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Source: Journal of Shellfish Research, 35(4):841-849.
Published By: National Shellfisheries Association
DOI: http://dx.doi.org/10.2983/035.035.0412
URL: http://www.bioone.org/doi/full/10.2983/035.035.0412

Journal of Shellfish Research, Vol. 35, No. 4, 841–849, 2016.

OYSTER HABITAT SUITABILITY IN THE NORTHERN GULF OF MEXICO

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ABSTRACT Oysters provide a wide variety of ecosystem services including furnishing habitat, supporting an economic industry, and enhancing water quality. To identify suitable areas for oyster restoration and aquaculture, areas of oyster-suitable habitat must first be identified. A habitat suitability model is an ideal tool for identifying sites for species restoration. Because it relies on presence-only data, MaxEnt is a particularly useful habitat-suitability model for identifying restoration and species introduction sites. Habitat suitability models rely on the selection of environmental factors, which are assumed to be important for the target species; however, this selection of environmental factors is often arbitrary and there are few existing guidelines. This work applies an oyster habitat suitability model to the St. Louis Bay in the northern Gulf of Mexico. Six environmental factors, namely average salinity, maximum temperature, minimum temperature, water depth, minimum dissolved oxygen, and average total suspended solids were chosen to simulate habitat suitability. The environmental factors were obtained from a calibrated hydrodynamic and water quality model of the estuary. The habitat suitability model was run with every possible combination of environmental factors, including one, two, three, four, five, and six inputs. Model results showed that at this location, salinity is the most important environmental input. Furthermore, model results showed that increasing the number of inputs optimizes model results. There is a diminishing return on the addition of environmental factors and there is a point at which the continued addition of environmental factors will not continue to notably improve model optimization. The ranges of simulated suitable values for the environmental factors were contextualized within measured values. This study shows how a statistical model can be used to identify restoration locations. It is a particularly compelling methodology because (1) it does not require prior information regarding suitable ranges of environmental factors; (2) it does not require information regarding the level of importance for those environmental factors; (3) it requires presence-only data; (4) results are based on spatiotemporal data at a finer scale than is generally measured in the field; and (5) model results can provide an additional line of evidence that complements knowledge by biologists and oystermen.

KEY WORDS: environmental factors, MaxEnt, habitat suitability, *Crassostrea virginica*, salinity, model

INTRODUCTION

The species *Crassostrea virginica* (eastern oyster) is a foundational species in the northern Gulf of Mexico where it provides a number of important ecosystem services such as fish habitat, water filtration, shoreline and habitat stabilization, sedimentation, carbon sequestration, food security, economic industry, and cultural symbology (Grabowski & Peterson 2007, Grabowski et al. 2012, Volety et al. 2014). Oysters depend on a number of environmental factors including water depth, salinity, temperature, dissolved oxygen (DO), and total suspended solids (TSS). The eastern oysters *Crassostrea virginica* are subtidal and intertidal and can generally survive at depths between 0.6 and 8.0 m (NOAA 2007). The species grows normally in salinities between 12 and 27, grows more slowly between 7 and 12, and is stressed in salinities below 6 (Butler 1954, Cake 1983, Kennedy et al. 1996). Respiration and feeding may be disrupted at temperatures over 32°C and feeding can stop at temperatures below 6°C (Kennedy et al. 1996). Calcification can also be inhibited at temperatures below 20°C (Waldbusser et al. 2011). The species is fairly tolerant of low levels of DO (Kennedy et al. 1996). The eastern oyster *Crassostrea virginica* has been shown to survive up to 5 days in waters with less than 1.0 mg/l DO but prefer at least 20% saturation (Sparks et al. 1958, NOAA 2007). Oysters have been shown to decrease their filtration rate when TSS is lower than 5 mg/l and higher than 25 mg/l (Cerco & Noel 2005). This suite of environmental factors is important for defining the habitat suitability for *C. virginica*.

Habitat suitability models simulate where species are likely to occur based on existing species occurrence data and pertinent environmental factors. An important question in habitat suitability modeling is which environmental variables should be considered. There is not a consistent conclusion in the literature regarding the importance of using different sets of environmental variables in habitat suitability model. Parra et al. (2004) assessed the behavior of BIOCLIM, an ecological niche model, using individual environmental datasets and all possible combinations of the same datasets. They showed that the combination of datasets gave an insignificant improvement to the model results. Peterson and Nakazawa (2008) showed that the choice of environmental datasets can exert an important influence on the results of ecological niche models. Jiménez-Valverde et al. (2011) showed that habitat suitability models should only use environmental factors that are directly linked to a species' physiological requirements.

A number of habitat suitability models have been applied to oysters in a variety of locations. Soniat and Brody (1988) developed a habitat suitability model for *Crassostrea virginica* in Galveston Bay, Gulf of Mexico that investigated the following environmental factors: bottom substrate, summer and mean salinity, surveyed oyster abundance, and frequency of killing floods. Barnes et al. (2007) created a habitat suitability model for *C. virginica* in southwest Florida based on salinity, depth, substrate, and flow. Theuerkauf and Lipcius (2016) developed a habitat suitability model for *C. virginica* in the Great Wicomico River, Chesapeake Bay, based on bottom type,

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DOI: 10.2983/035.035.0412

salinity, and water depth. Starke et al. (2011) created a habitat suitability model for *C. virginica* in the Hudson River based on sedimentary environment, sediment type, depth, and salinity. Soniat et al. (2013) developed a habitat suitability model for *C. virginica* in the Lower Brenton Sound, LA, based on salinity, substrate, and percent land. There are several limitations to these models. They define suitable ranges of environmental factors based on literature values. They also weight each environmental factor either equally or based on expert opinion.

MaxEnt is a popular habitat suitability model that simulates probability distributions of species occurrence using the principle of maximum entropy and presence-only data (Phillips et al. 2004, Phillips et al. 2006, Phillips & Dudík 2008). The two types of model inputs required by MaxEnt are species occurrence data and environmental factors, both of which are spatially explicit. MaxEnt has been applied to a wide variety of ecological conditions (Kumar and Stohlgren 2009, Azaele et al. 2010, Jones et al. 2013, Pitchford et al. 2016). MaxEnt has also been shown to perform well when compared with other habitat suitability models (Loarie et al. 2008, Elith et al. 2010, Jones et al. 2013). Two characteristics of MaxEnt that make it appealing is that it statistically and automatically weights the importance of environmental factors and it automatically develops suitable ranges of environmental factors for a given species without prior information.

The MaxEnt habitat suitability model was specifically applied to the Pacific oyster (*Crassostrea gigas*) in the United Kingdom (Jones et al. 2013). Although the study of Jones et al. is very useful in understanding the environmental requirements for oyster habitat, it was based on data with course resolution. For example, the grid angle was 0.5° in latitude and longitude and environmental data were derived from downscaled climate models.

In this study, MaxEnt was used to simulate the spatial habitat suitability of *Crassostrea virginica* in the Bay St. Louis estuary, northern Gulf of Mexico. The factors investigated as controlling mechanisms of habitat suitability included water depth, salinity, minimum temperature, maximum temperature, DO, and TSS. A calibrated and validated hydrodynamic and water quality model of the estuary (Liu et al. 2008, Camacho & Martin 2013) was used to obtain the environmental inputs for MaxEnt. The objectives of this study were to determine (1) suitable habitat for oysters in the St. Louis Bay, northern Gulf of Mexico; (2) use model results to identify the important environmental factors for oysters in the same area; and (3) investigate how maps of habitat suitability vary depending on the modeled environmental factors.

MATERIALS AND METHODS

Study Site

The St. Louis Bay estuary study site (168 km^2) is located in the Mississippi Sound, which feeds into the Gulf of Mexico (Fig. 1). The estuary receives freshwater drainage from a number of watersheds comprising approximately 1,840 km^2. The Jordan River and Wolf River, whose combined watersheds encompass 1,333 km^2, are the two dominant subwatersheds. Average combined flows from the Jordan and Wolf rivers deliver 37 m^3/s of freshwater into the estuary. Drainage from an additional 507 km^2 comes from ungauged adjacent tidal wetlands and bayous. At mean low water, the average depth of the estuary is 1.4 m. Oyster reefs occupy 16.9 km^2 of the study site and include the Waveland, Waveland Clutch, St. Stanislaus, Henderson Pass, and Henderson Point reefs as well as portions of the Pass Marianne and Telegraph reefs (NOAA 2011).

Environmental Input Data

Habitat suitability environmental factor inputs that were investigated included water depth, average salinity, maximum temperature, minimum temperature, and minimum DO. There is correlation between several of these parameters, which may influence the results. The environmental factors were obtained from outputs of a linked hydrodynamic and water quality model (Liu et al. 2008, Camacho & Martin 2013). This linked model was based on the Environmental Fluid Dynamics Code (EFDC) and the Water Quality Analysis and Simulation Program (WASP).

Environmental Fluid Dynamics Code is a hydrodynamic model that resolves the equations of fluid motion and mass transport in three-dimensional aquatic systems. The model solves the vertically hydrostatic, free surface, and turbulent-averaged equations of motion for a variable-density fluid. Turbulence at the subgrid scale is simulated using a turbulence closure scheme, which dynamically couples transport equations for turbulent kinetic energy and turbulent length scale. Salinity, temperature, and dye are also simulated by the model. The EFDC model in St. Louis Bay simulated hydrodynamic conditions during the year 2011. The model grid was made up of 750 horizontal cells, each of which were divided into two equal vertical layers (Liu et al. 2008). Freshwater inputs into the EFDC model were derived from the Hydrological Simulation Program-Fortran watershed model. Surface elevation was calibrated to the National Oceanic and Atmospheric Administration (NOAA) 8,747,766 oceanographic gauge. Salinity and temperature were calibrated to records collected by the Mississippi Department of Environmental Quality (MDEQ) at 52 monitoring stations during the period March to November 2011 (Camacho et al. 2014). For the calibration period, measured water levels at the NOAA gauge ranged between approximately –0.3 and 0.7 m. Measured temperature ranged between approximately 20°C and 30°C. Measured salinity ranged between approximately 1 and 25 with higher values recorded outside the embayment area toward Mississippi Sound. The root mean square error for water level during the model calibration was 0.08 m and the correlation coefficient was 0.99.

Water Quality Analysis and Simulation Program is a water quality model that simulates eutrophication processes in aquatic systems including water column and benthos interactions. Water Quality Analysis and Simulation Program can simulate time varying advection, dispersion, mass loading, and boundary exchanges. The St. Louis Bay WASP model was calibrated against field collected measurements of organic and inorganic nitrogen and phosphorus, chlorophyll a, biological oxygen demand, DO, and TSS collected at 52 Mississippi Department of Environmental Quality stations over the year 2011 (Camacho et al. 2014). For the calibration period, measured DO ranged between 6 and 9 mg/l. Overall, the model performed well with most water quality parameters having small root mean square errors and absolute percentage

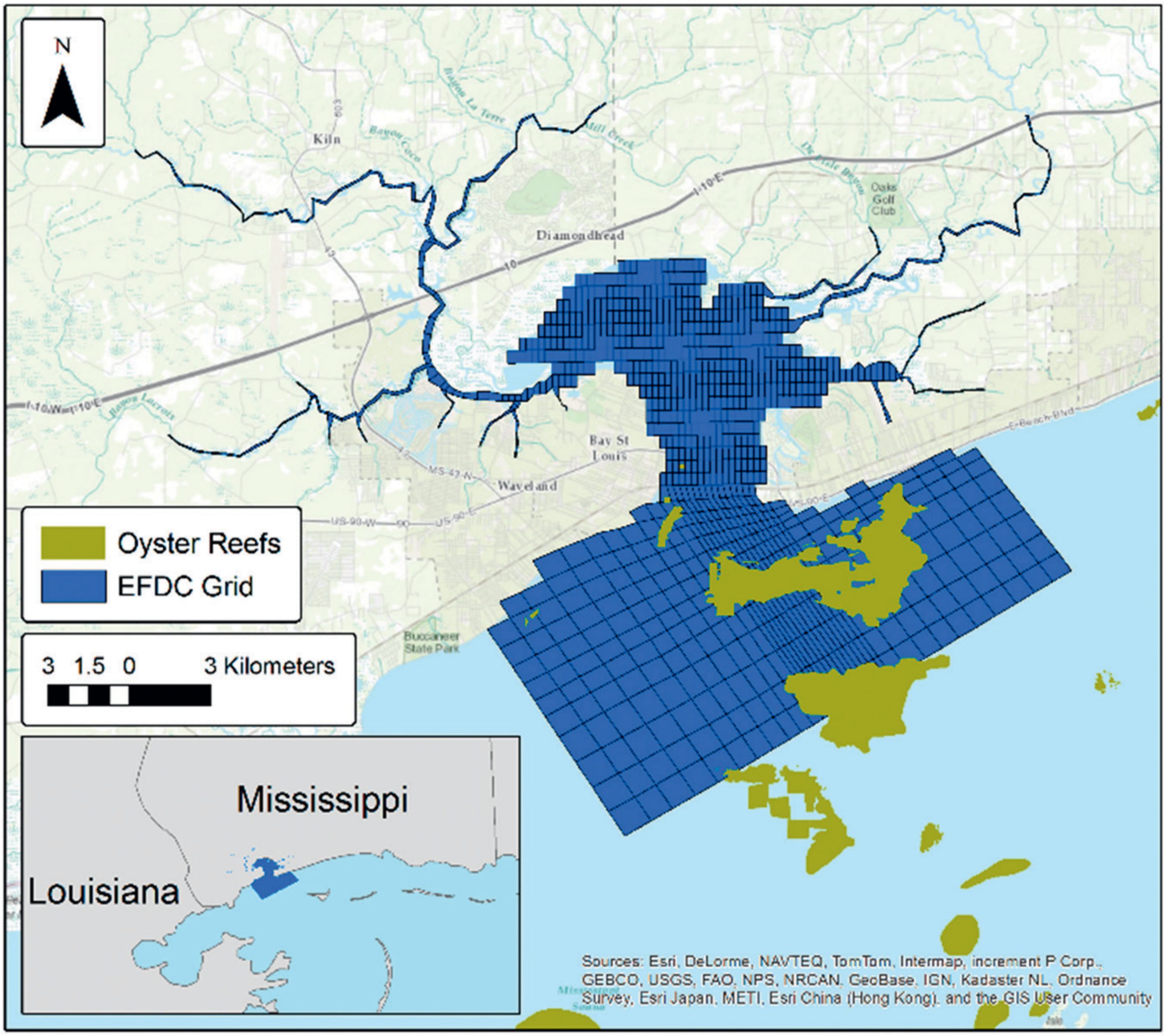

Figure 1. St. Louis Bay study site with oyster reefs and EFDC grid.

biases below 10%. Specifically for salinity, the average root mean square error was 2.3 and the absolute percent bias was 1.1%. For temperature, the average root mean square error was 2.5°C and the absolute percent bias was 6.5%. For DO, the average root mean square error was 1.4 mg/l and the absolute percent bias was 6.9%. For TSS, the average root mean square error was 13.4 mg/l and the absolute percent bias was 23%.

Environmental Fluid Dynamics Code and WASP model outputs including average salinity, maximum temperature, minimum temperature, minimum DO, and average TSS were converted to a uniform 30 × 30 m grid for inputs into the habitat suitability model (Fig. 2). A 30 × 30 m bathymetry dataset was based on the hydrodynamic input bathymetry. Although bathymetry datasets exist that have much better resolution, the use of the varying scales proved to be problematic and resulted in poorer model results. Oyster reef shapefiles (NOAA 2011) were converted to point data as per the requirements of MaxEnt for species occurrence data. A species occurrence point was assigned to each EFDC/WASP model cell whose area was more than 50% oyster habitat. Water depth within the study site ranged between 0.1 and 6.9 m. Average modeled salinity ranged between 0.0 and 20.0 mg/l. Minimum modeled temperature ranged between 1.0°C and 11.6°C. Maximum modeled temperature ranged between 30.4°C and 37.4°C. Minimum modeled DO ranged between 0.0 and 5.2 mg/l.

Habitat Suitability Model

An oyster habitat suitability model was developed using MaxEnt (Phillips et al. 2004, 2006). Results from MaxEnt give land cover suitability maps for a given study site. A total of 64 model simulations were run ranging from the use of one, two, three, four, five, and six environmental factors. The six-factor simulation used every available environmental factors and will be referred to as the "combined" run.

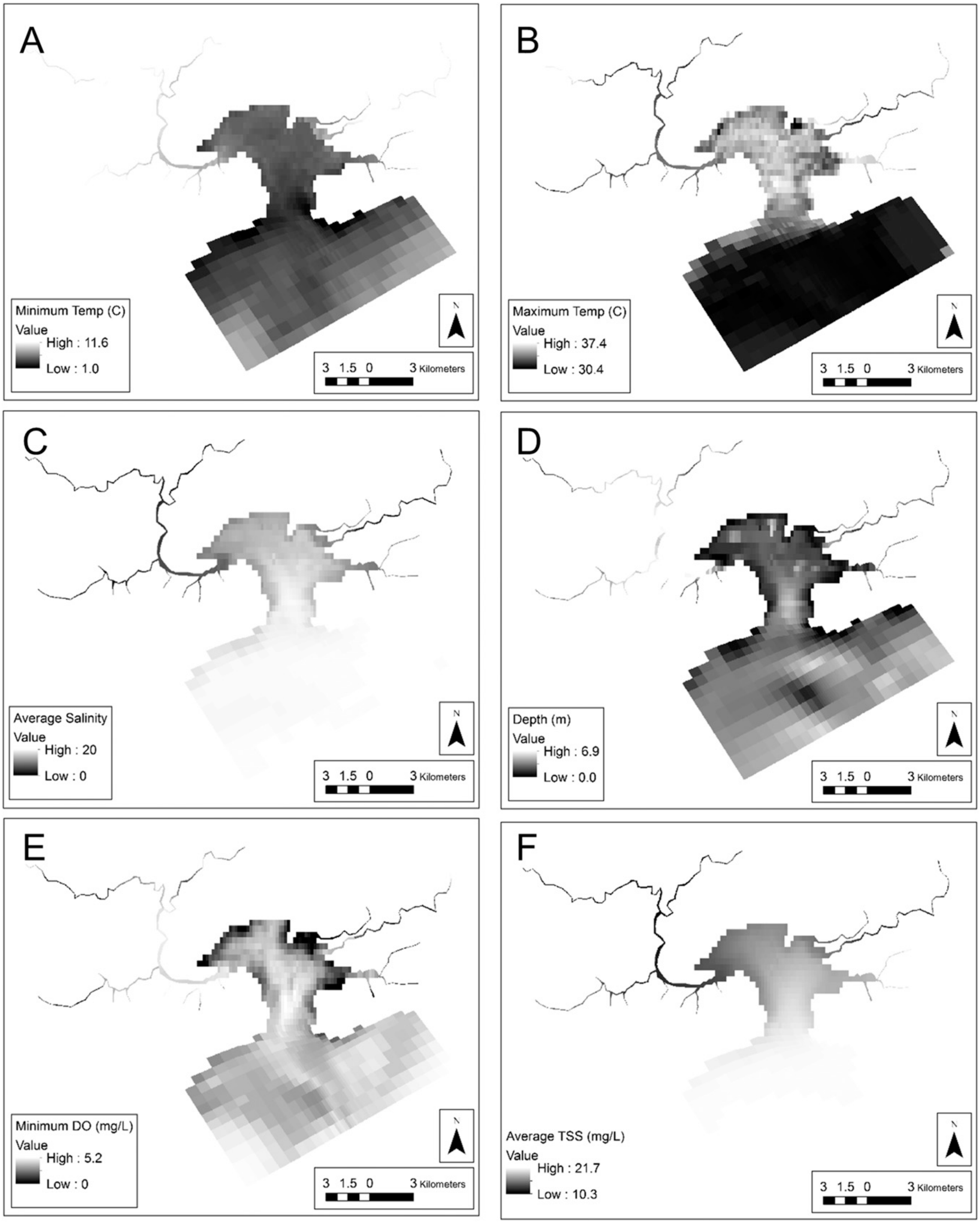

Figure 2. Environmental factors including (A) minimum temperature, (B) maximum temperature, (C) average salinity, (D) water depth, (E) minimum DO, and (F) average TSS.

The model was assessed using the receiver operating curve (ROC) statistic (Zweig & Campbell 1993). The ROC plots the rate of true positives (sensitivity) against false positives (one specificity). The area under the curve (AUC) for ROC provides a single statistic for interpreting the ROC and represents how well the model fits that data. A value of 1.0 for the AUC ROC indicates perfect model performance, 0.5 indicates that the model performs as well as a random variable, and 0.0 indicates a perfectly inverse model performance. The AUC ROC is correlated to the number of species occurrence points and also the size of the study area. Localized species occurrence data or a small study area will return a high AUC ROC (Phillips 2005, Allouche et al. 2006). The study site shows that the oyster reefs are indeed localized and so a high AUC ROC is expected.

The ROC plots true positives versus false positives and is an indication of model optimization; however, when multiple models are run, the AUC ROC statistic does not give any information regarding the spatial variance between simulations. It is very possible that two simulations give reasonable AUC ROCs, but map habitat suitability outside of the occurrence data in very different ways. This is especially problematic in this case study because the localized nature of the occurrence data will return artificially high AUR ROCs. As such, the combined run was used as a reference run and a basis by which all of the runs can be compared for spatial variance. We calculated the coefficient of determination (R^2) between the combined run and each of the other 63 runs for the simulated habitat suitability value in each grid cell. We will refer to this statistic as the "spatial variance statistic." A value of 1 for the spatial variance statistic indicates an exact match between two habitat suitability maps. A value of 0 for the spatial variance statistic indicates a purely random relationship between two habitat suitability maps.

RESULTS

Model results include simulations based on every possible combination of the six environmental factors including minimum temperature, maximum temperature, minimum DO, water depth, average salinity, and average TSS. The results of the AUC ROC ranged between 0.71 and 0.94. The lowest AUC ROC was for the single factor minimum temperature simulation and the highest was for the combined simulation.

In the combined model run, average salinity was the most important environmental factor contributing 67% to the model predictions. The second and third most important factors were depth, which contributed 16%, and minimum DO, which contributed 10%. Total suspended solids contributed 5%, minimum temperature 1.2%, and maximum temperature only 0.2%.

Although it is not feasible to graphically present the spatial maps of the 64 runs, Figure 3 does show the mapped results from the single-model runs and the combined run. These figures show that the spatial model results varied depending on the choice of environmental factors. For example, the results from the single environmental factor model runs for minimum temperature, minimum DO, and water depth simulations show extensive areas of suitable habitat within the bay (Fig. 3A, D, E); however, the results from the maximum temperature, average salinity, and average TSS single environmental factor simulations show suitable habitat only being located outside of the bay (Fig. 3B, C, F). The results from the combined-run show suitable habitat largely confined to the existing areas of habitat (Fig. 3G).

The spatial variance statistic, applied between the combined simulation and the remaining 63 simulations, ranged from 0.08 to 0.99. The lowest spatial variance statistic, and therefore the most different map compared with the combined run, was for the single minimum temperature simulation. The highest spatial variance statistic, and therefore the most similar map compared with the combined run, was for the simulation that contained five environmental factors including average salinity, average TSS, maximum temperature, depth, and minimum DO. This same simulation produced the second highest AUC ROC behind the combined run.

A plot of the AUC ROC versus the spatial variance statistic shows a logarithmic relationship ($R^2 = 0.93$, Fig. 4). Figure 4 shows that adding environmental factors optimizes the model results and also decreases the spatial variance. Specifically, the minimum AUC ROC was investigated for model runs involving a sweet of one to six variables. This analysis showed that the minimum AUC ROC increased from 0.71 to 0.81, to 0.85, to 0.88, to 0.91, and to 0.93 when the number of environmental inputs was increased from 1 to 2, to 3, to 4, to 5, and to 6 variables, respectively. Furthermore, the minimum spatial variance statistic increased from 0.08 to 0.33, to 0.42, to 0.61, and to 0.77 by increasing the environmental inputs from one to five. Because the combined simulation was used as the reference point, the spatial variance statistic cannot be considered for this simulation. The relationship is subject to the law of diminishing returns and there is some point at which continuing to include more environmental inputs will not yield better results.

Plots of probability presence versus environmental factor for the combined model show the ranges of suitable habitat for the oysters at the study site (Fig. 5). Here, the probability of presence for maximum temperature shows that cooler maximum temperatures are more suitable habitat at this site. The probability of presence for salinity shows that higher salinities are more suitable habitat at this site. The probability of presence for water depth shows that deeper water is more suitable habitat at this site. The probability of presence for minimum DO indicates that higher levels of DO are more suitable habitat at this site. The same graph indicates that the probability of presence goes down at the highest levels of DO. This is because the areas with the highest DO occur inside the bay and in the tributaries where salinities are lower. The probability of presence for average TSS indicates that levels of TSS below 22 mg/l are more suitable habitat at this site. The probability of presence for minimum temperature shows a slightly higher preference for cooler temperatures. This is a function of the correlation between minimum temperature and other environmental factors such as depth, salinity, maximum temperature, and DO. Minimum temperature only contributes 1.2% to the combined model results, and is not an important factor at this site.

The results from the ranges in suitable environmental factors for oyster habitat can be contextualized within the study site and also within literature values for acceptable ranges (Fig. 6). These results show that oysters in St. Louis Bay are constrained by the maximum depth in the area. The modeled maximum depth is equal to the maximum depth at

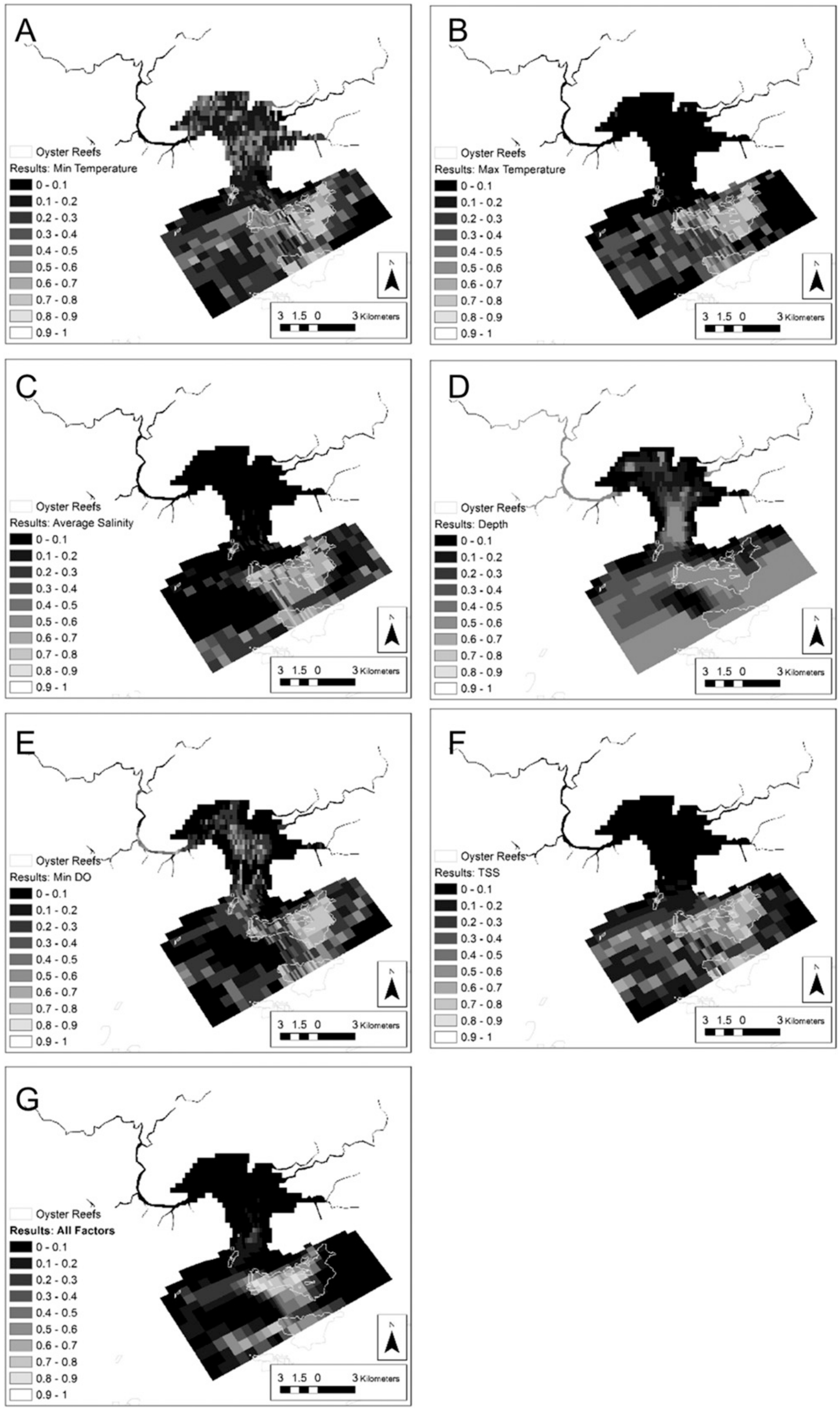

Figure 3. A selection of the habitat suitability model results from the (A) minimum temperature, (B) maximum temperature, (C) average salinity, (D) water depth, (E) minimum DO, (F) TSS, and (G) all of the environmental factors combined. The shaded scale indicates the Maxent habitat suitability score with 1.0 being very good habitat and 0 being very poor habitat.

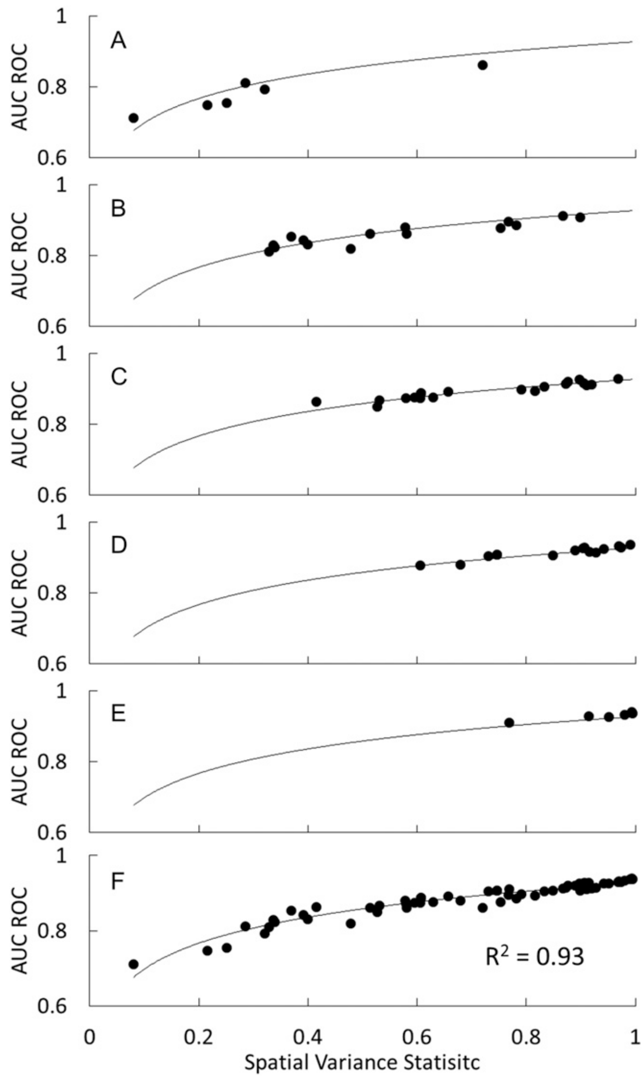

Figure 4. The AUC ROC versus the spatial variance statistic for model runs with (A) one environmental factor, (B) two environmental factors, (C) three environmental factors, (D) four environmental factors, (E) five environmental factors, and (F) all of the 64 model runs with all combinations of environmental factors.

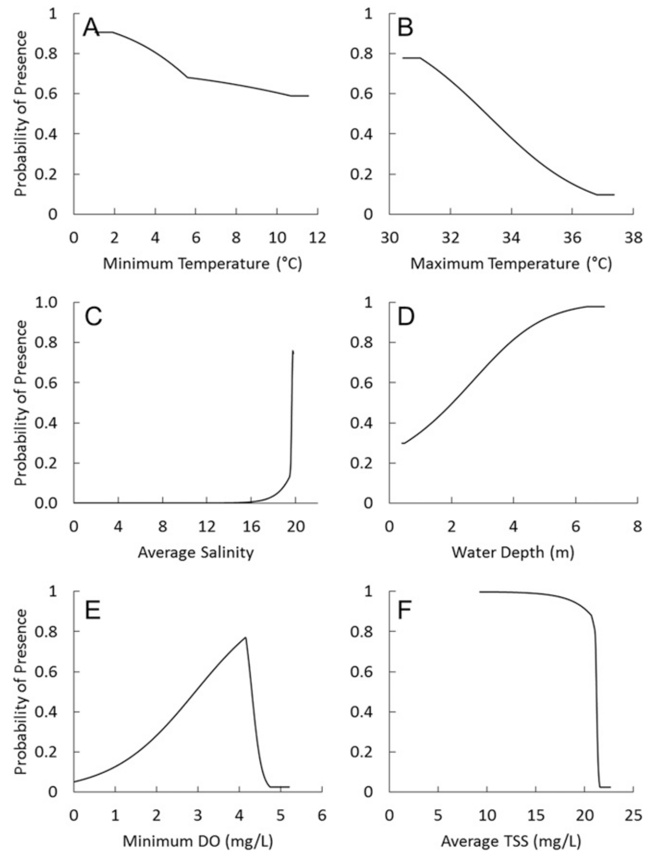

Figure 5. Probability of occurrence versus environmental factor range for the combined model: (A) minimum temperature, (B) maximum temperature, (C) average salinity, (D) water depth, (E) minimum DO, and (F) average TSS.

the site, which is 0.9 m lower than the literature values for suitable water depth for oyster habitat. The modeled minimum depth for suitable oyster habitat is 1.1 m higher than what is citied in the literature. Similarly, oysters in St. Louis Bay are constrained by the maximum salinity in the area and furthermore, the range of modeled suitable sanity is quite narrow. The modeled maximum salinity is equal to the maximum salinity at the site, which is 6, lower than the literature values for suitable salinity for oyster habitat. The modeled minimum salinity for suitable oyster habitat is 6.3 higher than what is citied in the literature. Suitable habitat for oysters is not limited by maximum or minimum temperature in the study area and the suitable modeled temperature range actually exceeds the literature range. The minimum suitable DO is 2 mg/l higher in the habitat suitability model compared with the literature. Oysters in St. Louis Bay are not constrained by TSS in the study site.

DISCUSSION

Average salinity, depth, and minimum DO were the most important environmental factors in the model. TSS and maximum temperature were not as important. The importance of minimum temperature was negligible. The importance of these environmental factors is likely dependent on the ranges in the factors at the study site. For example, a site that included deeper waters that were not within the biological ranges for oysters would likely show depth as a more important factor.

Salinity and temperature have been suggested to be the most important environmental factors for oyster habitat suitability (Kennedy et al. 1996). A synergistic impact of the combination of multiple environmental factors has also been cited as driving habitat suitability (Kennedy et al. 1996). Our results do confirm the importance of salinity in defining oyster habitat suitability; however, these results do not show oyster habitat as being critically influenced by temperature at this particular study site, with maximum and minimum temperature being the two least important environmental factors. This lack of importance may simply reflect the fact that the range of temperature in St. Louis Bay is not a limiting factor for oyster biology; however, the ranges of modeled maximum and minimum temperatures at the study site are somewhat wider than the ranges cited in the literature. Further studies need to be conducted to assess the range of suitable temperatures for oyster habitat suitability. The

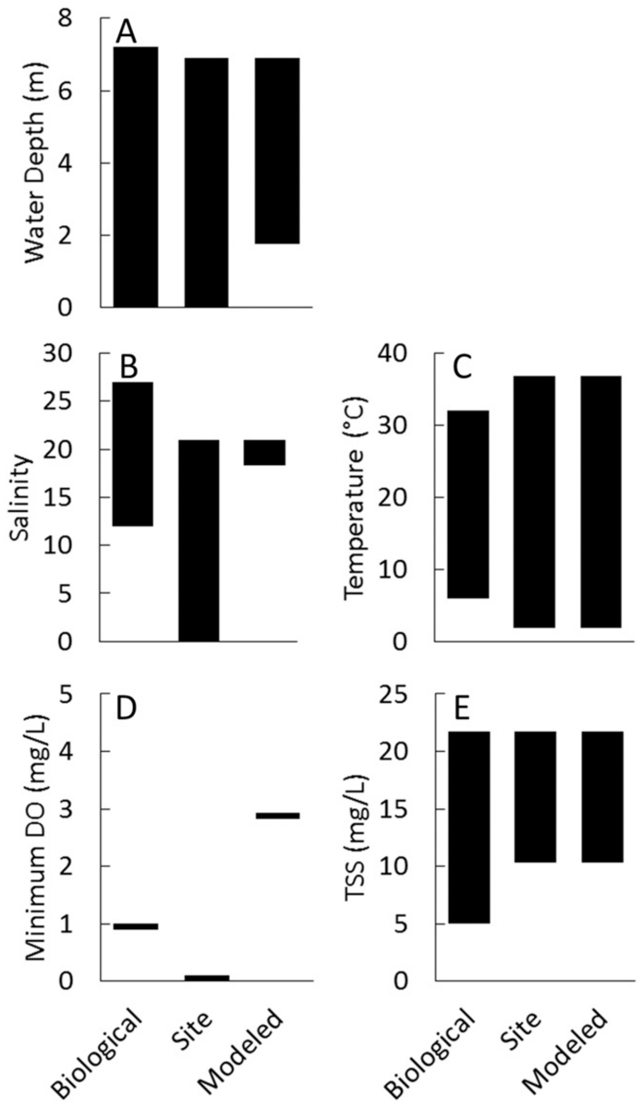

Figure 6. Values for environmental factors. The *X* axis shows values that are (A) suitable for oyster biology based on the literature, (B) within the St. Louis Bay study site, and (C) derived from the habitat suitability model-based results on a probability of presence greater than 50% from Figure 4. Note that water depth, salinity, temperature, and TSS refer to ranges, whereas DO refers only to a minimum level. Literature values from Butler 1954, Gunter and Geyer 1955, Sparks et al. 1958, Henryk 1971, Cake 1983, Cerco and Noel 2005, NOAA 2007, and Waldbusser et al. 2011 as described in the introduction.

study also shows how multiple environmental factors drive habitat suitability. This can be seen in the trend of increasing values for the AUC ROC and the spatial variance statistic with an increase in environmental factors.

Model results showed that simulations that investigated salinity and multiple environmental factors achieved the best AUC ROC and spatial variance statistic. This shows that it is critical that habitat suitability models investigate as many relevant environmental factors as is feasible. The importance of each environmental factor may not be known when the model is being set up. As such, to err on the side of caution, habitat suitability models such as MaxEnt, which automatically weight environmental factors, should investigate as many environmental factors that the modeler thinks may be important. The results also show a diminishing return on the number of environmental inputs, whereby the more the inputs are added the smaller the increase in model optimization and spatial similarity.

The results show that comparing suitable environmental factor ranges between the modeled results and the literature values is useful. Where ranges overlap, the model provides support of the literature values (e.g., maximum TSS). Where ranges vary, more monitoring will be useful to better understanding the suitable range for a given environmental factor (e.g., minimum salinity). In this way, statistical models can be combined with monitoring data to provide independent, converging lines of evidence for habitat preference.

An important limitation in this study is the size of the Bay St. Louis study area. Oysters are influenced by freshwater inputs and larvae transportation both of which may have sources that exist outside of the Bay St. Louis study area. For example, openings of the Bonnet Carre Spillway, which is a water diversion designed to protect New Orleans from flooding, has been shown to have a negative impact on oysters in the western Mississippi Sound because of changes in salinity (DeHaan et al. 2012). One such opening of the Bonnet Carre Spillway in 2011 was estimated to cause more than 85% mortality in Mississippi oysters and resulted in $60 million in losses through the oyster industry (DeHaan et al. 2012). In other cases, it has been shown that low salinity pulses can benefit oysters through decrease protist infection (La Peyre et al. 2009). Oysters also tend to colonize areas other than their home reefs and thus rely on external sources of larvae that are delivered by currents. For example, one study found that 96% of the larvae did not colonize the reef from which they were released (North et al. 2008). Future work may involve the development of a larger scale hydrodynamic model that would be able to simulate larvae transport. This would enable the identification of where suitable habitat intersects larvae trajectories and how freshwater diversions impact survivability.

In spite of the limitations, this study adds value to the practice of identifying restoration locations for several reasons. The method does not require prior information regarding suitable ranges of environmental factors nor does it require information regarding the level of importance for those environmental factors. The method also requires presence-only data and absence data are not needed. The results are based on spatiotemporal data at a finer scale than is generally measured in the field. Modeling is done without the necessity of field work, which may save time and money. And finally, the method provides an additional line of evidence that complements knowledge by biologists and oystermen. This method and these benefits can be applied to many species and restoration projects beyond that of *Crassostrea virginica*.

ACKNOWLEDGMENTS

This publication is a contribution of the Mississippi Agricultural and Forestry Experiment Station. This material is also based on work that is supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, Hatch project under accession number MIS-033160. This research was also funded by NOAA project "Expanding the Integrated Ecosystem Assessment in the Northern Gulf of Mexico," awarded through the Northern Gulf Institute (award number NA110AR4320199).

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