007; Minello and Rozas, 2002; Zimmerman et al., 2002). However, while applying edge response curves for species in the model improved six species-specific goodness-of-fit statistics (RMSE), the actual change when compared to the ‘no edge response curve’ scenario was trivial. For instance, under the linear scenario, blue crab and brown shrimp produced a RMSE of 0.78 and 0.22, respectively. But when these two species are compared with the RMSE under the ‘no edge response curve’ model run, the values are 0.79 and 0.27, respectively. So, in essence, the amount of marsh edge available does not appear to be accounting for a large portion of variation in the model.

One possible explanation for the lack of a strong relationship between edge and species’ biomass over time is that the amount of marsh edge in each cell, as a proportion of total area in each cell, is extremely low, less than 4% of the total cell area (Fig. 10). It could be that edge is not readily assessable in an approximately 1 km² area that any one fish or shellfish could be occupying.

However, we reason that the differences seen in this study when compared with previous studies are even more complicated. Organisms in estuarine systems respond to more than just the linear distance of marsh edge, which we acknowledge in this work by using an ecosystem model to incorporate trophic interactions, changes in environmental variables like salinity and anthropogenic impacts such as fishing pressure. In fact, the amenable fit of brown shrimp in this modeling effort appears to be largely driven by fishing effort, which was incorporated as monthly time steps in the model. So, while the loss of marsh area and edge is indeed catastrophic by most measures, and while previous studies have shown that in some estuaries, decapod crustaceans are found in higher densities near the edge, other environmental pressures are at work in the system and may have a stronger influence on population trends than changes in marsh habitat.

As seen in the survey data (Figs. 11–14; observed data represented as points), general observed trends in species relative biomass appear to be stable or even increasing from 2000 to 2009. So considering the fact that marsh edge and marsh area have both decreased over the 10 year period of the model run (Fig. 9), coupled with the fact that the modeled edge curves do not significantly improve model fits when incorporated in Ecospace, it stands to reason that estuarine nekton may not be as dependent on marsh edge

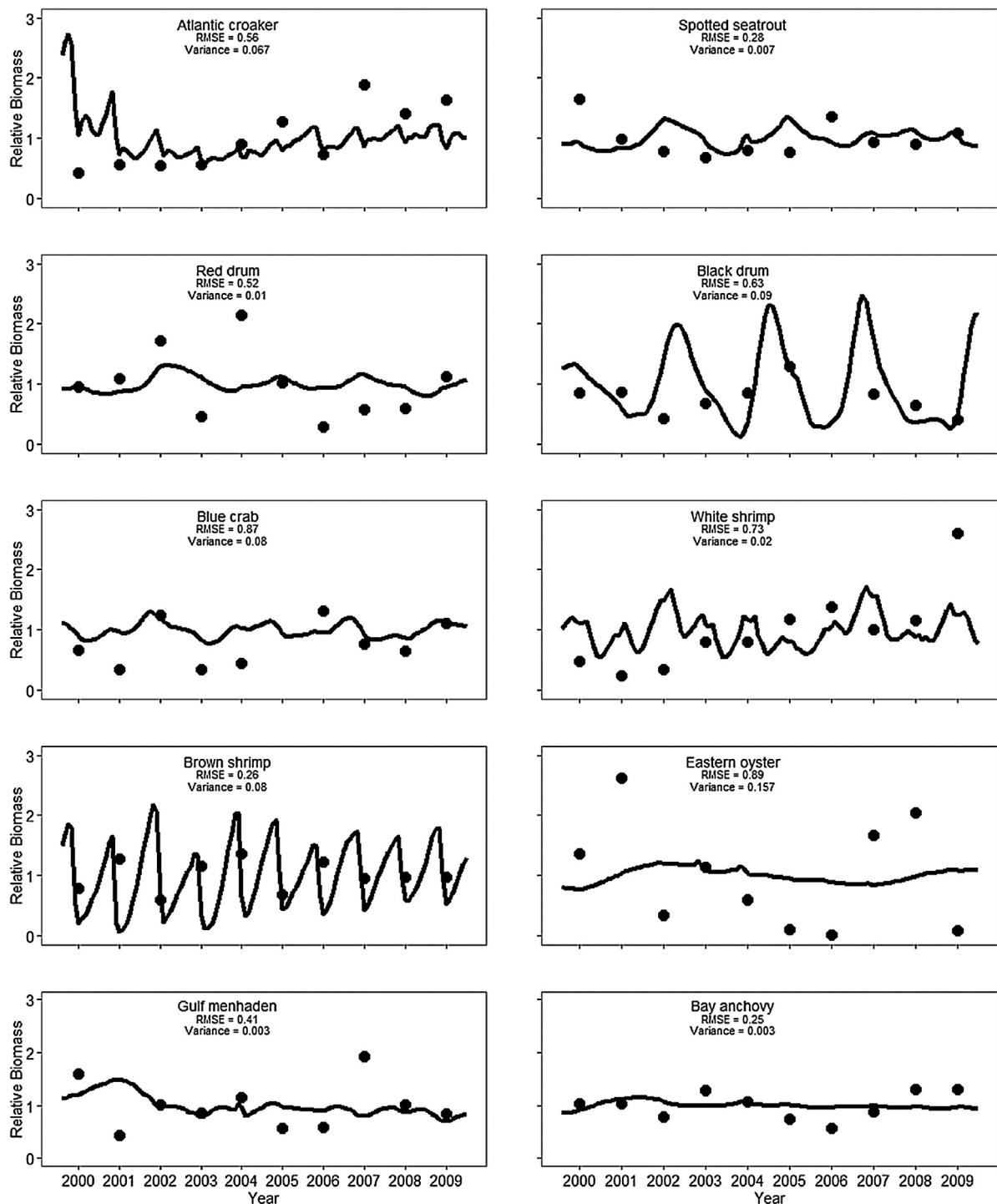


Fig. 11. Observed data versus Ecospace model predicted relative biomasses applying the asymptotic edge response function. Points indicate observed data derived from LDWF survey data and the solid line indicates Ecospace modeled biomasses aggregated over the entire model area.

as once thought. We contend that a possible explanation for the resilience seen in many estuarine species could be derived from their adaptations to dynamic deltaic ecosystems over thousands of years. Even though the delta cycle has effectively stopped in coastal LA, it is clear that habitat change has been and is still occurring, albeit at potentially higher rates because of the synergistic effects of multiple perturbations. Estuarine species may already be well adapted for a constantly changing ecosystem, and in this case, land loss may not affect nekton in this estuary as severely as once hypothesized. In addition, while previous studies have found

that densities of some species are indeed greater at the marsh edge interface, it would be difficult to determine what percentage of the population is actually utilizing the edge.

Evidence is emerging to support the notion that the dependence of some nekton species on the area of intertidal marsh or edge may be less important, at least in Barataria Bay, LA. Fry (2008) used shrimp density and stable isotope studies to show that open bays potentially support 50% of brown shrimp production in Barataria and Terrebonne Bays. If a large proportion of brown shrimp production can originate from open bays, Fry hypothesizes, the prediction

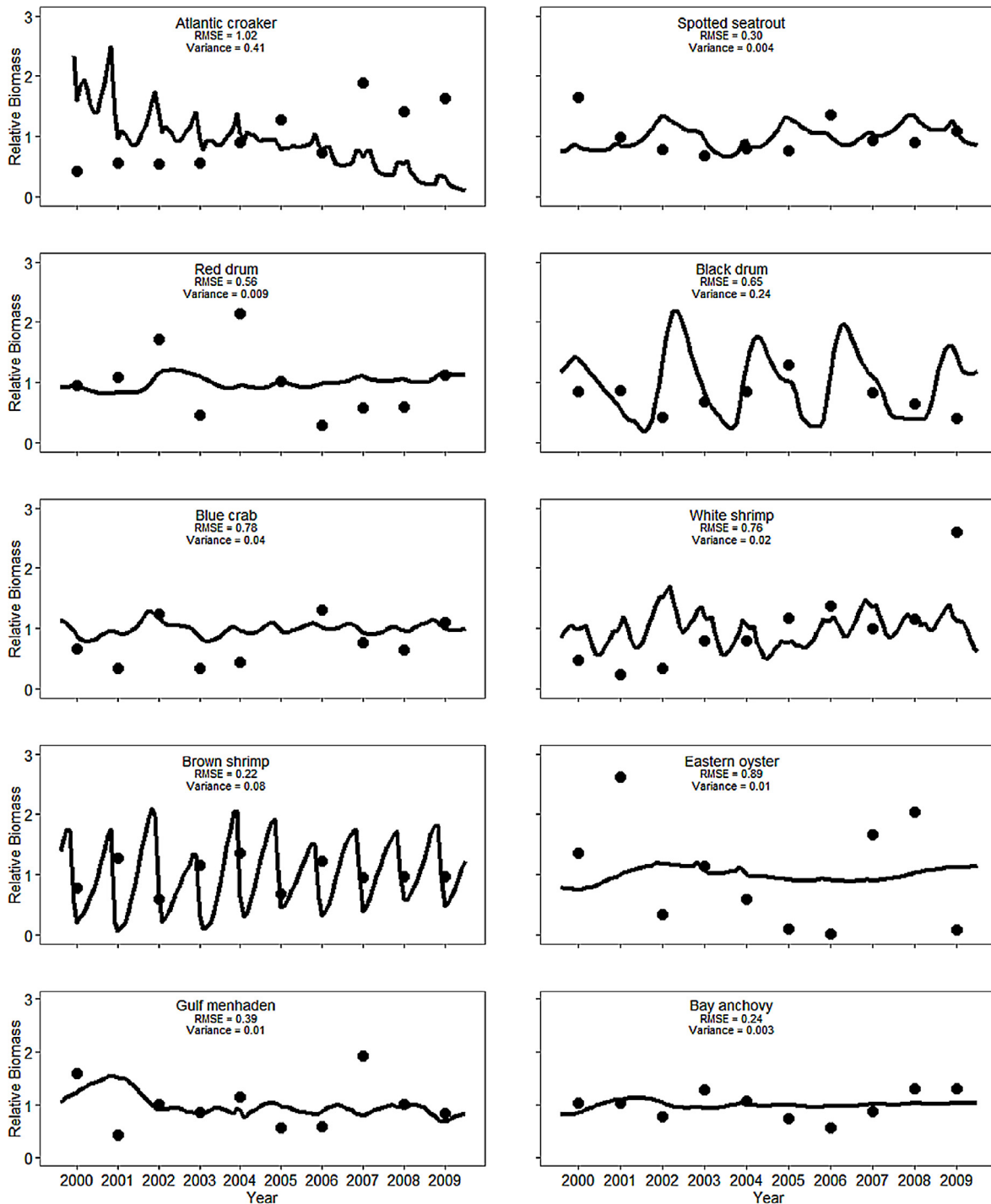


Fig. 12. Observed data versus Ecospace model predicted relative biomasses applying the linear edge response function. Points indicate observed data derived from LDWF survey data and the solid line indicates Ecospace modeled biomasses aggregated over the entire model area.

of a fisheries collapse with increased marsh loss may not be realized. Most recently, [Rozas and Minello \(2015\)](#) suggest that findings in their previous studies from Galveston Bay, Texas, noting that decapod crustaceans are found in higher densities nearer to the marsh interface, may not be applicable in Barataria Bay. Specifically, brown shrimp, blue crab and white shrimp were not found in higher densities near the marsh edge when those species were in the highest abundance in the estuary. Rozas and Minello put forth a number of explanations for this disparity, such as differences in marsh slope and flooding during between the two systems, in addition to a density dependent threshold near the marsh

edge that causes organisms to select for other habitats once that threshold has been exceeded. We suspect that the differences, to a larger extent, have more to do with the influence of the Mississippi River on Barataria Bay. With the combination of marsh loss and lack of fluvial input into upper reaches of Barataria Bay, long-shore currents flowing from east to west could be responsible for transporting nutrients and phytoplankton from the Mississippi River into the estuary, benefiting estuarine organisms and counteracting negative impacts of marsh loss. Another study suggests that resilience in fisheries production in coastal LA, could be a result of estuarine-like conditions on the shallow shelf during

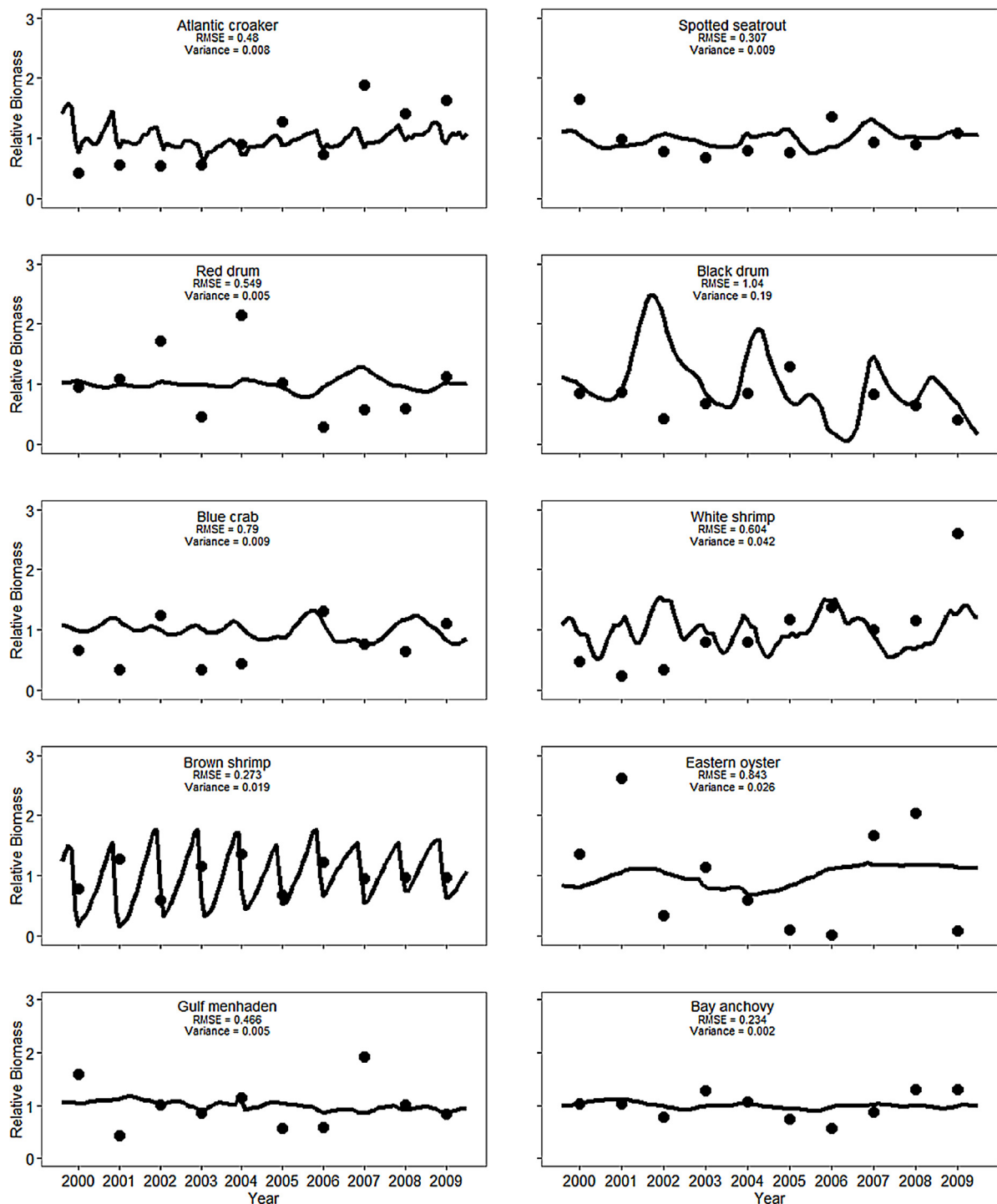


Fig. 13. Observed data versus Ecospace model predicted relative biomasses from the “no edge response function” scenario. Points indicate observed data derived from LDWF survey data and the solid line indicates Ecospace modeled biomasses aggregated over the entire model area.

periods of increased flow from the Mississippi River (Cowan et al., 2008). This hypothesis is corroborated by the fact that many of these species move off-shore at some point in their life history. Due to their close proximity to the river, therefore, LA estuaries could potentially exhibit a weaker nursery function signal because of the bottom-up influences generated by the transport of nutrients into the bays and onto the shallow-shelf where these organisms frequent. So, the question is not whether the nursery hypothesis is true, the question rather, is if the value of marsh vegetation to the production of estuarine nekton changes depending

on the regional hydrodynamic mechanisms influencing that system.

While results of this study indicate that edge may not be influencing estuarine nekton to the degree once hypothesized, a need still exists to examine this question further. As previously mentioned, organisms in estuarine systems respond to numerous environmental parameters, even more than the salinity, edge and fishing pressure introduced in this model. But in an effort to isolate the response of marsh edge, we chose to only include salinity as an environmental driver, as salinity regimes are well known in

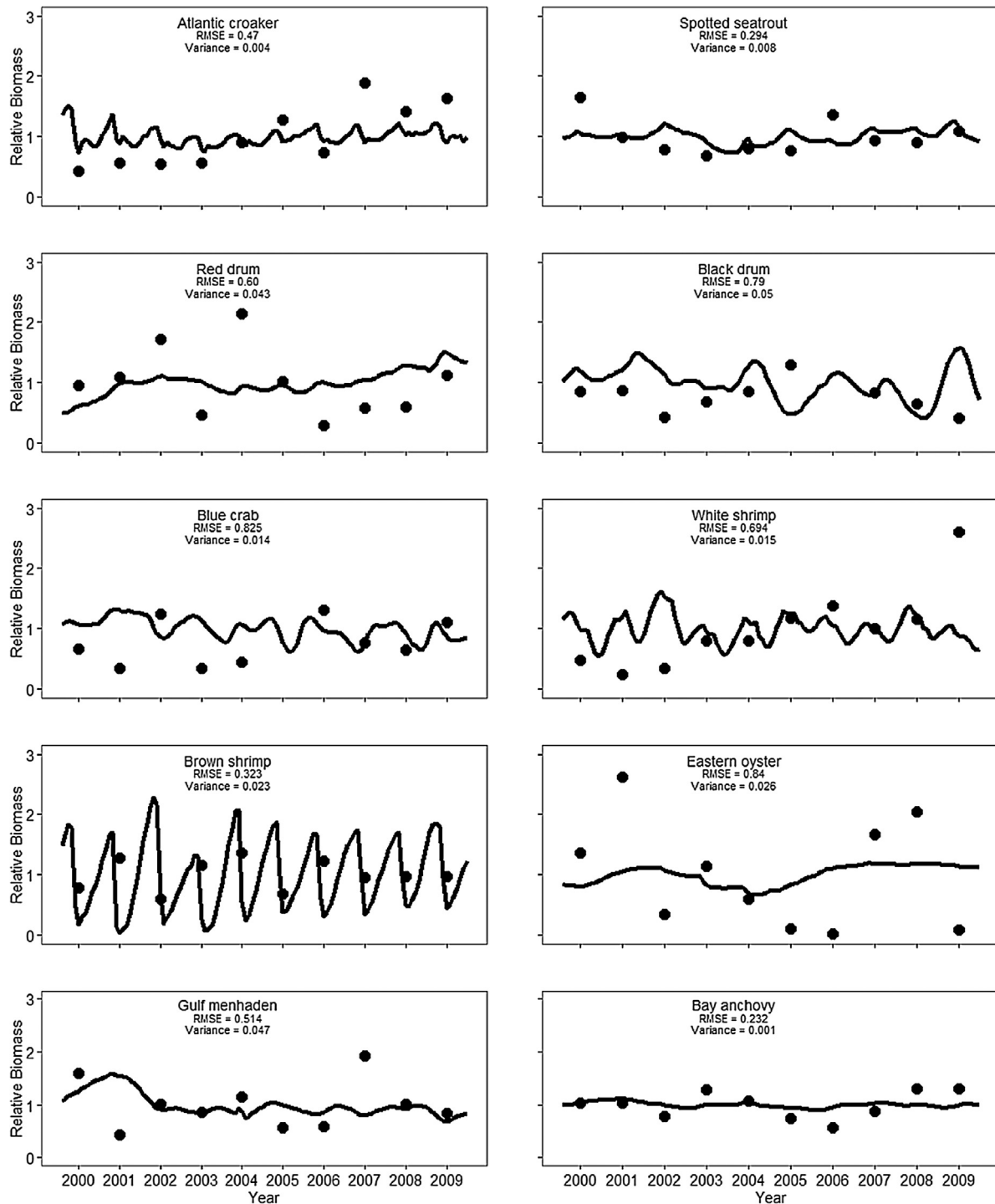


Fig. 14. Observed data versus Ecospace model predicted relative biomasses applying the best-fitting response functions for each species. If species performed better in previous scenarios without an edge response function, no function was applied in that case. Points indicate observed data derived from LDWF survey data and the solid line indicates Ecospace modeled biomasses aggregated over the entire model area.

estuarine systems to be a primary parameter in organismal distribution. In later iterations of this model, however, it will be important to investigate and include other drivers within the system, such as total suspended solids, temperature, and primary production. Furthermore, it will be critical to evaluate other basins within coastal LA to determine if the trends in Barataria Bay are unique. Caution must be taken when expanding these patterns to larger regional scales. It is well known that patterns of land loss and salinity differ widely from basin to basin within LA, so it will

be important moving forward to conduct these analyses in other areas to determine if the same relationships hold true. Considering the differences seen between Galveston Bay and Barataria Bay, a broader investigation is warranted.

This approach by no means represents all responses of organisms to the linear distance of marsh edge in the estuary, but it provided insight on how sensitive nekton were to this particular driver. Additional simulations are needed to test various other response curves. Estuarine system dynamics are complicated and

disentangling the mechanisms driving trends in nekton populations will continue to be a challenge. Continued advancements in ecosystem modeling, including coupling EwE models to hydrodynamic models, may help provide greater insight to these complex ecological interactions (De Mutsert et al., 2014).

Louisiana's wetland loss is of great concern for more reasons than fisheries production. Wetlands function to improve water quality, protect inland areas from storm surges and flooding, help to prevent shoreline erosion, in addition to providing habitat for numerous other forms of wildlife such as birds, mammals and amphibians. While the influence of marsh loss on fisheries may be less significant than once thought in Barataria Bay, the importance of protecting coastal wetlands remains vital to the health and prosperity to both the ecosystem and the people that utilize coastal marshes for both recreation and economic benefit.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2016.01.017>.

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