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SPATIAL BIODIVERSITY PATTERNS OF FISH WITHIN THE ARANSAS BAY COMPLEX, TEXAS

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ABSTRACT: The goal of this study was to consider the effects of habitat type and environmental conditions on the biodiversity of fishes within the Aransas Bay Complex, Texas and provide a management framework and an ecosystem examination of Essential Fish Habitat (EFH). A stratified, randomized experimental design was used to collect fishes from seagrass, oyster, and non-vegetated habitats within the Aransas Bay Complex from February through May 2010 over large spatial scales at the “bay-complex” level. We developed a biodiversity habitat model using Boosted Regression Trees (BRT). Fitted functions from the “best” fit BRT habitat model indicated that fish biodiversity was greatest in seagrass areas closest to the inlet (< 80 cost–distance units) during early spring, with temperatures < 18°C and dissolved oxygen levels between 7–8 mg O₂/L in shallow depths (< 0.5 m). Results from community assemblage analyses showed significant differences among habitats with highest abundance of fishes found in seagrass, followed by non-vegetated substrate, and oyster reef. The relatively high abundance of fishes at non-vegetated bottom compared to the low abundance found at the oyster reef was most likely due to the spatial location of the habitats sampled. Our results indicate that future conservation measures should focus along the eastern and southern areas of Aransas Bay to protect EFH with highest levels of biodiversity. The modeling approach developed in this study provides a framework for natural resource managers to identify habitats supporting the greatest biodiversity of juvenile fishes.

KEYWORDS: Boosted Regression Trees, estuarine nursery habitat, essential fish habitat, fish community assemblage, biodiversity–habitat model

INTRODUCTION

Estuaries are among the most productive aquatic ecosystems and are obligate habitats for many marine species. Given the proximity to human population centers and the influence of freshwater as a determinant to both physical (e.g., salinity regime) and biotic (seagrass abundance and distribution as affected by freshwater inflow and nutrient loading) components, these ecosystems provide an ideal research laboratory to investigate modern paradigms in biodiversity and conservation (Lotze et al. 2006). The Gulf of Mexico (GOM) includes over 200 estuarine systems that are impacted by human population growth (which is predicted to increase 40% by 2025; <http://www.unwater.org/index.html>). Current and potential threats include increased waste production and urban non-point runoff, loss of wildlife habitat, water quality decline, and reduced sediment quality. Additionally, increased demands for wastewater treatment, irrigation, energy sources, and potable water of the GOM (<http://www.lme.noaa.gov/>) can all have profound effects on the biodiversity of estuaries within the GOM (Worm et al. 2006).

Human populations and their demands for land, energy, and natural resources are growing exponentially, creating pressures on ecosystems that were not anticipated by conventional approaches to natural resource management (Arkema et al. 2006). Human impacts have altered the distribution, quantity, and quality of marine habitats (Pyke 2004, Lotze et al. 2006, Nobre 2011), and these impacts have contributed to the depletion of more than 90% of estuarine species,

degraded water quality, accelerated species invasions, and destroyed greater than 65% of seagrass and wetland habitat among estuaries and coastal seas (Jackson et al. 2001, Lotze et al. 2006, Worm et al. 2006). These losses have decreased marine biodiversity, which impairs the estuaries’ capacity to maintain ecological health (provide food, maintain water quality etc.; Worm et al. 2006, Hector and Bagchi 2007) and the provision of ecosystem services like nursery habitats (Worm et al. 2006). Thus, there is a need for increased measurement of biodiversity across estuarine landscapes and in particular for fishes.

In the United States and territories, legislative mandates have required resource managers to identify Essential Fish Habitat (EFH) for fish, and take measures to restore, protect, and preserve these areas (2007 Magnuson–Stevens Fishery Conservation and Management Act Public Law 94–265). Estuarine habitat types such as submerged aquatic vegetation (e.g., seagrasses), emergent intertidal marshes, and non-vegetated bottom have been thoroughly investigated, and their role as EFH is well documented (Waycott et al. 2009). It is assumed that there is a positive relationship between the quantity of EFH and fish abundance or productivity (Hayes et al. 1996). However, this assumption is not often tested as research on EFH has focused on density patterns within habitat types (Gallaway and Cole 1999). This information is important, but EFH extends well beyond simple habitat–density relationships and includes interactions among biotic and abiotic components of the habitat (Hayes et al. 1996).

Therefore, modeling species–environment relationships is crucial for examining EFH.

The objective of this study was to compare fish communities among estuarine habitat types (seagrass, oyster, and non-vegetated bottom) and to determine spatial biodiversity patterns by developing a biodiversity model that predicts a Shannon–Wiener index within the Aransas Bay Complex, Texas. Specifically, the relationship among abiotic factors (temperature, salinity, turbidity, dissolved oxygen, and pH), biotic factors (habitat type, depth, and organic content), and the Shannon–Wiener biodiversity index were investigated within the Aransas Bay Complex (Mission–Aransas National Estuarine Research Reserve; MANERR), Texas. We also characterized monthly community structure (February, March, April, and May) as well as examined assemblages for each habitat type (seagrass, oyster, and non-vegetated bottom). The biodiversity–habitat model and related community level analyses will provide crucial information needed to identify and describe EFH within the Aransas Bay Complex, TX.

MATERIALS AND METHODS

Study site

Field collections were conducted in the estuarine waters of the northern GOM in Aransas Bay Complex (Figure 1) within the MANERR. The reserve encompasses 752 km² of seagrass beds (primarily *Halodule wrightii*), oyster reefs (*Crassostrea virginica*), salt marsh (*Spartina alterniflora*), and non-vegetated bottom (sediment consisting of sand with small amounts of clay and silt). Aransas Bay contains extensive coastal wetlands and submerged aquatic vegetation, while Copano Bay is the largest secondary bay connected to Aransas Bay, and freshwater inflow (mean daily inflow of 28 m³/s) occurs primarily via the Aransas and Mission Rivers, and virtually all of the saltwater exchange occurs via the Aransas Pass tidal inlet (Figure 1).

Field collection

A stratified and randomized experimental design was used to classify fish community structure among seagrass, oyster, and non-vegetated bottom habitats within the Aransas Bay Complex from February through May 2010. Sites were selected by converting the study area into 100 m² grid cells. Habitat type for each cell was determined using existing habitat maps (<http://www.csc.noaa.gov/digitalcoast/data/benthiccover/download.html>), with the first available seagrass nearly 10 km from the inlet. Using this grid, forty 100 m² sites were sampled each month in 3 habitat types, seagrass (n=10), oyster (n=10), and non-vegetated bottom habitats (n=20). Sample sites were selected without replacement using a randomized selection of sites from the sampling grid.

Physical environment

Prior to sampling at each site, environmental variables

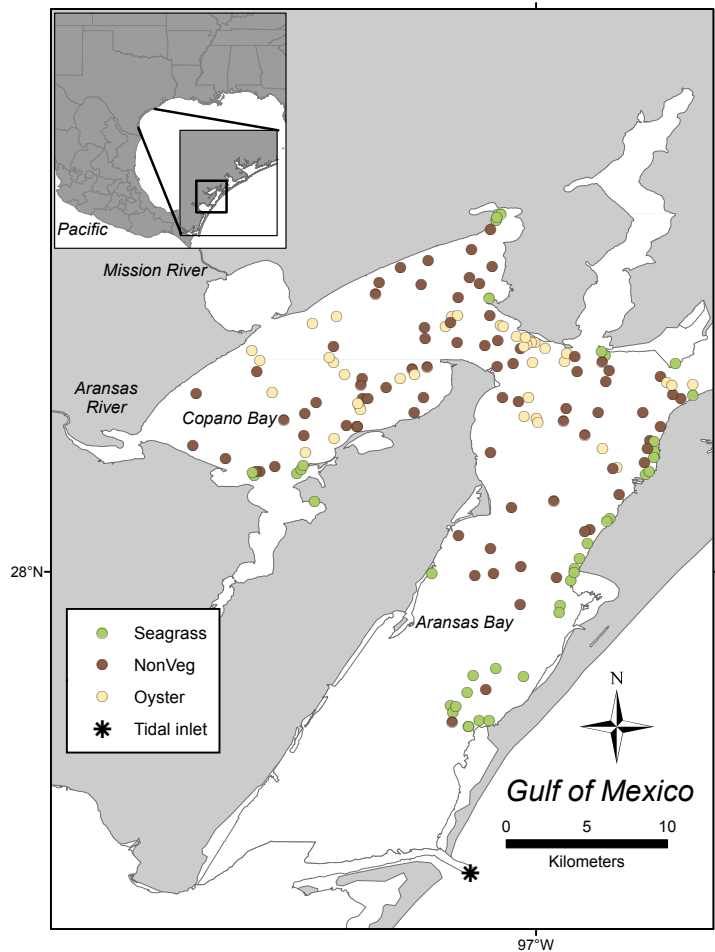


FIGURE 1. Map of Aransas Bay Complex located along the northwestern Gulf of Mexico. Sampling locations ($n = 160$ sites) within the Aransas Bay Complex from February–May 2010, 80 non-vegetated bottom (NonVeg, brown circles), 40 seagrass sites (green circles), and 40 oyster sites (tan circles).

were measured just above the substrate using a Hydrolab 5S Sonde. Variables measured included water temperature (°C), dissolved oxygen (DO) in mg O₂/L, pH, salinity, and depth (m). Turbidity was measured using a Secchi disk (cm). Sediment samples were taken at non-vegetated and seagrass sites using a modified Van–Veen grab. Sediment samples were not collected at oyster sites as shells prevented sediment collection. Sediment samples were placed on ice and transported back to the laboratory for dry weight analysis as an indication of organic content. Analyses were conducted by placing 25g of sediment from each sample into an oven at 104°C for 24 hours. After drying, samples were re-weighed and the dry weight was subtracted from the original wet weight, using the following formula: Percent dry weight = (Sediment after drying (g)) / (wet weight (g)).

Samples with a low percent of dry weight were considered to have a higher percentage of organic content than samples with a higher percent of dry weight. Thus, low percentage of dry weight is correlated with higher sediment quality (Froeschke et al. 2013a).

Fish sampling

Fishes were collected using a 2 m wide beam trawl with 6 mm stretch mesh liner towed for 50 m (total area 100 m²) at a constant speed (5 kt). Trawl samples were rough-sorted in the field to remove excessive algae, seagrass, and debris, then preserved in 10% formalin and returned to the laboratory for further processing. All fishes were identified, enumerated, and measured to the nearest mm standard length (SL).

Spatial Analyses

Saltwater and larval exchange (ingress pathway during the larval stage) occurs via the Aransas Pass tidal inlet. To examine a potential relationship between biodiversity of fishes with the connection to the GOM, the distance from the Aransas tidal inlet to each sampling location was calculated using the cost distance function in the spatial analyst extension in ArcGIS (ESRI, Redlands CA, USA), using the shoreline as a buffer (Whaley et al. 2007). The cost-distance function is used to calculate the shortest distance between 2 points that are constrained within a geographic boundary to provide more accurate relative distance estimates than Euclidian methods (Froeschke et al. 2010, 2013a, b).

Boosted Regression Trees

The relationship between Shannon–Wiener index of biodiversity of fishes and biological, physical, spatial and temporal variables were determined by developing spatially explicit distribution patterns of biodiversity of fishes. We used a forward fit, stage-wise, binomial boosted regression tree model (De'ath 2007, Elith et al. 2008), which is a powerful, yet relatively new, approach to modeling species–environment relationships. Boosted regression trees (BRT) is an ensemble method that combines statistical and machine learning techniques; it has shown to be an effective method for identifying relationships between fish distribution patterns and environmental predictors (Leathwick et al. 2006, 2008, Froeschke et al. 2010, 2013a, b, Froeschke and Froeschke 2011). Boosted regression trees: 1) accept different types of predictor variables; 2) accommodate missing values through the use of surrogates; 3) resist the effects of outliers; and 4) automatically fit interactions between predictors (Elith et al. 2006, 2008, Leathwick et al. 2006, 2008). Unlike traditional regression techniques, BRTs combine the strength of two algorithms, regression trees and boosting, to combine large numbers of relatively simple tree models instead of a single “best” model (Elith et al. 2006, 2008, Leathwick et al. 2006, 2008). Each individual model consists

of a simple regression tree assembled by a rule-based classifier that partitions observations into groups having similar values for the response variable based on a series of binary splits constructed from predictor variables (Friedman 2001, Leathwick et al. 2006, Elith et al. 2008). The BRTs often have a higher predictive performance than single tree methods due to the inherent strengths of regression trees and the robustness of model averaging that improves predictive performance. Overfitting is minimized by incorporating 10-fold cross validation into the model fitting process (Elith et al. 2006, 2008, Leathwick et al. 2006, 2008).

Analyses were conducted in R (version 3.01, R Core Team 2013) using the ‘gbm’ library supplemented with functions from Elith et al. (2008). Initially, 10 predictors were included in the model: habitat type, organic content (%), depth (m), dissolved oxygen (mg O₂/L), temperature (°C), turbidity (cm), salinity, pH, distance to the inlet, and month (treated as a categorical variable; Figure 2). The adjustable model parameters for BRT are tree complexity (*tc*), learning rate (*lr*), and bag fraction, where *tc* controls whether interactions are fitted, *lr* determines the contribution of each tree to the growing model, and *bf* specifies the proportion of data to be selected at each step (Elith et al. 2008). Model selection was based on 2 performance metrics: 1) area under the receiver operating characteristic curve (ROC) and 2) explained deviance on cross-validated data. Selection of predictor variables was done using the *gbm.simplify* function from Elith et al. (2008), while the tuning parameters were optimized by cross-validation selecting a final model larger than 1,000 trees with maximum explained deviance on cross-validated data. Model validation was done by testing the null hypothesis that the slope of the trend line for

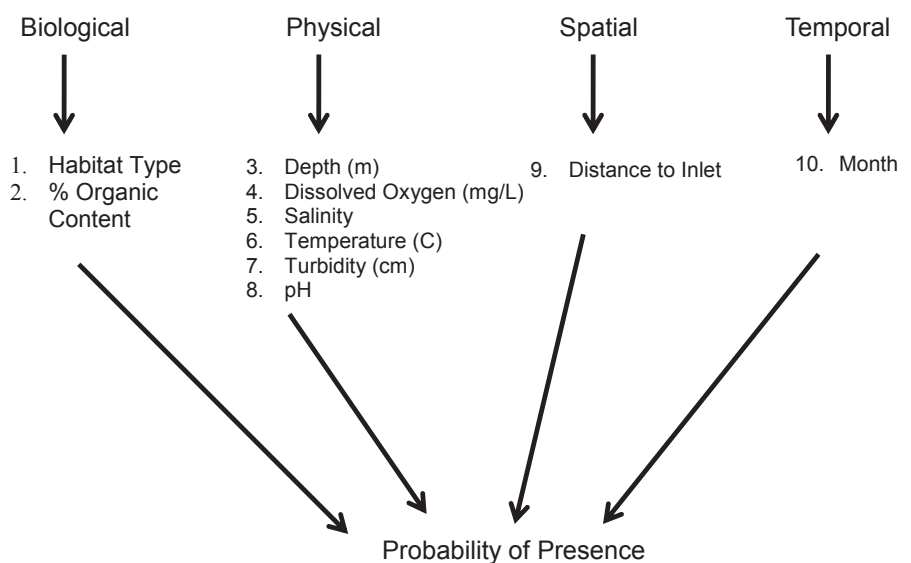


FIGURE 2. Flowchart for Boosted Regression Trees to identify biodiversity hotspots within the Aransas Bay Complex.

predicted biodiversity versus actual calculated biodiversity was not significantly different from one and the intercept parameter was not significantly different from zero. A least-squares linear regression was used: $\text{Predicted}_i = \text{Intercept} + C_i + \text{Residuals}_i$ where Predicted_i equals predicted Shannon–Wiener index of biodiversity of fishes from the BRT model, and C_i equals the calculated Shannon–Wiener index of biodiversity of fishes from the data collected.

Community Analysis

A multivariate analysis (PRIMER v.6; Clarke and Gorley 2006) was conducted to test for significant differences in community assemblages among habitat types (Greenstreet and Hall 1996, Fisher and Frank 2002). The goal of this analysis was to test for differences in community assemblages among habitats by using several routines from PRIMER v.6 (Ludwig and Reynolds 1988, Catalán et al. 2006). The mean monthly abundance of each species collected was examined for each habitat (12 total samples). Data were 4th root transformed prior to analysis to reduce the differential effects of dominant species and differentiate among habitat types having many or few rare species (Clarke and Green 1988). The community assemblage patterns among habitat types were determined using non-metric multidimensional scaling (nMDS) based on Bray–Curtis similarity with Bray–Curtis cluster groups superimposed for interpretation (Clarke and Warwick 2001). Additionally, the SIMPER routine (similarity percentages) was used to determine the species contribution to the within group (habitat) similarity (Clarke and Warwick 2001). Along with the SIMPER routine, the BVSTEP procedure was used in the BEST routine (random selection) to identify the species that contributed the most to the whole community pattern. Using the identified species, another resemblance matrix based on Bray–Curtis similarity was created and compared to the original matrix (all species included) with the RELATE routine, with the null hypothesis that there is no relationship between the two similarity matrices, to determine if we find a similar community pattern with only the selected species (Clarke and Gorley 2006).

RESULTS

Abiotic and Biotic Parameters

During this study abiotic and biotic parameters varied seasonally and mean values differed among habitats (Table 1). Temperature ranged from 12.88°C (February) to 30.48°C (May), and the depth across sites ranged from 0.08 m (seagrass) to 3.54 m (non-vegetated bottom). The lowest salinity (6.22) occurred in an oyster reef in Copano Bay sampled in February, and the highest salinity (33.50)

TABLE 1. Mean (\pm se) parameter ranges by habitat from 160 sites (seagrass $n = 40$, oyster reef $n = 40$, and non-vegetated bottom $n = 80$) sampled from February to May 2010 within the Aransas Bay Complex.

	Non-vegetated	Oyster	Seagrass
Water temperature (°C)	21.55 \pm 2.41	21.97 \pm 3.47	22.99 \pm 3.64
Salinity	14.74 \pm 1.65	13.13 \pm 2.08	18.93 \pm 2.99
Turbidity (cm)	81.12 \pm 9.07	73.10 \pm 11.56	56 \pm 8.85
Depth (m)	3.59 \pm 0.40	2.78 \pm 0.44	2.15 \pm 0.34
Dissolved oxygen (mg O ₂ /L)	7.26 \pm 0.81	7.89 \pm 1.25	9.03 \pm 1.43
pH	8.14 \pm 0.91	8.22 \pm 1.30	8.44 \pm 1.33
Dry weight (%)	47.83 \pm 5.49	N/A	29.06 \pm 4.59

occurred in seagrass in Aransas Bay sampled in March. The lowest dissolved oxygen (2.72 mg O₂/L) occurred in April in seagrass in Copano Bay, and the highest dissolved oxygen (14.49 mg O₂/L) also occurred in April but in non-vegetated bottom in Aransas Bay. Percent dry weight was lowest (10.09%; highest organic content) in March in Copano Bay at a non-vegetated site and highest (75.58%; lowest organic content) in May in Aransas Bay at a non-vegetated site. Turbidity ranged from 20–200 cm with the lowest turbidity occurring in seagrass in February in Copano Bay, and the highest turbidity occurring in non-vegetated sites in May in Aransas Bay.

Summary of collections

A total of 5,789 fishes were collected from February to May 2010 from 160 sites (80 non-vegetated, 40 seagrass, and 40 oyster) within the Aransas Bay Complex. The fish assemblage included 35 species from 22 families. Seagrass sites supported the largest abundance of fishes ($n = 3,797$) and individual species ($n = 27$), followed by non-vegetated sites (1,487 fishes, 23 species), and then oyster reef sites (505 fishes, 16 species). The most abundant fish collected was *Micropogonias undulatus* ($n = 984$) comprising 17% of the fishes sampled (Table 2). *Syngnathus* sp. (mean = 18.55 \pm 2.36), *Lagodon rhomboides* (mean = 16.75 \pm 6.06), and *Ctenogobius boleosoma* (mean = 13.53 \pm 5.41) were the most abundant fish at seagrass sites (Table 2). *Micropogonias undulatus* (mean = 8.84 \pm 3.53), *Citharichthys spilopterus* (mean = 3.40 \pm 0.74), and *Gobiosoma bosc* (mean = 2.30 \pm 0.89) were the most abundant fish at non-vegetated sites (Table 2). *Micropogonias undulatus* (mean = 5.30 \pm 2.50), and *G. bosc* (mean = 4.13 \pm 1.40) were the 2 most abundant fish species at oyster sites (Table 2).

Boosted Regression Trees (Biodiversity Model)

The simplified habitat BRT model for prediction of the Shannon–Wiener Diversity Index incorporated 6 out of 10 variables and was determined as the “best” fit model (ROC = 0.87) as compared to the full model (ROC = 0.85, tree

complexity = 2, learning rate = 0.001, bag fraction = 0.5). Model validation using linear regression demonstrated an approximate 1:1 relationship between the calculated Shannon–Wiener Diversity Index values versus the predicted Shannon–Wiener Diversity Index values from the BRT ($r^2 = 0.92$, $F_{1,159} = 1,927$, $p < 0.05$, Slope = 0.90; Figure 3) Within the BRT biodiversity model, habitat type explained the most deviance in the model (29.2%) followed by temperature (22.3%), distance to the nearest inlet (18.8%), month of collection (13.7%), dissolved oxygen (8.7%), and depth (7.3%; Figure 4). The fitted functions from the “best” fit

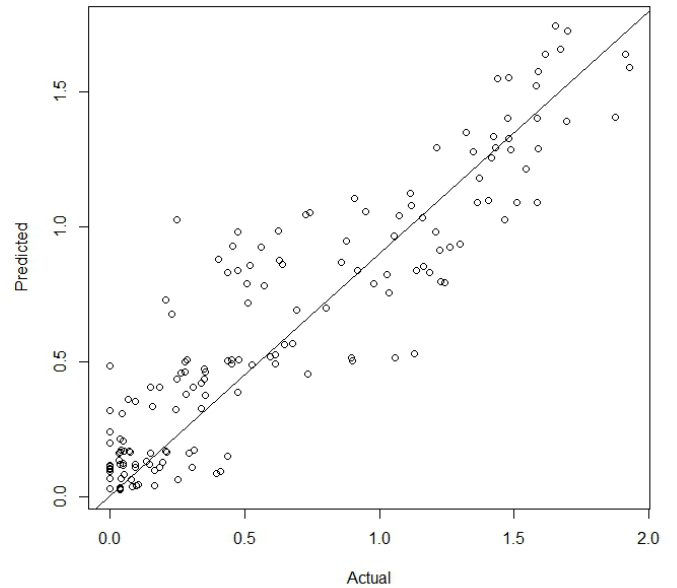


FIGURE 3. Predicted values of biodiversity from the Boosted Regression Tree model versus the actual biodiversity values. Trend line was determined from the linear regression model ($r^2 = 0.92$, $F_{1,159} = 1,927$, $p < 0.05$, Slope = 0.90).

TABLE 2. Overall mean abundance and standard error (SE) of all collected fishes in 3 habitat types including seagrass, oyster reef (Oyster), and non-vegetated bottom (Nonveg). The total number and relative abundance (number of individuals/total number of animals collected \times 100) also are given. Species are listed in order of total and relative abundance.

Common Name	Scientific Name	Total Number	Relative Abundance (%)	Seagrass		Oyster		Nonveg	
				Mean	SE	Mean	SE	Mean	SE
		5,789							
Atlantic Croaker	<i>Micropogonias undulatus</i>	984	17	1.63	(0.55)	5.30	(2.50)	8.84	(3.53)
Pipefishes	<i>Syngnathus</i> sp.	800	13.8	18.55	(2.36)	0.58	(0.18)	0.44	(0.14)
Bay Whiff	<i>Citharichthys spilopterus</i>	715	12.4	10.33	(2.58)	0.75	(0.22)	3.40	(0.74)
Pinfish	<i>Lagodon rhomboides</i>	675	11.7	16.75	(6.06)	0.00	(0.00)	0.06	(0.05)
Darter Goby	<i>Ctenogobius boleosoma</i>	580	10	13.53	(5.41)	0.08	(0.06)	0.45	(0.34)
Naked Goby	<i>Gobiosoma bosc</i>	531	9.2	4.55	(2.73)	4.13	(1.40)	2.30	(0.89)
Spot	<i>Leiostomus xanthurus</i>	447	7.7	10.35	(4.01)	0.15	(0.07)	0.34	(0.10)
Code Goby	<i>Gobiosoma robustum</i>	416	7.2	7.90	(1.68)	0.65	(0.18)	0.93	(0.29)
Pigfish	<i>Orthopristis chrysoptera</i>	139	2.4	3.45	(1.36)	0.00	(0.00)	0.01	(0.01)
Blackcheek Tonguefish	<i>Symphurus plagiosa</i>	105	1.8	1.98	(0.75)	0.05	(0.03)	0.30	(0.10)
Silver Perch	<i>Bairdiella chrysoura</i>	103	1.8	2.58	(1.14)	0.00	(0.00)	0.00	(0.00)
Green Goby	<i>Microgobius thalassinus</i>	93	1.6	0.18	(0.08)	0.35	(0.13)	0.90	(0.18)
Seahorses	<i>Hippocampus</i> sp.	43	0.7	1.08	(0.27)	0.00	(0.00)	0.00	(0.00)
Southern Flounder	<i>Paralichthys lethostigma</i>	32	0.6	0.50	(0.14)	0.08	(0.06)	0.11	(0.06)
Sheepshead	<i>Archosargus probatocephalus</i>	31	0.5	0.78	(0.37)	0.00	(0.00)	0.00	(0.00)
Bay Anchovy	<i>Anchoa mitchilli</i>	24	0.4	0.08	(0.08)	0.25	(0.12)	0.14	(0.06)
Gulf Menhaden	<i>Brevoortia patronus</i>	23	0.4	0.05	(0.03)	0.15	(0.15)	0.19	(0.11)
Inshore Lizardfish	<i>Synodus foetens</i>	10	0.2	0.20	(0.11)	0.05	(0.03)	0.00	(0.00)
Gray Snapper	<i>Lutjanus griseus</i>	7	0.1	0.18	(0.11)	0.00	(0.00)	0.00	(0.00)
Gulf Toadfish	<i>Opsanus beta</i>	7	0.1	0.03	(0.03)	0.00	(0.00)	0.03	(0.02)
Inland Silverside	<i>Menidia beryllina</i>	4	0.1	0.08	(0.08)	0.00	(0.00)	0.01	(0.01)
Lined Sole	<i>Achirus lineatus</i>	3	0.1	0.00	(0.00)	0.03	(0.03)	0.03	(0.02)
Sheepshead Minnow	<i>Cyprinodon variegatus</i>	3	0.1	0.08	(0.08)	0.00	(0.00)	0.00	(0.00)
Rock Sea Bass	<i>Centropristis philadelphica</i>	2	0	0.03	(0.03)	0.00	(0.00)	0.01	(0.01)
Crested Blenny	<i>Hypseurochilus geminatus</i>	2	0	0.00	(0.00)	0.00	(0.00)	0.03	(0.03)
Shrimp Eel	<i>Ophichthus gomesii</i>	2	0	0.05	(0.05)	0.00	(0.00)	0.00	(0.00)
Ocellated Flounder	<i>Ancylosetta quadrocellata</i>	1	0	0.03	(0.03)	0.00	(0.00)	0.00	(0.00)
Frillfin Goby	<i>Bathygobius soporator</i>	1	0	0.00	(0.00)	0.03	(0.03)	0.00	(0.00)
Striped Blenny	<i>Chasmodes bosquianus</i>	1	0	0.03	(0.03)	0.00	(0.00)	0.00	(0.00)
Striped Burrfish	<i>Chilomycterus schoepfii</i>	1	0	0.03	(0.03)	0.00	(0.00)	0.00	(0.00)
Fringed Sole	<i>Gymnachirus texae</i>	1	0	0.00	(0.00)	0.00	(0.00)	0.01	(0.01)
Skilletfish	<i>Gobiosox strumosus</i>	1	0	0.00	(0.00)	0.03	(0.03)	0.00	(0.00)
Atlantic Midshipman	<i>Porichthys plectrodon</i>	1	0	0.00	(0.00)	0.00	(0.00)	0.01	(0.01)
Least Puffer	<i>Sphoeroides parvus</i>	1	0	0.00	(0.00)	0.00	(0.00)	0.01	(0.01)

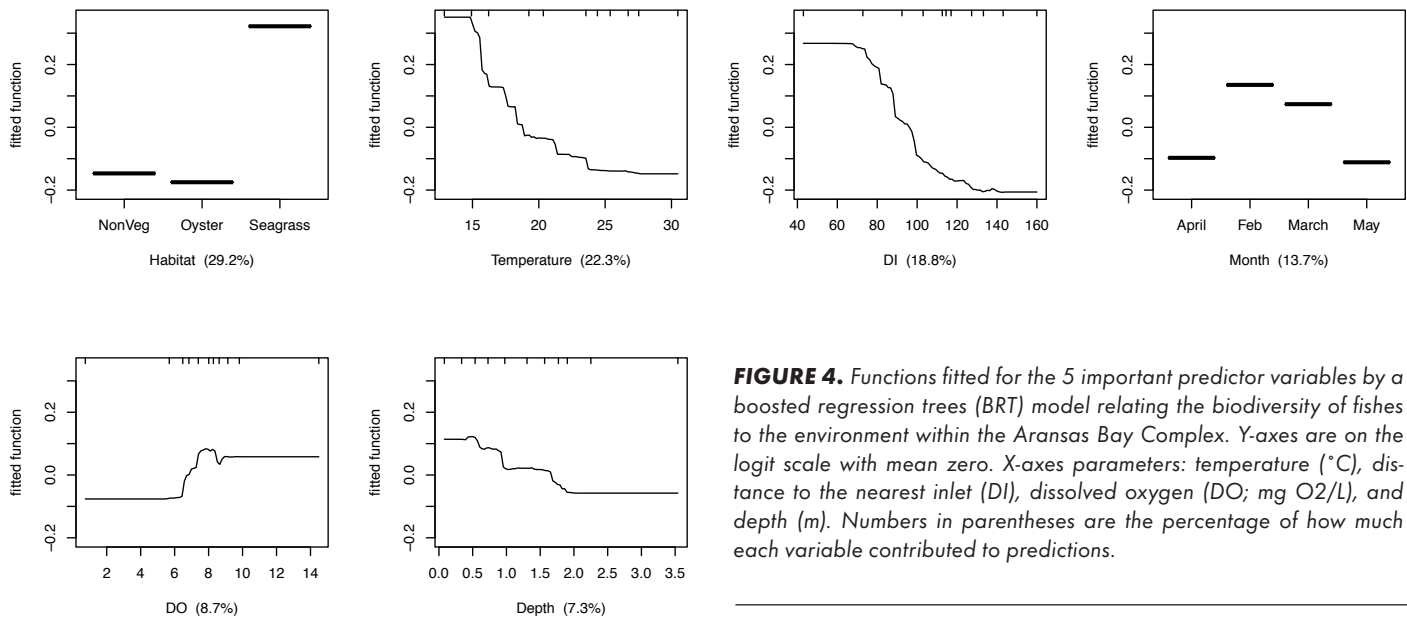


FIGURE 4. Functions fitted for the 5 important predictor variables by a boosted regression trees (BRT) model relating the biodiversity of fishes to the environment within the Aransas Bay Complex. Y-axes are on the logit scale with mean zero. X-axis parameters: temperature ($^{\circ}\text{C}$), distance to the nearest inlet (DI), dissolved oxygen (DO; mg O_2/L), and depth (m). Numbers in parentheses are the percentage of how much each variable contributed to predictions.

BRT habitat model indicated that the greatest biodiversity of fishes occurred in seagrass meadows closest to the inlet (< 80 cost–distance units) during the months of February and March, with temperatures $< 18^{\circ}\text{C}$ and dissolved oxygen levels between 7–8 mg O_2/L in shallow depths (< 0.5 m; Figure 4).

Spatial prediction of biodiversity of fishes from the BRT model demonstrated similar values between the calculated (Figure 5A) and predicted (Figure 5B) Shannon–Wiener

Diversity Index values. Furthermore, spatial prediction indicated the highest biodiversity would occur in seagrass habitat along the eastern and southern areas of Aransas Bay (Figure 5B). Moderate biodiversity values (1.1–1.4) of fishes occurred in seagrass within Copano Bay and non–vegetated sites closest to the tidal inlet in Aransas Bay. The lowest biodiversity values (< 0.35) of fishes occurred along oyster and non–vegetation in the northern portions of Aransas and Copano Bays (Figure 5B).

Community Analysis

Our community analysis revealed differences in community assemblages both monthly and among habitats. Bray–Curtis cluster analysis found 3 groups at the 60% similarity level: 1) seagrass, 2) oyster and non–vegetated bottom, and 3) a second oyster group. The nMDS ordination indicated the same separation among habitats, but also revealed seasonal differences, which is very clear within the cluster analysis superimposed at the 60% level (Figure 6). Oyster samples collected during April and May have a different assemblage than during cooler months when they are more similar to non–vegetated bottom. Additionally, the nMDS plot reveals seasonal differences among seagrass samples with clear separation within the group from February through May. Non–vegetated bottom also reveals a similar seasonal trend with monthly differences in a similar pattern as seagrass habitat (Figure 6). The SIMPER analysis was used to determine which species were contributing to the community structure within each habitat. Estuarine–dependent species had the greatest contribution to the percent similarity among

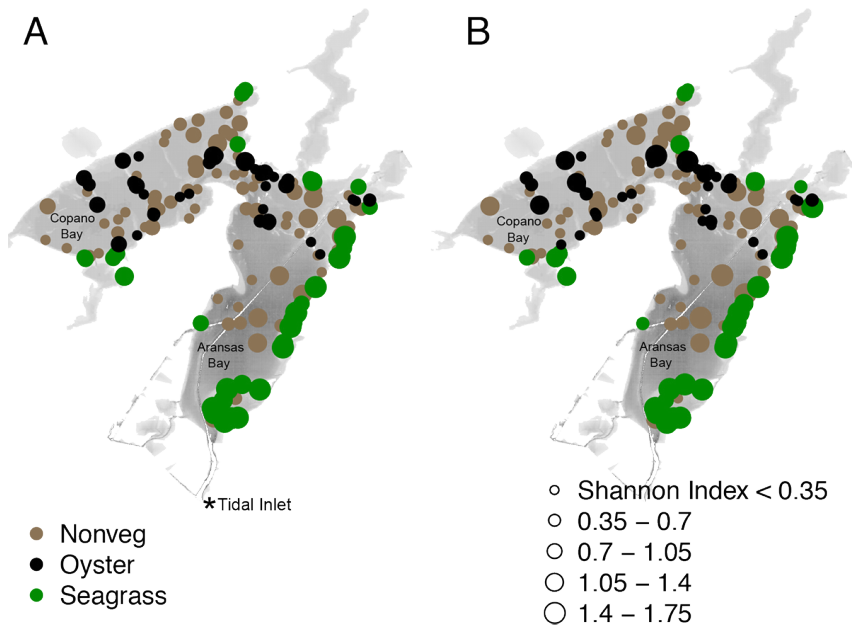


FIGURE 5. Diversity of fishes in the Aransas Bay, TX complex. A. Calculated Shannon–Wiener Diversity Index at each site sampled. B. Spatial prediction of biodiversity of fishes from the boosted regression trees (BRT) model indicating the highest biodiversity would occur among seagrass along the east and south areas of Aransas Bay. Moderate values of biodiversity of fishes occurred in seagrass within Copano Bay and non–vegetated (Nonveg) sites closest to the tidal inlet in Aransas Bay. The lowest biodiversity values of fishes occurred along oyster and non–vegetation in the northern portions of Aransas and Copano Bays.

Habitat

- Seagrass
- ▲ Oyster
- ◇ Nonveg

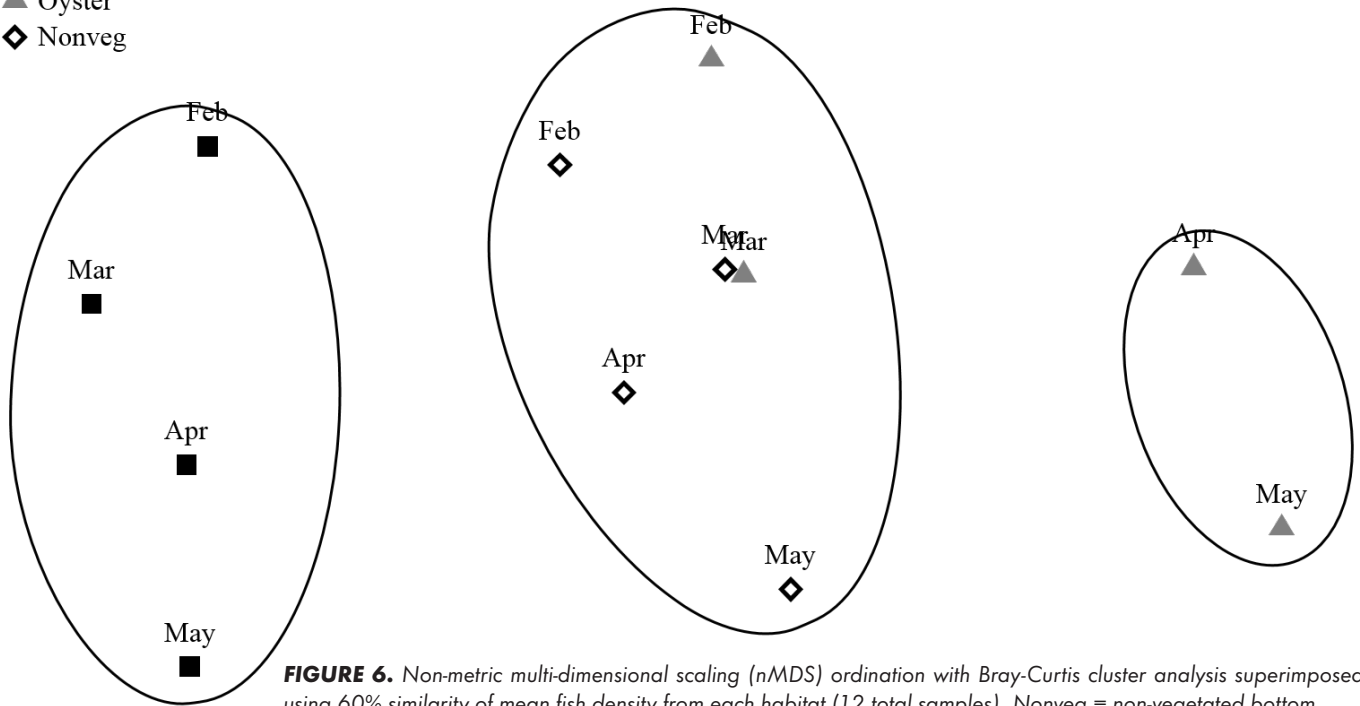


FIGURE 6. Non-metric multi-dimensional scaling (nMDS) ordination with Bray-Curtis cluster analysis superimposed using 60% similarity of mean fish density from each habitat (12 total samples). Nonveg = non-vegetated bottom.

habitats. In seagrass, *Syngnathus* sp., *L. rhomboides*, and *C. boleosoma* had the greatest contribution to the within-group similarity (Table 3). Whereas, in oyster reefs *G. bosc*, *Gobiosoma robustum*, and *Syngnathus* sp. had the greatest contribution to the within group similarity and in non-vegetated habitat, *C. spilopterus*, *G. bosc*, and *M. undulatus* had the greatest contribution to the within group similarity (Table

3). Using the BEST routine, we found 7 species that correlated 95.1% of the community assemblage. We also found a strong correlation between the original matrix (all species) and the BEST matrix (selected species) using the RELATE routine indicating that the matrices were similar ($r = 0.95$, $p = 0.001$). Generally, the most abundant species were identified in the BEST routine as contributing to the community

TABLE 3. SIMPER summaries showing species that contributed to the within group average similarity for each habitat type. * denotes species that did not contribute to the within group average similarity. Nonveg = nonvegetated bottom.

		Seagrass		Oyster		Nonveg	
		Mean Abundance	% Similarity	Mean Abundance	% Similarity	Mean Abundance	% Similarity
Pipefishes	<i>Syngnathus</i> sp.	18.55	15.93	0.58	15.31	0.44	9.23
Pinfish	<i>Lagodon rhomboides</i>	16.75	12.74	0.00	*	0.06	*
Darter Goby	<i>Ctenogobius boleosoma</i>	13.53	11.81	0.08	*	0.45	7.39
Code Goby	<i>Gobiosoma robustum</i>	7.90	11.58	0.65	16.63	0.93	9.37
Bay Whiff	<i>Citharichthys spilopterus</i>	10.33	10.31	0.75	14.61	3.40	15.66
Spot	<i>Leiostomus xanthurus</i>	10.35	7.28	0.15	8.07	0.34	8.25
Blackcheek Tonguefish	<i>Symphurus plagiusa</i>	1.98	6.85	0.05	*	0.30	7.18
Seahorses	<i>Hippocampus</i> sp.	1.08	5.49	0.00	*	0.00	*
Atlantic Croaker	<i>Micropogonias undulatus</i>	1.63	5.40	5.30	9.92	8.84	10.78
Naked Goby	<i>Gobiosoma bosc</i>	4.55	2.91	4.13	24.54	2.30	10.96
Green Goby	<i>Microgobius thalassinus</i>	0.18	*	0.35	*	0.90	10.38
Bay Anchovy	<i>Anchoa mitchilli</i>	0.08	*	0.25	6.94	0.14	3.56

assemblage (Table 3), which is similar to the SIMPER findings. *Lutjanus griseus* was the only species that had relatively low abundance and was not identified by SIMPER but was found to also contribute to the community assemblage in the BEST routine (Table 3).

DISCUSSION

It has been hypothesized that an increase in biodiversity increases ecosystem function and services (Worm et al. 2006, Hector and Bagchi 2007) and has a direct impact on the number of viable fisheries, provision of nursery habitats, and water quality (Worm et al. 2006). This study supports these hypotheses and demonstrates the importance of incorporating biological, physical, and spatial variables to identify biodiversity hotspots. We found that biodiversity was most strongly influenced by the interaction among habitat type, water temperature, distance to the nearest inlet, month of sampling, dissolved oxygen, and depth. Results from this study also show the importance of determining which species are driving biodiversity along with spatial differences by combining diversity metrics with community assemblage techniques over a relatively large spatial scale.

Our results revealed that habitat type, specifically seagrass, was the most important predictor of biodiversity in this sub-tropical estuarine system. Given the importance of habitat on biodiversity patterns, projected habitat loss of a high biodiversity habitat (seagrass) to a lower biodiversity habitat type (non-vegetated) is concerning. Further, habitat loss due to human impacts is a primary cause of population depletion in fishes (Ruckelshaus et al. 2002, Pyke 2004, Levin and Stunz 2005, Lotze et al. 2006) and threatens the health of marine ecosystems (Pauly et al. 2002, Hilborn et al. 2003, Crowder et al. 2008, Halpern et al. 2008, Zhou et al. 2010). Water temperature was also a very important predictor of biodiversity. The relationship with temperature was most likely a result of seasonal temperature variance, which is certainly linked to annual fish recruitment patterns. For example, in the Aransas Bay Complex, occurrence of juvenile *Paralichthys lethostigma* were found in cooler water temperatures (Froeschke et al. 2013a) because their peak recruitment occurs between January and March each year (Nañez-James et al. 2009, Neahr et al. 2010).

Distance to the nearest inlet was also an important predictor of biodiversity. These results are consistent with other studies that show many estuarine species increase in abundance near inlets (Whaley et al. 2007, Reese et al. 2008, Froeschke et al. 2010, 2013b). Previous studies have identified EFH in habitats closest to the tidal inlet in the Aransas Bay Complex, TX (Nañez-James et al. 2009, Froeschke et al. 2013a, b). Moreover, our results suggest that inlet proximity remains an important feature of habitat quality across biotic habitat types. Month was the fourth most important predictor of biodiversity, with the highest biodiversity occur-

ring in February and March. These results are most likely due to recruitment patterns of winter spawning species (*M. undulatus*, *P. lethostigma*, and *L. rhomboides*). Although decreasing biodiversity at lower salinities (greater distance from a tidal inlet) is a natural phenomenon, this is less pronounced in Texas secondary bays (e.g., Copano Bay) because they are greatly influenced by rainfall (Britton and Morton 1989). For example, during periods of drought, communities of secondary bays are characteristic of higher salinity environment (e.g., closer to the tidal inlet). Additionally, salinity was not a predictor in biodiversity, which shows that this parameter most likely did not greatly contribute to the distance pattern found.

Dissolved oxygen and depth were the least important predictors of biodiversity in this study. While dissolved oxygen levels can influence the distribution, abundance, and diversity of organisms (Breitburg 2002, Vaquer-Sunyer and Duarte 2008, Montagna and Froeschke 2009), this primarily occurs at much lower oxygen levels (i.e., < 2 mg O₂/L) (Froeschke and Stunz 2012) than observed in this study. In this study, few samples were collected in low dissolved oxygen conditions, however, low dissolved oxygen events (e.g., hypoxia) are increasing in frequency and spatial extent in Texas estuaries (Applebaum et al. 2005, Montagna and Froeschke 2009). These data suggest that oxygen levels could influence the distribution and abundance of biodiversity and that dissolved oxygen should be included as a variable in future studies. While depth may be important, these are relatively shallow estuarine well-mixed systems where depth likely has little effect.

Using community analyses we were able to determine what species were contributing to the differences in biodiversity among habitats and over time by the BRT model. Overall, both resident species (*Syngnathus* sp., *C. spilopterus* and several goby species) as well as estuarine-dependent species (*M. undulatus*, *L. rhomboides*, *Leiostomus xanthurus*) equally dominated the catch. However, the highest abundances of both of these groups of fishes were found in submerged seagrass vegetation, which is similar to many other studies (Day et al. 1989, Beck et al. 2001, Stunz et al. 2002, 2010, Reese Robillard et al. 2010). We found a low biodiversity of fishes on oyster reefs, which contrasts with numerous studies finding that structurally complex oyster reef systems support high density, biomass, and richness of estuarine nekton (Coen et al. 1999, Coen and Grizzle 2007, Stunz et al. 2010). The comparatively low biodiversity we observed could be a result of the spatial distribution of oyster reefs in the Aransas Bay Complex because the majority of oyster reefs are located in areas furthest away from the inlet in the northern portion of Aransas Bay and the northern and east portions of Copano Bay. Many estuarine species increase in abundance near inlets (Whaley et al. 2007, Froeschke et al. 2010), and Froeschke et al. (2013a) reported an in-

creased probability of flatfish occurrence closest to the inlet in the Aransas–Bay Complex, TX. The other reason for a low number of fish collected from oyster reefs could be because the reefs sampled were subtidal. Reese Robillard et al. (2010) showed similar results with deep subtidal reefs having much lower densities of nekton than shallow estuarine habitats, which may be due to lower vertical relief because these reefs are commercially fished. This similar study concluded that deep reefs may not be as important habitat for newly recruiting estuarine fishes, but are very important for resident oyster–reef species, as well as important foraging grounds for large transient fishes. It should also be noted that there could be a gear effect of using a towed gear over these complex habitats, which may also have caused the low biodiversity found. However, distance from a tidal inlet is an important factor as many estuarine–dependent species may not be able to access these habitats, thus lowering the overall biodiversity.

Despite the strengths of using BRT modeling approach, there are some inherent limitations. Cross–validated model evaluation indicated good performance of the BRT for biodiversity of fishes. It is possible other factors affecting biodiversity of fishes may not have been incorporated into the model, such as biotic components: spawning location, prey and predator density. However, we were able to examine several variables simultaneously that were related to habitat suitability, providing timely information for conservation and management of biodiversity within the Aransas Bay Complex. Furthermore, results from the BRT model were supported by the multivariate community analysis. Nonetheless, future studies of biodiversity should incorporate these abiotic parameters into the models when possible.

Although we collected the fewest number of fishes from oyster reefs, we found they had a similar community assemblage to non–vegetated bottom during February and March. *Micropogonias undulatus* was one of the most abundant species collected among all 3 habitats during this time, particularly in oyster and non–vegetated habitats, and its seasonal recruitment was most likely the driving factor for

this community assemblage pattern (Rooker et al. 1998). The other evidence that *M. undulatus* was driving the community patterns is that their recruitment typically ends in March (Rooker et al. 1998), and the April and May oyster community assemblages were no longer similar to non–vegetated habitats. Seagrass samples were the most different from the other habitats among all months sampled. However, they were more closely related to non–vegetated bottom than oyster reefs, which could be because fish abundance was high at the non–vegetated sites closest to the inlet and adjacent to seagrass beds, highlighting the importance of the spatial arrangement of habitat types within ecosystems (Reese Robillard 2010). Finally, we did not directly assess the predation fields among these habitat types, and there is potential that very different trophic dynamics may exist in different habitats that may affect community structure and abundance (Grabowski 2004, Grabowski and Powers 2004). Several studies have demonstrated that different trophic linkages and connectivity between different estuarine habitats can affect nekton assemblage, density, prey mortality, and growth (Irlandi and Crawford 1997, Micheli and Peterson 1999, Grabowski et al. 2005).

A positive linkage among biodiversity, productivity, and stability across trophic levels in marine ecosystems has been demonstrated (Worm et al. 2006). Therefore, it is critical to maintain/increase the biodiversity of fishes. This study demonstrated the importance of incorporating environmental and biological variables into species biodiversity habitat models to identify areas suitable for EFH designation. The modeling approach, combined with community analyses developed in this study, provide a framework for natural resource managers to identify habitats supporting the greatest biodiversity of juvenile fishes, and to identify which species are contributing to the diversity among habitats. Marine biodiversity loss is increasingly impairing the ocean's capacity to provide food, maintain water quality, and recover from perturbations; therefore, we must understand the importance of these changes to develop a more management approaches to better maintain fish biodiversity.

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