A Restoration Suitability Index Model for the Eastern Oyster (Crassostrea virginica) in the Mission-Aransas Estuary, TX, USA

Jennifer Beseres Pollack¹, Andrew Cleveland², Terence A. Palmer², Anthony S. Reisinger²,³, Paul A. Montagna²

¹ Department of Life Sciences, Texas A&M University-Corpus Christi, Corpus Christi, Texas, United States of America, ² Harte Research Institute for Gulf of Mexico Studies, Texas A&M University-Corpus Christi, Corpus Christi, Texas, United States of America, ³ Department of Physical and Environmental Sciences, Texas A&M University-Corpus Christi, Corpus Christi, Texas, United States of America

Abstract

Oyster reefs are one of the most threatened marine habitats on earth, with habitat loss resulting from water quality degradation, coastal development, destructive fishing practices, overfishing, and storm impacts. For successful and sustainable oyster reef restoration efforts, it is necessary to choose sites that support long-term growth and survival of oysters. Selection of suitable sites is critically important as it can greatly influence mortality factors and may largely determine the ultimate success of the restoration project. The application of Geographic Information Systems (GIS) provides an effective methodology for identifying suitable sites for oyster reef restoration and removes much of the uncertainty involved in the sometimes trial and error selection process. This approach also provides an objective and quantitative tool for planning future oyster reef restoration efforts. The aim of this study was to develop a restoration suitability index model and reef quality index model to characterize locations based on their potential for successful reef restoration within the Mission-Aransas Estuary, Texas, USA. The restoration suitability index model focuses on salinity, temperature, turbidity, dissolved oxygen, and depth, while the reef quality index model focuses on abundance of live oysters, dead shell, and spat. Size-specific Perkinus marinus infection levels were mapped to illustrate general disease trends. This application was effective in identifying suitable sites for oyster reef restoration, is flexible in its use, and provides a mechanism for considering alternative approaches. The end product is a practical decision-support tool that can be used by coastal resource managers to improve oyster restoration efforts.

Introduction

Oyster reefs are one of the most threatened marine habitats on earth, with an estimated 15% remaining worldwide [1]. Within the Gulf of Mexico, an estimated 50 to 80 percent of native oyster populations have been lost relative to historic levels [2]. Declines in the abundance of oysters are a consequence of habitat loss due to historical shell dredging [3], water quality degradation [4], disease [5], oil spill effects [6], and hurricanes [7]. In Galveston Bay, Texas, approximately 50%, or 32 km² (8,000 acres) of oysters were lost as a result of Hurricane Ike in 2008 [8]. The resulting sediment deposition smothered live oysters, submerged available hard substrate, and inhibited larval oyster settlement and natural recovery processes. In Louisiana, an estimated 50% of oysters were lost after the Deepwater Horizon oil spill in response to freshwater releases that decreased salinity below oyster tolerance levels [9]. Despite recent and historical losses, there is hope that restoration efforts and adaptive management approaches can revitalize oyster populations in the Gulf of Mexico [10].

For successful and sustainable oyster reef restoration efforts, it is necessary to choose sites that support long-term growth and survival of oysters [11,12]. Selection of suitable sites is an important first step in the restoration process as it can greatly influence mortality factors and may largely determine the ultimate success of the restoration project. Habitat suitability indices are a common tool used by natural resource managers for habitat mapping, conservation and restoration planning [13,14,15]. The Gulf of Mexico coast is ideally suited to developing a standardized site selection framework because areas of relatively abundant oyster populations still exist (Fig. 1). In addition, a substantial long-term database is available from the Texas Parks and Wildlife Department’s (TPWD) Resource Monitoring Program that describes oyster characteristics and hydrological parameters.
The aim of this study was to develop a restoration suitability index model and reef quality index model to characterize locations based on their potential for successful reef restoration within the Mission-Aransas Estuary, Texas, USA, using a Geographic Information System (GIS)-based approach. GIS is an effective tool that can be used in identifying suitable sites for oyster reef restoration and removes much of the uncertainty involved in the somewhat trial and error selection process that currently exists. The rationale for this study is similar to that used in previous oyster habitat/restoration suitability studies [16,17,18], where areas are selected based on the highest potential for successful recruitment, growth, and persistence of oyster populations. Long-term data on oyster populations and environmental variables were integrated within a GIS to characterize locations based on their potential for successful restoration programs.

Methods

Study site

The Mission-Aransas Estuary is a shallow, bar built estuary located in the coastal bend region of the Texas Gulf coast (Fig. 2). The estuary is approximately 540 km² with an average depth of 2 m [19]. The two largest bays in the system are Aransas Bay, which is located closest to the Gulf inlets of Aransas Pass and the intermittently open Cedar Bayou, and Copano Bay, which is located closest to the Mission and Aransas Rivers. The estuary experiences a typical salinity gradient from the river mouths to the Gulf of Mexico, which is driven by episodic freshwater pulses [20]. Oysters occur primarily on large subtidal reefs in the low- to moderate-salinity regions of the estuary, with vertical relief ranging from ~0.3 to 1.5 m.

Field surveys

Oysters were collected from January 1986 through December 2009 as part of a fisheries-independent survey conducted by the TPWD Resource Monitoring Program within the Mission-Aransas Estuary (Fig. 2). All necessary collecting permits were obtained from TPWD. Samples were collected by oyster dredge (0.5 m wide, 5 cm diameter mesh) at 20 randomly selected locations on known reefs in Copano Bay and Aransas Bay each month. Latitude and longitude coordinates were recorded using a Garmin GPSMap Geographic Positioning System (GPS) unit. Dredges were towed for 30 s in duration at a speed of 1.3 m s⁻¹ for approximately 40 m in distance. Because oysters were collected by oyster dredge, which is a relatively inefficient gear, these data represent a relative index of abundance and oyster size [21]. At each location, 19 live oysters (approx. 95% of all oysters collected) were randomly selected and measured for shell length. A subset of 5 live oysters was also examined for quantification of spat (shell length ≥25 mm) settlement. The amount of dead shell (>25 mm) in each sample was enumerated and a subset of 5 shells was also examined for spat settlement.

Spatially resolved environmental measurements of salinity, dissolved oxygen (mg/l), temperature (℃), and turbidity (NTU) were collected throughout the bay system from January 1975 through April 2009 as part of the TPWD Resource Monitoring Program (Fig. 2). The Aransas Bay bathymetric digital elevation model from the National Oceanic and Atmospheric Administration – National Ocean Service [22] was used to represent depth.

Oysters were sampled quarterly from December 2004 through 2009 and examined for the presence of Perkinsus marinus, a protozoan parasite that causes severe mortalities in Gulf of Mexico oyster populations [23]. Ten submarket (26–75 mm) and 10 market-size (≥76 mm) oysters were collected from 8 fixed sampling locations on reefs in Copano Bay and Aransas Bay in each quarterly sampling event (Fig. 1). The southernmost site was discontinued because of difficulties locating live oysters; therefore only 7 sites are reported here. A section of mantle tissue was removed and incubated in thioglycollate medium for 2 weeks following the culture method of Ray [23]. Tissue cultures were stained with Lugol’s solution and examined under the microscope. The percentage of oysters infected by P. marinus was calculated by dividing the number of oysters infected by the number of oysters tested. Infection intensity was ranked using a 5-point scale (after

![Figure 1. Commercial oyster landings.](image)

**Figure 1. Commercial oyster landings.** Commercial oyster landings (metric tons) from the U.S. Atlantic and Gulf of Mexico from 1950–2009 (NOAA 2011).

**PLoS ONE | www.plosone.org 2 July 2012 | Volume 7 | Issue 7 | e40839**
Spatial analysis

Environmental measurements collected by TPWD were imported as point data into a Geographic Information System (GIS; ArcGIS 10, ESRI) and temporally aggregated based on TPWD sampling stations. A new point dataset was created from these aggregations to represent the temporal variability and average conditions at each sampling station. At each TPWD sampling station, mean and standard deviation were generated for salinity, turbidity, and temperature, as well as frequency of occurrence (\%) of low dissolved oxygen measurements (<4 mg/l). Dissolved oxygen concentrations of <4 mg/l (instead of 2 mg/l) were selected because all samples were collected during the day and may therefore have resulted in hypoxic conditions at night. New aggregated environmental measurements were spaced 1 minute of longitude on average from each other (approximately 1.8 km), representing the spatial resolution of the TPWD environmental sampling scheme. Although higher resolution data would potentially reveal more localized patterns and processes, finer scale data were not available. However, the available data accurately represent field observations.

Environmental data were spatially interpolated over the area of the estuary. Root mean square error was used to compare and select interpolation methods. The best interpolation method was local polynomial interpolation (1st order polynomial with barriers) weighted by temporal frequency of sampling each station. This model is a good candidate for mapping data regularly collected from the environmental monitoring networks [26]. Rasters were created using a 0.1 minute cell size (approximately 180 m) for mean and standard deviation of salinity, temperature (°C), and turbidity (NTU), as well as frequency of occurrence (\%) of low dissolved oxygen measurements (>4 mg/l). For depth, the Aransas Bay bathymetric digital elevation model from NOAA-NOS was resampled to 0.1 minute cell size to match the spatial resolution and extent of the environmental variable rasters. Sediment grain size data available [27] had low spatial resolution and sampling points were avoided on reef areas, and therefore were not useful in the current study. Side scan sonar and sub-bottom profiling data were not available for the entire study area so were also not used.

Oyster data (except for disease data) from TPWD were imported as point data into the GIS. Where oyster samples were collected with the presence of live oysters, points were buffered by 80 m (the area covered by dredge sampling) to create polygons that represent live oyster reef. Live reef polygons were then used to aggregate oyster sampling data, where mean abundance of live oysters (>25 mm shell length), dead shell (>25 mm shell length), and spat (5–25 mm shell length) on live oysters and dead shell were calculated for each continuous reef polygon.

As for the environmental variable rasters, data were normalized by scaling from 0–1, where values of 1 are optimal, and values of 0 are unacceptable [17,18,28]. Specific environmental values used for generating the restoration suitability index are presented in Fig. 3.

Mean turbidity data were normalized using the following equation:

\[
\text{Normalized Turbidity} = \frac{\text{Turbidity} - \text{Min Turbidity}}{\text{Max Turbidity} - \text{Min Turbidity}}
\]
Normalized turbidity $e_t$ is defined as:

$$\text{Normalized}(e_t) = \frac{e_t - E_{\text{min}}}{E_{\text{max}} - E_{\text{min}}}$$

(1)

where $E_{\text{min}}$ and $E_{\text{max}}$ are the minimum and maximum values, respectively, for the variable $E$.

Higher values were assigned to high turbidities to maximize available suspended food particles.

Mean temperature data and standard deviation of temperature, salinity, and turbidity were normalized using the following equation:

$$\text{Normalized}(e_t) = \left( \frac{e_t - E_{\text{min}}}{E_{\text{max}} - E_{\text{min}}} - 1 \right)^-$$

(2)

where higher values were assigned to lower temperatures because the prevalence and intensity of $P. \text{marinus}$ infections increase with increasing temperature [29]. Higher values were assigned to low standard deviations to optimize areas with less environmental variability.

Mean salinity data were normalized using the following equation:

$$\text{Normalized}(e_{\text{sal}}) = \left( \frac{|\text{Salinity}_{\text{mean}} - \text{Salinity}_{\text{optimum}}|}{\max(\text{Salinity}_{\text{mean}} - \text{Salinity}_{\text{optimum}})} \right) - 1$$

(3)

where the optimum salinity value was 15. At salinities ranging from 10–20, oysters are present in dense populations, have high reproductive ability, and are subject to relatively lower densities of
predators and disease [30]. Higher values were assigned to moderate salinities because the relationship with oysters is nonlinear; moderate salinities are more favorable than are low or high levels.

Frequency of DO <4 mg/l was normalized using the following equation:

\[ \text{Normalizede}_{\text{DO}} = 1 - f_{\text{DO}<4} \]  

where \( f_{\text{DO}<4} \) is the frequency of dissolved oxygen <4 mg/l. Higher values were assigned to lower frequencies.

Continuous depth values were given 3 different index values. Depths of 1–2 m were given a value of 1 because of the feasibility of large-scale restoration using barges as well as the success of past restoration efforts within this depth range in the Mission-Aransas Estuary. Depths between 0.5 and 1 m were given a value of 0.5 because of suitability for oyster growth but limitations to construction methods. Depths of 2–3 m were also given a value of 0.5 because of suitability for oyster growth, but also increased construction costs and observations of higher proportions of fine sediment accumulation at these depths within the Mission-Aransas Estuary. Depths of <0.5 and depths of >3 m were given values of 0 because of being too shallow or too deep for long-term reef sustainability as observed in previous unsuccessful restoration efforts in this estuary.

The normalized environmental rasters were then combined using a weighted geometric mean function [17,18] using the equation:

\[ RSI = \left( \prod_{i=1}^{n} \text{NEV}_{wi} \right)^{1/n} \]  

where \( w_i \) is the relative weight of importance of the normalized environmental variables (NEV), producing a restoration suitability index (RSI). Using this method, the overall suitability at a specific location is given a ranked value of 0 if any single parameter is unsuitable (has a value of 0). All NEV except salinity were given equal weights of 2 and all standard deviations were given equal weights of 1. Salinity plays the most important role in oyster health in the study area and thus was given a corresponding weight of 4.

The sensitivity of the model to particular environmental variables was assessed using the following equation:

\[ \text{Sensitivity} = \frac{RSI - RSI_{\text{NEV}}} {RSI} \]  

where \( RSI \) is the index of restoration suitability (Eq. 5) and \( RSI_{\text{NEV}} \) is RSI with an individual normalized environmental variable (NEV) removed, one at a time. The output of each scenario is presented in map form to allow for visual comparison of percent change in the base model resulting from removal of an individual variable.

The ratio of live oysters to total (live plus dead) was calculated. Mean abundance of spat was scaled from 0 to 1 using Eq. 1. An index of oyster reef quality (\( \text{Index}_{eq} \)) was then derived using the following equation:

\[ \text{Index}_{eq} = \text{LiveProportion} \times \text{NS} \]  

where \( \text{LiveProportion} \) is the ratio of live oysters to total and \( \text{NS} \) is the normalized spat value. Higher values of the index indicate oyster reefs with higher quality oyster populations (abundant live oysters and spat, moderate to few dead oysters).

Perkinsus marinus sampling occurred at fixed sampling stations throughout the Estuary; therefore these data were not integrated into the model, but were mapped as a series of bar charts to illustrate disease trends along a salinity gradient. Perkinsus marinus accumulates in oyster tissue over time and infections tend to be size-specific, with large oysters having higher infection levels and disease-related mortality than small individuals [31]. Therefore, \( P. \) marinus data were presented using percent infection and weighted prevalence of both submarket (<76 mm) and market (≥76 mm) size classes to demonstrate size-specificity.

Results

Environmental conditions were variable over the period of the study. Mean salinities ranged from 10.7–29.5 (Fig. 4A). Lower salinities were observed in the secondary bays (Copano and St. Charles) due to river inputs while higher salinities were observed in Aransas Bay, located closest to the Gulf of Mexico inlets. The highest salinity variability was observed in the northwest quadrant of Copano Bay, which is influenced by sporadic pulses of freshwater from the Mission and Aransas Rivers (Fig. 4B). Mean temperatures ranged from 21.9–26.0°C and were highest in the shallow margins of the estuary, adjacent to the slow-moving Aransas River and Copano Creek, and throughout relatively shallow St. Charles Bay (Fig. 4C). The highest temperature variability was observed in the central portion of Copano Bay, which is subdivided by several long oyster reefs that likely constrain water circulation (Fig. 4D). Mean turbidities ranged from 11.5–59.6 NTU and were highest and more variable along the northwestern edge of Copano Bay, where the Mission and Aransas Rivers and Copano Creek drain into the estuary (Fig. 4E, F). The frequency of low dissolved oxygen (≤4 mg/l) measurements was fairly small, ranging from 0–7.4% (Fig. 4G). Low dissolved oxygen levels were more frequent in the shallow portions of the estuary. Mean water depth ranges from 0–9.2 m (Fig. 4H). The deepest water occurs in the Gulf Intracoastal Waterway and in the southern portions of Aransas Bay, and the shallowest water exists in areas of existing oyster reef.

Live oyster abundance was highest (>80 oysters per 30 s tow) on several reefs in Copano Bay and at the confluence of Copano and Aransas Bays (Fig. 5A). Live oyster abundance was moderate to low (3–47 oysters per 30 s tow) throughout Aransas Bay. Moderate numbers of dead shell (>25 mm shell length) were observed throughout both Copano and Aransas Bays (Fig. 5B). Spat abundance was highest on several reefs in Copano Bay and moderate to low throughout Aransas Bay, similar to the distribution of live oysters (Fig. 5C).

The restoration suitability index illustrates the range of suitability of environmental variables throughout the Mission-Aransas Estuary (Fig. 6A). Highest index values often correspond with areas of existing oyster reef. Lowest index values occur in the southern, deeper portions of Aransas Bay and in the Gulf Intracoastal Waterway. The reef quality index quality was highest on reefs in Copano Bay (Fig. 6B). Along the 7 fixed sampling sites, Perkinsus marinus infection levels and weighted prevalence were highest for juvenile oysters (<76 mm shell length) at the southernmost location in Aransas Bay and at the confluence with Copano Bay (Fig. 6C). Infection levels and weighted prevalence of \( P. \) marinus in commercial oysters (≥76 mm shell length) were generally higher than in juvenile oysters. Weighted prevalence for commercial oysters was consistently high (>0.50) over 6 of the 7 sites and low (<0.26) at the upstream-most sampling station. The lowest disease levels for both juvenile and commercial oysters were observed at the upstream-most location.
The sensitivity analysis illustrates the percent change from the base restoration suitability index model when individual normalized environmental variables were removed, one at a time (Fig. 7). Removing mean salinity, mean temperature, or mean turbidity resulted in the greatest percent change in Copano Bay (Figs. 7A, C, E). Removing standard deviation of salinity, temperature, or turbidity, or frequency of low dissolved oxygen, resulted in relatively small changes from the base model throughout the estuary (Figs. 7B, D, F). Removing depth resulted in the greatest percent change in the southern, deeper portions of Aransas Bay.

**Discussion**

For successful and sustainable oyster reef restoration efforts, it is necessary to choose sites that support long-term growth and survival of oysters. In general, this requires suitable environmental conditions, adequate larval supply, sustained survival and growth of juvenile and adult oysters, and low disease levels. Proper site selection is one of the most important decisions that restoration groups have to make. Selection of suitable sites is critical as it can greatly influence mortality factors and may largely determine the ultimate success of the restoration project. The application of GIS provides an effective methodology for characterizing locations based on their potential for successful reef restoration and removes much of the uncertainty involved in the sometimes trial and error
selection. This GIS-based approach also provides an objective and quantitative tool for planning future oyster reef restoration efforts.

In this study, we sought to characterize locations within the Mission-Aransas Estuary based on their potential for successful oyster reef restoration. The justification for selecting sites based on their potential for successful recruitment, growth, and survival follows that used in previous restoration/habitat suitability studies [16,17,18]. Depending on project goals, map layers could be integrated in different ways to answer different questions or apply adaptive management strategies. For example, areas with relatively low spat abundance could be targeted for restoration using spat-on-shell [32], reefs with high levels of disease could be targeted for restoration using disease resistant oysters [33], and areas with persistent hypoxia could be restored using reefs with higher vertical relief [12]. This flexibility may be useful to resource management.
managers in dealing with local-scale issues in otherwise high-quality environmental conditions.

In the Mission-Aransas Estuary, it was strongly desired to select sites with moderate salinities to reduce oyster mortalities associated with the high and low ends of the salinity range. The Estuary is located in a semi-arid climate and regularly experiences prolonged droughts. Severe oyster mortalities can result from low flow periods as predators with higher salinity optima, such as the southern oyster drill *Stramonita haemastoma* and the stone crab *Menippe mercenaria* are favored [34,35]. In addition, *Perkinsus marinus* disease initiation and progression are favored by high salinities in combination with high temperatures [24,36]. However, it has also been suggested that it is critically important to protect and restore oyster populations in mesohaline waters, regardless of disease presence, to encourage the development of disease resistant populations [37]. At this time, no such *P. marinus*-resistant populations have been identified within the Mission-Aransas Estuary. At the low end of the salinity range, the Mission-Aransas Estuary is strongly driven by episodic freshwater pulses that depress and then maintain low salinities for a prolonged period [20]. When exposed to sustained periods of low salinities, oysters may reduce their feeding and growth rates, depress or arrest gametogenesis, delay spawning, and/or resorb gonadal material [38,39,40], which can lead to recruitment failure or post-settlement mortality. In general, within the Mission-Aransas Estuary, selecting restoration sites with historically moderate

Figure 6. Restoration suitability index and reef quality index. A) Restoration suitability index. Darker shading indicates higher index value. B) Reef quality index. Dark shading indicates higher index value. C) *P. marinus* disease levels: at each of 7 sampling stations, bar graphs illustrates percent infection and weighted prevalence for juvenile (<76 mm shell length; green-hued color bars) and commercial oysters (≥76 mm shell length; pink-hued bars).
doi:10.1371/journal.pone.0040839.g006
For oyster reef restoration in the Mission-Aransas Estuary, it was also desirable to select areas with low to moderate temperatures. Oysters in Gulf Coast estuaries experience extended periods of warm temperatures compared to northern USA estuaries. Because of the positive correlation with *P. marinus* infection, high temperature values were reclassified with low rankings. Reproduction of *P. marinus* increases at temperatures above 20°C and the parasite proliferates rapidly at temperatures of 25°C or higher [42,43]. Because water temperatures in Gulf of Mexico estuaries generally exceed 20°C for 6 months of the year, oysters do not receive the long reprieve from disease pressures experienced by oysters in northern USA and other high latitude estuaries [30]. Although temperature is a more difficult environmental parameter to control in terms of restoration site selection, particularly in sub-tropical and tropical regions, it is advisable to select locations with sufficient circulation to limit temperature extremes and reduce the probability of disease related mortalities.

Dissolved oxygen concentrations in estuarine waters are another critical component of water quality affecting the survival of oysters. Although the Mission-Aransas estuary has not historically experienced low dissolved oxygen concentrations (Fig. 4G), many estuaries (e.g. Chesapeake Bay) exhibit seasonal salinity and temperature stratification that can lead to hypoxic or anoxic bottom waters. Early developmental stages of oysters may experience negative effects on survival and feeding due to prolonged reductions in dissolved oxygen concentrations [44], whereas adult oysters are better able to survive extended anoxia through the use of anaerobic metabolic pathways [45]. However, the potential negative effects of bottom water hypoxia may be overcome through reef design, particularly increasing reef height, which can provide refuge for oysters and other reef organisms above hypoxic bottom waters [46]. Nevertheless, it is advisable to consider historical frequency of low dissolved oxygen concentrations/hypoxia when selecting the location for a restoration site [47].

The GIS approach employed in this study to characterize locations based on their potential for successful reef restoration in the Mission-Aransas Estuary is flexible and provides a mechanism for considering alternative approaches. Coastal resource or fishery managers can compare different preferred ranges of values for each variable, develop alternative restoration strategies based on these choices, and visualize the effects of these alternative strategies in real time.

The current study has attempted to include as much available and relevant information as possible in the analysis of sites for oyster reef restoration in the Mission-Aransas Estuary. Nevertheless, the approach could be refined further with additional information. For example, side scan sonar and sub-bottom profiling methods are being used more frequently to characterize the bottom and sub-bottom conditions of estuarine systems [50,51,52]. These data have been collected for a portion, but not all, of the Mission-Aransas Estuary and thus were not able to be included in this study [53]. Side scan sonar can cover large areas quickly and can produce a detailed picture of the bay bottom, which is useful for identifying the distribution and scale of oyster reefs and other surficial features. Sub-bottom profilers provide additional information about the shallow structure of the bay bottom, which is important for identifying the presence of

---

Figure 7. Sensitivity analyses. Percent change from the restoration suitability index base model due to removal of individual normalized environmental variables, one at a time. Removal of: A) mean salinity, B) standard deviation (SD) salinity, C) mean temperature, D) SD temperature, E) mean turbidity, F) SD turbidity, G) frequency of low dissolved oxygen; H) depth.
doi:10.1371/journal.pone.0040839.g007
hard substrates for supporting reef building materials. New reef materials may sink or experience high rates of sedimentation if an appropriate location is not selected [54]. In estuaries where bay bottom conditions are unknown, it is advisable that these methods be considered and utilized in advance of site selection. In general, the restoration suitability index model matches the current distribution of oyster reef throughout the Mission-Aransas Estuary. However, there are some differences, particularly in the NE region of the system, where the restoration suitability index predicts favorable conditions for oysters, yet there are few reefs. The reason behind this mismatch may be due, in part, to missing information on bay bottom conditions. Particularly within Aransas Bay, these areas tend to have softer sediments (personal observation) and therefore may not facilitate oyster reef development. Future collection of comprehensive side scan sonar and sub bottom profiling data throughout the Mission-Aransas Estuary and inclusion in the model could improve restoration suitability index results. In addition, we have ongoing restoration efforts throughout the estuary, and thus will be able to empirically test the suitability of the selected regions.

This study sought to support oyster reef restoration efforts by developing a GIS-based methodology for a priori improvement of restoration success via an informed site selection process. This approach provides an interactive and quantitative tool for planning future oyster reef restoration efforts. The proposed restoration suitability model could be further refined when additional data (e.g. sub-bottom conditions) become available. Although it is critically important to continue restoring degraded habitats, it is also essential to develop standardized, science-based tools to inform this process. This model provides a practical, objective, and quantitative decision support tool for assisting stakeholders and managers in planning for future oyster reef restoration efforts and for maximizing long-term sustainability of oyster resources.

Acknowledgments
We thank Texas Parks and Wildlife Department’s Coastal Fisheries Division in Rockport, Texas, especially Nick Ahrens, Willy Cuptit, Mark Fisher, Christopher Mace, Karen Meador, and Luis Ubalde. We also thank Rick Kalke for performing P. marinus oyster collections and Dr. Sammy Ray from Texas A & M University-Galveston for conducting the P. marinus assays (data available on OysterSentinel.org).

Author Contributions
Conceived and designed the experiments: JBP PAM. Performed the experiments: JBP AC TAP ASR. Analyzed the data: JBP AC TAP ASR. Contributed reagents/materials/analysis tools: PAM. Wrote the paper: JBP. Development of the modeling approach: AC ASR. Extensive editorial comments, insight into results: TAP PAM.

References
1. Beck MB, Brumbaugh RD, Airoldi L, Carranza A, Coen LD, et al. (2009) Shellfish Reefs at Risk: A Global Analysis of Problems and Solutions, Arlington, VA. 52 p.
2. Beck MW, Brumbaugh RD, Airoldi L, Carranza A, Coen LD, et al. (2011) Oyster Reefs at Risk and Recommendations for Conservation, Restoration, and Management. Bioscience 61:107–116.
3. Doran Jr E (1965) Shell roads in Texas. Geographical review 55: 223–240.
4. Powell EN, Klinck JM, Hofmann E, Wilson Ormond EA, Ellis MS (1995) Modelling oyster populations. V. Declining phytoplankton stocks and the population dynamics of American oyster (Crassostrea virginica) populations. Fish Res 24: 199–222.
5. Craig A, Powell EN, Fay EN, Brooks JM (1989) Distribution of P. marinus in gulf oast shell populations. Estuaries 12: 82–91.
6. Williams N (2010) Gulf braced for the big clean-up. Current Biology 20: R613–R614.
7. Haby MG, Miget RJ, Falconer LL (2009) Hurricane Damage Sustained by the Oyster Industry and the Oyster Reefs Across the Galveston Bay System with Recovery Recommendations. College Station, TX. TAMU-MG-09-201. The Texas A&M University System. 51 p.
8. McKinley JCJ, Crawley K (2009) Tough Season May Force Texas Oystermen to Fold. New York. New York ed. New York. A16 p.
9. Upton HF (2011) The Deepwater Horizon Oil Spill and the Gulf of Mexico Fishing Industry. Congressional Research Service. R41649 R41640 14 p.
10. Breitburg DL, Coen LD, Luckenbach MW, Mann R, Posey MH, et al. (2000) Oyster reef restoration: convergence of harvest and conservation strategies. J Shellfish Res 19:371–377.
11. Hargis WJ, Haven DS. (1999) Chesapeake oyster reefs, their importance, destruction, and guidelines for restoring them. In: Luckenbach MW, Mann R, Wesson JA (eds) Oyster reef habitat restoration: a synopsis and synthesis of approaches. Virginia Institute of Marine Science, Gloucester Point, VA.
12. Schulte DM, Burke RP, Lipschutz RN (2009) Unprecedented restoration of a native oyster metapopulation. Science 325: 1124–1128.
13. Soniat TM, Brody MS (1988) Field validation of a habitat suitability index model for the American oyster. Estuaries 11(2): 87–95.
14. Currant JL, Cominsky J, Nott PM, Gross LJ (2000) Landscape-based spatially explicit species models for Everglades restoration. Ecol Appl 10(6): 1849–1860.
15. Brown SK, Buja K, Hury SH, Monaco ME, Banner A (2008) Habitat suitability index models for eight fish and invertebrate species in Casco and Sheepscot Bays, Maine. Am Fish Manage 20: 407–415.
16. Batista TA (1999) Habitat suitability index model for the eastern oyster (Crassostrea virginica), in Chesapeake Bay: A geographic information system approach. M.S. Thesis. University of Maryland. 117.
17. Barlow TK, Volery AK, Chartier K, Mazzoni FJ, Prchalotine I. (2007) A habitat suitability index model for the eastern oyster (Crassostrea virginica), a tool for restoration of the Caloosahatchee Estuary, Florida. J Shellfish Res 26(4): 949–957.
18. Starks A, Levinson JS, Deoil M (2011) Restoration of Crassostrea virginica (Gmelin) to the Hudson River. USA: A spatio-temporal modeling approach. J Shellfish Res 30(5): 671–684.
19. NOAA (1990) Estuaries of the United States: vital statistics of a national resource base. Rockville, MD: National Oceanic and Atmospheric Administration, Strategic Assessments Division. 79 p.
20. Orlando SFJ, Rozas LP, Ward GH, Klein CJ (1993) Characteristics of Gulf of Mexico estuaries. Silver Spring, MD: National Oceanic and Atmospheric Administration, Office of Ocean Resources Conservation and Assessment. 209 p.
21. Powell EN, Ashdon-Alcox KA, Kraeuter JN (2007) Realization of eastern oyster dredge efficiency in survey mode: Application in stock assessment. North American Journal of Fisheries Management 27: 492–511.
22. NOAA and National Oceanic and Atmospheric Administration – National Ocean Service (1990) Aransas Bay, TX (G300) Bathymetric Digital Elevation Model (30 m resolution) derived from source hydrographic survey. soundings collected by NOAA, NOAA’s Ocean Service, Special Projects (SP), Silver Spring, MD.
23. Ray SM (1966) A review of the culture method for detecting Dermatophyton marinum, with suggested modifications and precautions. Proc Natl Shellfish Assoc 54: 55–69.
24. Mackin J (1962) Oyster disease caused by Dermatophyton marinum and other microorganisms in Louisiana. Publications of the Institute of Marine Science of the University of Texas 7: 132–229.
25. Craig A, Powell EN, Fay EN, Brooks JM (1989) Distribution of P. marinus in Gulf coast oyster populations. Estuaries 12: 82–91.
26. Grishov A, Krivoruchko K (2011) Local polynomials for data detrending and interpolation in the presence of barriers. Stoch Environ Res Risk Assess 25:1027–1063.
27. Kuczkowski BJ, Reid JA, Jenkins CJ, Reid JM, Williams SJ, et al. (2006) uSSEABED: Gulf of Mexico and Caribbean (Puerto Rico and U.S. Virgin Islands) Offshore Surficial Sediment Data Release: U.S. Geological Survey Data Series 146, version 3.0.
28. Cake EW (1983) Habitat suitability index models: Gulf of Mexico American oyster. U.S. Dept Int Fish Wildl Serv FWS/OBS-82/10.57. 37.
29. Villalba A, Reece KS, Oradas MC, Canas SM, Figuerras A (2004) Perkinosoma in molluscs: a review. Aquatic Living Resources 17: 411–420.
30. Slumway SE (1996) Natural environmental factors. In: Kennedy VS, Newell RIE, Ehle AF, editors. The Eastern Oyster Crassostrea virginica, College Park, MD: Maryland Sea Grant. 734 p.
31. Andrews JD, Ray SM (1998) Management strategies to control the disease caused by Perkinsus marinus. Am Fish Soc Spec Pub 18: 257–264.
32. Carlson J, Carnegie RB, Cordes JF, Hare MP, Leggett AT, et al. (2008) Evaluating recruitment contribution of a selectively bred aquaculture line of the oyster, Crassostrea virginica used in restoration efforts. J Shellfish Res 27(5): 1117–1124.
33. Economou VG, Stockler SM, Allen SK, Chu F-L (2005) Performance of “natural Dermo-resistant” oyster stocks – survival, disease, growth, condition, and energy reserves. J Shellfish Res 24(1): 143–153.
34. Menzel RW, Hulings NC, Hathaway RR (1958) Causes of depletion of oysters in St. Vincent Bay, Apalachicola Bay, Florida. Proc Natl Shellfish Assoc 48: 66–71.

35. MacKenzie CL Jr (1977) Development of an aquaculture program for rehabilitation of damaged oyster reefs in Mississippi. US Fish Wildl Serv Mar Fish Rev 39: 1–13.

36. Soniat TM (1996) Epizootiology of *Perkinsus marinus* disease of eastern oysters in the Gulf of Mexico. Journal of Shellfish Research 17: 1149–1165.

37. Carnegie RB, Burreson EM (2011) Declining impact of an introduced pathogen: *Haplosporidium nelsoni* in the oyster *Crassostrea virginica* in Chesapeake Bay. Mar Ecol Prog Ser 432:1–15.

38. Loosanoff VL (1953) Behavior of oysters in water of low salinities. Proc Natl Shellfish Assoc 43: 135–151.

39. Allen RL, Turner RE (1989) Environmental influences on the oyster industry along the west coast of Florida. J Shellfish Res 8: 95–104.

40. Livingston RJ, Niu XF, Lewis FG, Woodsum GC (1997) Freshwater input to a gulf estuary: Long-term control of trophic organization. Ecol Appl 7: 277–299.

41. Levinton J, Doall M, Ralston D, Starke A, Bassem A (2011) Climate change, precipitation and impacts on an estuarine refuge from disease. PLoS ONE 6: e18849.

42. Chu FLE (1996) Laboratory investigations of susceptibility, infectivity and transmission of *Perkinsus marinus* in oysters. J Shellfish Res 15: 57–66.

43. Ford SE, Tripp MR (1996) Diseases and defense mechanisms. In: Newell RIE, Kennedy VS, Eble AF, editors. The Eastern Oyster *Crassostrea virginica*. College Park, MD: Maryland Sea Grant College.

44. Widdows J, Newell RC, Mann R (1989) Effects of hypoxia and anoxia on survival, energy metabolism, and feeding of oyster larvae (*Crassostrea virginica*, Gmelin). Biol Bull 177: 154–156.

45. de Zwaan A (1983) Carbohydrate catabolism in bivalves. In: Wilbur KM, Hochachka PW, editors. The Mollusca, Metabolic Biochemistry and Molecular Biomechanics. New York: Academic Press. 137–175.

46. Lenihan HS, Peterson CH (1998) How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. Ecological Applications 8: 128–140.

47. Brumbaugh RD, Beck MW, Coen LJ, Craig I, Hicks P (2006) A practitioners’ guide to the design and monitoring of shellfish restoration projects: an ecosystem services approach. The Nature Conservancy, Arlington, VA. 32.

48. Loosanoff VL (1947) Effects of turbidity on feeding of oysters. Proc Natl Shellfish Assoc 1947: 40–44.

49. Schoenharecier C, Guthrie CG, Lu Q (2011) Coastal hydrology for the Mission-Aransas Estuary. Texas Water Development Board, Austin, Texas. 15. Available at http://midgewater.twdb.texas.gov/bays_estuaries/hydrology/reports/TWDB_MissionAransas_Hydrology_20110222.pdf.

50. Smith RW, Bergen M, Weisberg SB, Cadien D, Dalkey A, et al. (2004) Benthic response index for assessing infaunal communities on the southern California mainland shelf. Ecol Appl 11:1073–1087.

51. Allen YC, Wilson CA, Roberts HH, Supan J (2005) High resolution mapping and classification of oyster habitats in nearshore Louisiana using sidescan sonar. Estuaries 28: 435–446.

52. Grizzle RE, Ward LG, Adams JR, Dijkstra SJ, Smith B (2005) Mapping and characterizing subtidal oyster reefs using acoustic techniques, underwater videography, and quadrat counts. American Fisheries Society Symposium 41: 153–159.

53. Dellapenna TM, Weaver E, Simons J, Simms A, Traviani T (2007) Oyster reef and seabed mapping of Copano Bay. Texas General Land Office – Coastal Management Program Cycle 11 Final Report: 92 p.

54. Kennedy RJ, Roberts D (1999) A survey of the current status of the flat oyster (*Ostrea edulis*) in Stamford Lough, Northern Ireland. Proceedings of the Royal Irish Academy 99B: 79–88.