9-1-2017

Non-Linear Thresholds Characterize the Relationship Between Reef Fishes and Mangrove Habitat

Geoffrey S. Shideler
University of Miami

Rafael J. Araujo
University of Miami

Brian K. Walker
Nova Southeastern University, walkerb@nova.edu

Jeremiah Blondeau
National Oceanic and Atmospheric Administration; University of Miami

Joseph E. Serafy
National Oceanic and Atmospheric Administration; University of Miami, joe.serafy@noaa.gov

esa

ECOSPHERE

Non-linear thresholds characterize the relationship between reef fishes and mangrove habitat

GEOFFREY S. SHIDELER,[1,†] RAFAEL J. ARAÚJO,[1] BRIAN K. WALKER,[2] JEREMIAH BLONDEAU,[1,3] AND JOSEPH E. SERAFY[1,3]

[1]*Rosenstiel School of Marine & Atmospheric Science, University of Miami, Miami, Florida 33149 USA*
[2]*Halmos College of Natural Sciences and Oceanography, Nova Southeastern University, Dania Beach, Florida 33004 USA*
[3]*National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, Florida 33149 USA*

Citation: Shideler, G. S., R. J. Araújo, B. K. Walker, J. Blondeau, and J. E. Serafy. 2017. Non-linear thresholds characterize the relationship between reef fishes and mangrove habitat. Ecosphere 8(9):e01943. 10.1002/ecs2.1943

Abstract. A significant obstacle to evaluating the importance of mangrove habitat to coral reef fishes has been the difficulty of disentangling its effects from other subtidal/nearshore habitats or human population pressures. Florida's seascape, unlike most others, has been extensively surveyed and mapped, and there are reliable estimates of human population density. Despite many studies that have correlated reef fish abundance with nearby mangrove habitat, some researchers continue to question the importance of mangroves to reef fishes. Previous studies that have investigated the mangrove–reef fish subsidy effect have applied methods that either compared averages or examined linear relationships; yet there is a body of literature that indicates that the effects of habitat are characterized by thresholds and limiting functions. Here, we employed a generalized additive model to investigate whether species richness of 106 mangrove-associated reef fishes is related to thresholds in the extent of nearby mangrove forests along the Florida Keys Reef Tract. In addition, we used linear discriminant analyses (LDAs) to examine the relationships between the occurrence of 77 reef fish species and extent of Florida mangrove forests. We found that after accounting for confounding factors, at scales <20 km^2, species richness declines with decreasing mangrove extent, whereas richness increases with increasing mangrove extent at scales >80 km^2. Results of our LDA suggested that at least 49 reef fish species (64% of focal species) were associated with higher nearby mangrove forest extent. Our results indicate that of all habitat attributes considered, mangroves played the most substantial role in the diversity of nearby reef fish populations. These apparent thresholds (i.e., non-linearities) in the extent of mangrove forests should be incorporated into fisheries critical habitat management and emphasize the need to consider non-linear relationships between fishes and their habitat.

Key words: Florida Reef Tract; habitat thresholds; mangroves; reef fish; species richness.

Received 13 July 2017; accepted 17 July 2017. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** geoffreyshideler@gmail.com

INTRODUCTION

Researchers have sought for decades to investigate the role that mangrove forests play on the abundance of specific reef fishes (for reviews, see Faunce and Serafy 2006, Nagelkerken 2007). Studies have ranged from small (10s of km), island-scale investigations (Parrish 1989, Nagelkerken et al. 2002, Dorenbosch et al. 2004, Halpern 2004, Mumby et al. 2004) to region-wide (1000s of km), country-level analyses (Serafy et al. 2015), with the objective of evaluating the role that mangroves serve as fish habitat. In the Caribbean region, mangroves and seagrass beds have been shown to function as habitat for juveniles of many reef fishes, with each species exhibiting a different

level of dependence on shoreline and benthic vegetation (Nagelkerken et al. 2001, 2002, Nagelkerken and van der Velde 2002). In actuality, Nagelkerken et al. (2001) demonstrated that juveniles of certain reef fishes were largely absent at fish survey sites lacking mangroves, a finding boosted by Mumby et al. (2004) uncovering that reef sites nearer to mangroves had enhanced biomass of coral reef fishes. Mumby et al. (2004) hypothesized that mangrove prop roots may provide a refuge from predators and/or plentiful food that increases the survivorship of juveniles, or that detritus and nutrients may enrich primary production in neighboring ecosystems. In fact, there are species (e.g., *Epinephelus itajara*) for which quantity and quality of mangrove habitat have been identified as a "bottleneck" to offshore adult fish populations (Koenig et al. 2007).

There have been a variety of approaches to investigating the mangrove–reef fish subsidy effect (i.e., biotic export and trophic subsidy; see Saenger et al. 2013), including examination of otolith isotopic signatures (Chittaro et al. 2004, Gerard et al. 2015), correlations of fish abundance with temporal lags (Jones et al. 2010), examination of fish biomass near areas either with and without mangroves (Nagelkerken et al. 2001, Mumby et al. 2004), and relating indices of fish abundance with annual, country-level mangrove forest size estimates (Serafy et al. 2015). A majority of the studies in the tropical western Atlantic have found mostly positive relationships between fish abundance and mangroves (see Table 3 in Serafy et al. 2015). However, after evaluating more than 200 publications from across the world, Saenger et al. (2013) concluded that it was misleading to generalize a prevailing effect of mangrove areas as nursery areas or enhancers of the species that associate with them. It is important to note that the majority of (if not all) studies that have investigated the reef fish–mangrove relationship have utilized methods that either compared average abundances or examined for linear effects (e.g., analyses of variance and linear models), and these approaches may miss or obscure real relationships, and it is on these studies that generalizations have been made. A departure from examining average fish abundance responses was employed by Serafy et al. (2015) at the Caribbean-wide scale by using a quantile regression approach, and thus estimating the constraining effects of the variable. They found that using a quantile regression at the 90th quantile, the relative abundance of a majority of focal species was limited primarily by mangrove forest extent. However, no previous study has sought to investigate whether the relationship between reef fishes and quantity of nearby mangrove habitat is non-linear, or whether there is a threshold of nearby mangrove forest extent required to detect a mangrove–reef fish subsidy effect. Conservation biology literature has long sought to answer the question of how much habitat is necessary to maintain a viable population (Fahrig 2001). This is an important caveat to the generalizations of the effect of mangroves, especially because studies examining the ecological value of mangrove ecosystems have largely cautioned against assuming linearity since natural processes are characterized by thresholds and limiting functions (Barbier et al. 2008, Koch et al. 2009).

While doubt has been cast on the generalization of the mangrove–reef fish subsidy effect, there largely has been consensus on the roles that seagrass habitats and anthropogenic influences have on reef fishes. For example, seagrasses have long been thought to substantially contribute to coral reef fish populations (Orth et al. 1984, Serrano et al. 2017), both through functioning as juvenile resident areas (Orth et al. 1984, Verweij et al. 2008) and as feeding habitats (Zieman 1982, Verweij et al. 2006). In addition, anthropogenic pressures (via higher levels of nearby human population density) have been universally linked to declines in fish populations via fishing pressure, water quality impacts, and habitat degradation (Stallings 2009, Advani et al. 2015, Serafy et al. 2015). However, while many studies have investigated the contribution of mangrove forests to reef fish abundance, they have been limited by the fact that seagrass beds grow in close proximity to mangrove forests, which complicates interpretation (Nagelkerken et al. 2002, 2012, Dorenbosch et al. 2004, Serafy et al. 2015). Another limitation to previous comprehensive examinations of the effects that mangroves and seagrasses have on fishes is that although mangrove forests have been readily identifiable via remote sensing (Hamilton 2013), seagrass extent estimates in the Caribbean region (and throughout the world) are only more recently available,

albeit at coarse resolutions (see Green and Short 2003, UNEP-WCMC and Short 2016).

Unlike many parts of the Caribbean region, much of Florida's coastal landscape, seascape, and human population has been surveyed and comprehensively mapped. This includes extents of mangrove forest, seagrass, coral reef, and hardbottom, as well as thousands of reef fish surveys and human population census data. Collectively, the habitat, reef fish, and human population data provide an opportunity to examine how coastal and benthic habitats influence fishes occupying nearby reefs, including the effect that mangrove forest extent has on the offshore adult reef fish populations and assemblages after accounting for other influencing factors. Also, while much of the world's mangroves experience large tidal ranges, exposing the prop roots making them generally unavailable as fish habitat (Igulu et al. 2014), the Caribbean region experiences near amphidromic tidal ranges, and it is an excellent place to examine the general impacts of mangroves without that influence. Furthermore, Florida's exhaustive fish surveys allow for the examination of a wide array of species, whereas most previous studies have analyzed fewer than 20 focal species associated with these bosky shorelines (Nagelkerken et al. 2002, Mumby et al. 2004, Serafy et al. 2015).

Given the opportunity presented by Florida's highly mapped and wide-ranging habitat characterizations, we used a generalized additive model (GAM) to ask (1) whether mangrove extent explains a substantial proportion of the spatial variation in the structure (species richness and composition) of mangrove-associated coral reef fishes, (2) whether that proportion is greater than other habitats, and (3) whether that relationship is non-linear (including thresholds). We hypothesized that (1) mangrove extent contributes substantially, and more than other habitats, to explaining spatial variation in the species richness of nearby coral reef fish assemblages and (2) the relationship is non-linear (including the presence of habitat thresholds).

Next, we sought to examine whether mangrove extent and other habitats are a strong predictor of the occurrence of these reef fish species on coral reefs, and whether mangroves are stronger predictors than other habitats. To accomplish this, we used a linear discriminant analysis (LDA) on the occurrence of mangrove-associated reef fish species along the Florida Reef Tract.

Our study is the first to investigate a non-linear influence of nearby mangrove habitat on reef fishes. If non-linear thresholds are revealed in the relation between reef fishes and mangrove extent, this information could be incorporated into fisheries critical habitat management that includes habitat preservation and mangrove restoration, in other words the totality of the landscape. Results of these analyses could also provide guidance for future studies with regard to those species that most benefit from mangrove forest habitat, providing information for species-specific management strategies and conservation. Additionally, this study is the first to examine the influence of mangroves on a comprehensive inventory of reef fish species (>100) on a reef tract that extends for nearly 250 km.

Methods

Study location

The contiguous Florida Reef Tract extends on the Atlantic coast of Florida, USA (Fig. 1), and contains a complexity of geomorphologies and habitats that are relatively close to shore (<7 km), with an extent and proximity to shore that vary in space (Lidz et al. 1991, Rohmann et al. 2005, Lirman and Fong 2007, Walker 2012). The length of the entire reef tract is approximately 250 km, and it is home to stony corals, octocorals, seagrasses, and hardbottom (FDEP 2016). South Florida's coasts also contain the preponderance of the United States' mangrove forest extent, and the southeast coast (adjacent to the reef tract) is home to approximately 6 million people.

Reef fish data

We conducted an exhaustive search for fish surveys in South Florida coastal waters to compile a list of fish species that have been observed to occur nearby to mangrove forests; in total, this led to a list of 254 species of both cartilaginous and bony fishes (see Appendix S1 for the complete list of species and list of references from literature search). We then downloaded fish survey data for the Florida Reef Tract from the Reef Visual Census (RVC), now called the National Coral Reef Monitoring Program. The RVC is a long-term reef fish monitoring program supported mainly by the

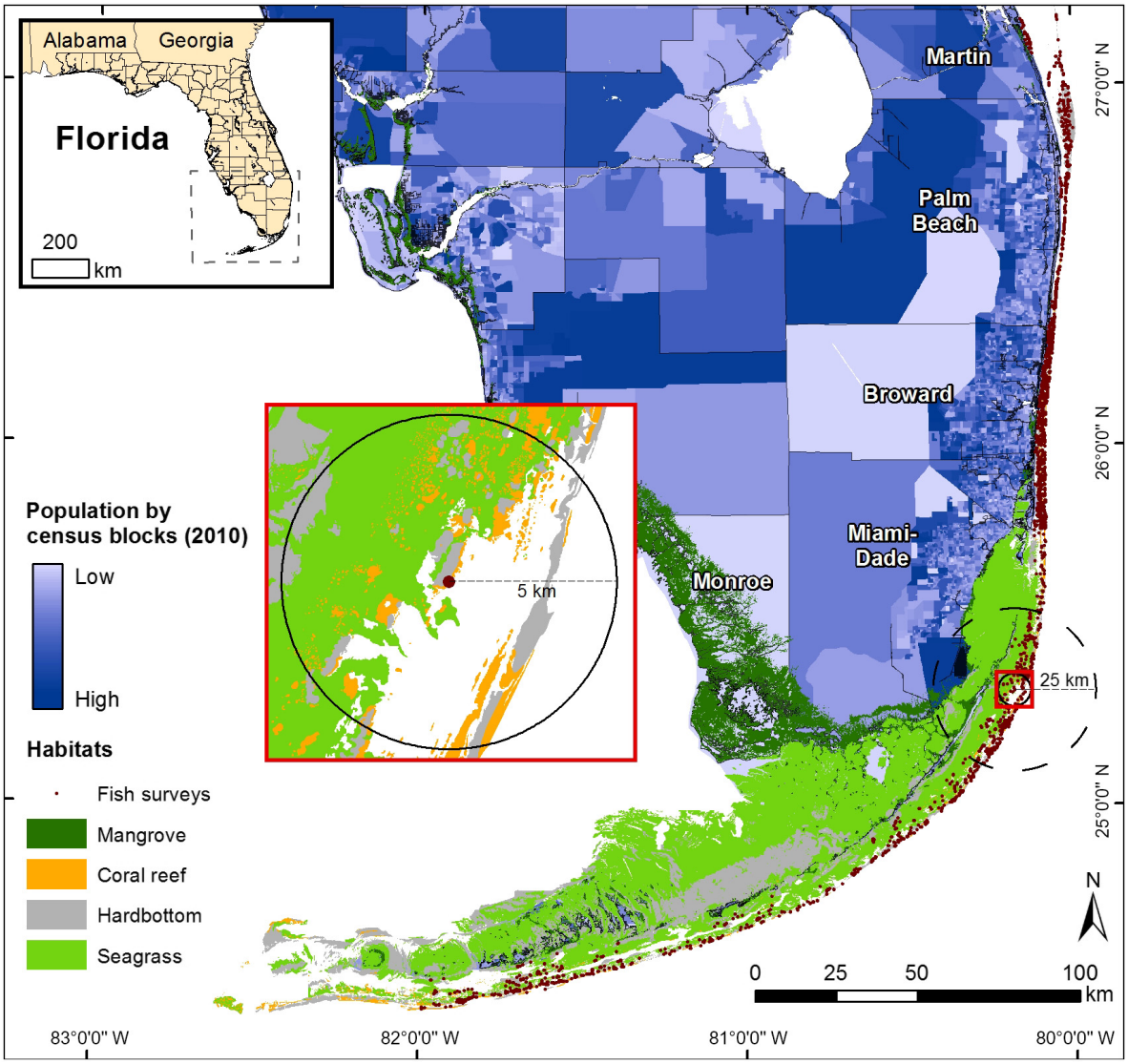

Fig. 1. Map of the Florida Reef Tract showing Reef Visual Census (RVC) survey sites, as well as shapefiles used to approximate their habitat attributes: mangrove extent (dark green), seagrass extent (light green), coral reef extent (orange), and hardbottom extent (gray). Also shown are the census blocks used to calculate anthropogenic pressures (from U.S. Census Bureau, darker shades of blue are higher densities of human population). For each RVC data point, a buffer (circle) was used to estimate its nearby habitat, conducted at three different scales: 0.5, 5, and 25 km (as an example: 5 km shown in inset, 25 km shown as dashed line for one of the RVC survey points).

National Oceanic and Atmospheric Administration's Coral Reef Conservation Program. The RVC method utilizes two scientific divers ("buddy pair") to each census a 15 m diameter cylinder sampling unit in standardized time blocks, which is used to create a probabilistic survey of the Florida Reef Tract for both abundance and size of reef fishes (see Smith et al. 2011 for more information on this long-term survey design). The database consists of approximately 30 yr of data for the Florida Keys; however, beginning in 2012, the survey was expanded to include the northern third of the reef tract system from Miami to St. Lucie Reef (Kilfoyle et al. 2015). Thus, we downloaded all available data for the years 2012 to 2014 from the RVC database using the package rvc in R

(Ganz 2015). The rvc package downloaded a total of 3341 RVC surveys for the Florida Keys and southeast Florida, for observations that included 401 unique taxa. We cross-referenced the two lists (from the literature search and from RVC database), which produced an overlapping list of 106 reef fish species of interest for analyses (hereafter "focal species").

Habitat and human population data

Habitat and human population data were compiled in a geographic information system (GIS) database (Fig. 1). Habitat polygon shapefiles for Florida mangroves, seagrass, coral (i.e., coral reef exhibiting rugosity), and hardbottom (labeled "pavement" in the database, referring to scoured, low/no rugosity hard substrate) were downloaded from the Florida Fish and Wildlife Conservation Commission (available from http://myfwc.com/research/gis/). RVC reef fish survey locations were buffered at three different distances (0.5, 5, and 25 km radius) to calculate the habitat potentially available for each fish species based on their home ranges. Buffer distances were based on a comprehensive review of reef fish movement by Green et al. (2015), who included general recommendations of marine reserve size for fish species based on species-specific home ranges (describing species movement generally as <0.1–0.5, 3–10, and 10s–100s of km; see Table 1 in Green et al. 2015). For species that were not explicitly mentioned, we used a congener or made inferences based on fish body size (see Figure 1 in Green et al. 2015; see also Welsh et al. 2013). The mapped habitat polygons for each habitat type were clipped at the buffer distances to calculate the area of each habitat within each distance. The smaller home-range scales of 0.5 or 5 km were not used for mangroves because there were little to no mangrove forests in proximity to the RVC sites at those scales. This is of little concern as the effect of mangroves on reef fish (even with smaller home ranges) in this system has been shown at the scale of tens of kilometers, primarily because many fishes make ontogenetic migrations from the mangroves to the offshore habitats tens of kilometers away (Serafy et al. 2003, Jones et al. 2010). The shortest distance between each RVC site and the nearest mangrove polygon edge (regardless of size) was measured in the GIS. To examine the potential of anthropogenic influences, we obtained human population density data by downloading the census block polygons from the state of Florida for the most recent national U.S. census in 2010 (available from http://www.fgdl.org/metadata/fgdl_html/cenblkgrp_2010.htm). Human population was considered at the 25-km scale so that their relative contribution was evaluated at the same spatial scale as mangroves.

Analysis approach

To determine the influence that mangrove forest extent has on the probability of occurrence for Florida reef fishes, we used a two-step approach. First, we used a GAM to examine (1) whether mangrove extent explains a substantial proportion of the spatial variation in the structure (species richness) of coral reef fishes (i.e., of the 106 reef fish species analyzed), (2) whether that proportion is greater than other habitats, and (3) whether that relationship is non-linear. Second, we used LDA to examine whether mangrove extent and other habitats are a strong predictor of the occurrence of these reef fish species on coral reefs, and whether mangroves are stronger predictors than other habitats.

For the GAM analysis, we modeled reef fish species richness of the focal assemblage using a Gaussian error distribution via the software package mgcv in R (Wood 2011). We began with a full model, investigating reef fish species richness as a function of year, mangrove extent, seagrass extent, coral extent, hardbottom extent, distance from mangroves, and human population density, utilizing the intermediate habitat circle size (5 km) for the relevant subtidal habitat parameters (seagrass, coral, and hardbottom extent), and the larger circles (25 km) for mangrove extent and human population density. We selected our final model using a backwards stepwise procedure, whereby we eliminated non-significant model terms (beginning with the highest P value) until we reached our final model. All model parameters were estimated using the GAM smoothing function (with the exception of year), using a cubic regression spline with a maximum of five degrees of freedom to guard against overfitting (five knots; i.e., the number of times the analysis will allow the smoothed curve to "kink" for each variable; Zuur et al. 2009). We used deviance explained as a measure of final

model fit to the data, and the relative importance of each covariate was evaluated by visually inspecting the response curves and evaluating the magnitude of each function's range on the *y*-axis, where larger magnitudes were considered to reflect greater explained deviance (Sagarese et al. 2014, Shideler et al. 2015).

For the species-specific analyses, we used a LDA to compare the habitat characteristics among survey sites where a specific fish species was present and those where it was absent. This established whether there was a significant difference between those habitats that had presences and absences, and identified which variables were involved in the discrimination (Jones et al. 1995, Coghlan 2014). For each of the 106 fishes, we paired the presence/absence data from the fish surveys with the appropriate home-range size (0.5, 5, 25 km; see *Habitat and human population data*) and the resulting circle's habitat attributes (mangrove extent, coral extent, distance from mangroves, etc.). When the analysis found that the habitat variables were significant discriminators of reef sites, a high positive coefficient indicated that higher values of a variable (e.g., high mangrove extent) were associated with the presence of a species, and a high negative coefficient suggested that lower values of a variable (e.g., low mangrove extent) were associated with species presence (Jones et al. 1995). Habitat attributes were considered "significant" for coefficients >0.20 following Jones et al. (1995). The LDAs provided predicted classifications and scored the percent correctly classified as a measure of discriminant performance. We omitted data for species that had fewer than 10 observations during the study period (following Peduzzi et al. 1996, Agresti 2007). After establishing this criterion, 29 reef fish species had insufficient positive observations (<10 sightings) to conduct analyses, resulting in 77 fishes for this analysis. Due to the risk of type I error associated with testing such a high number of species, we employed a Hochberg correction to control our false discovery rate (Benjamini and Hochberg 1995).

Due to issues of non-normality and heterogeneity of variance, we rank-transformed our habitat extent and human population data (Conover 2012) prior to any analysis. We initially investigated the effects of latitude; however, during data exploration, we found that latitude and seagrass were highly correlated ($P < 0.001$, Pearson's $r = -0.80$), primarily because the northern extent of the Florida Reef Tract is mostly devoid of offshore seagrass beds. Additionally, in exploratory models examining these two variables, they had very high variance inflation factors not found for other relationships. Though previous studies have found that latitude can play a role in smaller-scale reef fish distributions (Fisco 2016), we opted to omit the variable from our analyses to avoid issues of autocorrelation and variance inflation. We employed a Mantel's test based on 9999 Monte Carlo simulations to determine whether issues of spatial autocorrelation existed using the software package ade4 in R (Dray and Dufour 2007). Results of the Mantel's test suggested that while there was statistically significant spatial autocorrelation, the observed correlation in space was quite low (observed correlation: 0.09, simulated $P < 0.05$), which we interpreted as having minimal impact on interpretation of results. All statistical analyses were conducted in R (R Core Team 2016) and JMP Pro v12.0.1, with a family-wise $\alpha = 0.1$ for all hypothesis testing.

Results

Species richness

Mean species richness of the focal assemblage for the reef sites surveyed from 2012 to 2014 was 13.27 species per site (SD = 5.06, range = 0–30, $n = 3341$). Results of our GAM selection process indicated that year and distance from mangrove were not significant covariates explaining reef fish species richness and were removed from our final model (Table 1). We found that of all habitat variables, mangrove extent (within a 25 km radius of a reef survey site) had the strongest relationship with species richness; high mangrove extent was associated with higher levels of reef fish species richness. Our model suggested two apparent mangrove thresholds for reef fish richness: (1) a precipitous decline in species richness with decreasing mangrove extent below 20 km^2; and (2) a strong, almost linear, increase in richness with increasing mangrove extent above 80 km^2 (Fig. 2). The second strongest association was with seagrass, which the GAM reduced to a linear effect. At approximately 10 km^2 of seagrass extent, there is an increasing positive relationship

Table 1. Final model results from generalized additive model estimating the deviance in reef fish species richness of the focal assemblage explained by variation in the extent of mangroves, seagrass, reef, hardbottom, and nearby density of human population on the Florida Reef Tract from 2012 to 2014.

Smoothed model term	Coef	edf	*t*/*F*	*P*
Initial model				
Intercept	0.0004		1.08	0.276
Year†	0.0065		167.32	<0.001
Mangrove forest extent		3.394	8.41	<0.001
Distance from mangroves		1.000	0.36	0.546
Seagrass extent		1.000	32.37	<0.001
Reef extent		3.778	8.69	<0.001
Hardbottom extent		3.828	3.52	0.005
Human population		3.421	3.04	0.021
Final model				
Intercept	13.2700		167.30	<0.001
Mangrove forest extent		3.437	9.16	<0.001
Seagrass extent		1.000	36.60	<0.001
Reef extent		3.773	9.36	<0.001
Hardbottom extent		3.816	3.43	0.007
Human population		3.472	4.05	0.003

Notes: Seagrass, reef, and hardbottom were within 5 km of a survey site; mangrove extent and human population were within 25 km of a survey site. For the smoothed terms, shown are the estimated degrees of freedom (edf) for each model term, as well as the estimate for the *F* statistic. The intercept and year were parametric terms and are shown with estimated coefficients (coef) and *t* values. Deviance explained for the final model is 18.5%, $n = 3341$. Results of the additive effects are shown in Fig. 2. Year and distance from mangrove were not significant and removed from the final model (see *Methods* for details).

† Note that year was not significant after distance from mangroves was eliminated from model.

with species richness with increasing seagrass extent, whereas reef sites below that value were associated with lower species richness than average (Fig. 2). Our results suggested that species richness declined below the threshold of 3 km^2 of reef extent (Fig. 2). We did not detect a relationship between species richness and the extent of nearby hardbottom habitat. Lastly, our final model results indicated a negative relationship between species richness and human population density, especially at reef sites that were beyond the threshold of 1.5 million people (from Greater Miami to Pompano Beach; Fig. 2).

Species-specific presence and absence

For the 3341 surveys, the number of species sightings (i.e., the number of dives that a particular species was sighted) ranged from 0 to 2728 (Table 2). Results of our species-specific LDAs suggested that for 62 of the 77 (81%) focal reef fish species, presence at a reef site could be significantly determined based solely on habitat variables, while 15 fish species were not significantly related to the habitat attributes examined (Table 2). The percent correctly classified by the LDA procedures ranged from 55% to 94% (Table 2). Results for year were mixed, most having no significant effect ("significant" here defined as a coefficient >0.2), a result not surprising given the limited study period (2012–2014).

Mangroves and seagrasses.—Of the 62 reef fish species with significant results, 49 (79%) were more likely to occur at sites with higher mangrove extent, while five (8%) were more likely to occur at sites with lower mangrove extent (Table 2, Fig. 3A). We found that 42 of the 62 reef fish (68%) had a positive coefficient for distance from mangroves, indicating that increased distances from mangroves were associated with higher reef fish occurrences. Only two species (3%) had negative coefficient for distance from mangroves. For seagrass, higher frequencies of occurrence of 53 reef fish species (85%) were associated with greater extent of nearby seagrass, while eight species (13%) were associated with reef sites nearby to lower seagrass extent (Table 2, Fig. 3B). The presence of seagrass was the strongest discriminator for 18 reef fish species (17 positive and 1 negative), and for 11 reef fish species, mangroves was the strongest discriminating variable (10 positive and 1 negative). Only five species had distance from mangroves as the strongest discriminating variable (Table 2).

Coral reef and hardbottom.—We found that 37 of the 62 reef fish species (60%) had higher frequency of occurrence with greater extent of coral reef nearby, whereas five species (8%) had higher occurrence with lesser extent of coral reef. For 14 of the species (29%), coral reef extent was the strongest discriminating variable, all with positive relationships (Table 2, Fig. 3A). Results of the LDA found that 18 reef fish species (29%) had increased occurrence with greater extent of hardbottom nearby, while 16 species (26%) had higher occurrence with lesser extent of hardbottom. Only five species had hardbottom as the strongest discriminating variable in our analyses;

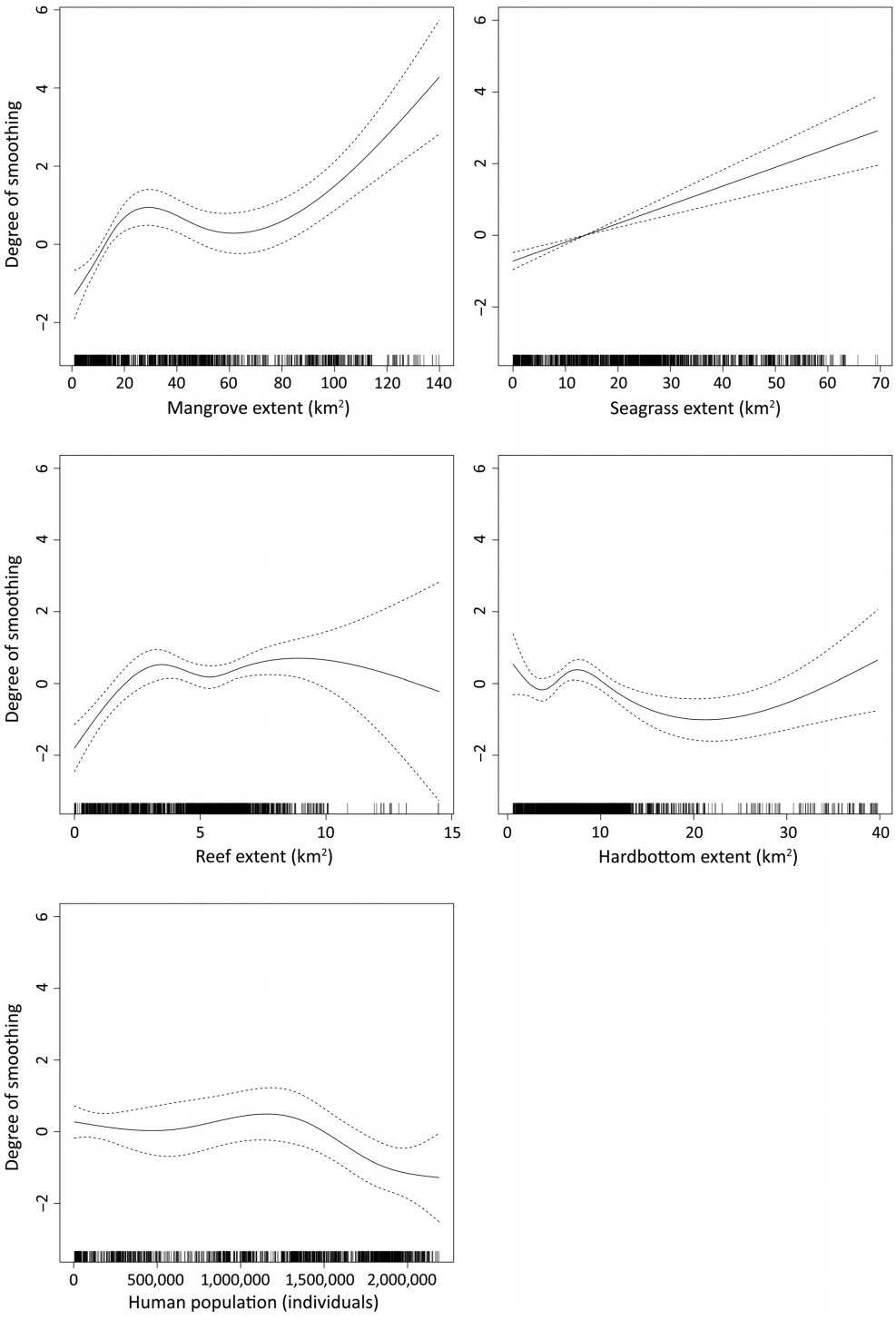

Fig. 2. Results of the generalized additive model showing the effect of mangroves, seagrass, reef, hardbottom, and human population on reef fish species richness of the focal assemblage on the Florida Reef Tract from 2012 to 2014. See *Methods* for information on model specification. The *y*-axis represents the model's degree of smoothing, and the range indicates the relative importance of the explanatory variable. The "rug" on the *x*-axis reflects the relative density of data points. Dashed lines are 95% confidence intervals around response curves.

Table 2. Results of the species-specific linear discriminant analysis (LDA) examining whether there was a significant difference between those habitats that had reef fish presences and absences on the Florida Reef Tract from 2012 to 2014, and identifying which variables were involved in the discrimination.

Species	No.	Dives present (%)	HR (km)	*P*	CC	Year	Dist	Habitat extent				HP
								M	S	CR	H	
Abudefduf saxatilis^{S+}	663	19.8	0.5	<0.001	67%	0.02	0.02	**0.55**	**0.96**	<0.01	**−0.23**	**−0.51**
Acanthostracion quadricornis^{M+}	254	7.6	5	<0.001	73%	0.01	**0.31**	**0.84**	**0.72**	**0.45**	**0.59**	**−0.33**
Acanthurus bahianus^{CR+}	2689	80.5	5	<0.001	65%	−0.18	**0.36**	0.18	**0.21**	**0.87**	**−0.26**	0.02
Acanthurus chirurgus^{S+}	1997	59.8	0.5	<0.001	61%	**−0.34**	0.04	**0.82**	**0.84**	−0.17	**−0.2**	**−0.74**
Acanthurus coeruleus^{CR+}	2312	69.2	0.5	<0.001	67%	−0.1	**0.5**	**0.61**	**0.61**	**0.63**	**−0.45**	**−0.56**
Aetobatus narinari	18	0.5	25	0.59	–	ns	ns	ns	ns	ns	ns	ns
Anisotremus virginicus^{CR+}	1454	43.5	5	<0.001	59%	0.11	**0.59**	**0.59**	**0.51**	**0.62**	**0.57**	**−0.2**
Archosargus probatocephalus^{CR+}	51	1.5	5	<0.001	85%	**−0.25**	−0.1	**0.25**	**0.45**	**0.69**	**0.33**	0.02
Archosargus rhomboidalis	5	0.1	5	–	–	–	–	–	–	–	–	–
Astrapogon stellatus	0	0.0	0.5	–	–	–	–	–	–	–	–	–
Balistes capriscus^{P-}	682	20.4	25	<0.001	65%	−0.1	**0.45**	**0.78**	**0.8**	**0.49**	**0.47**	**−0.82**
Balistes vetula^{CR+}	50	1.5	25	0.006	64%	−0.41	0.03	**0.7**	**0.67**	**0.72**	**0.21**	−0.04
Bothus ocellatus	2	0.1	0.5	–	–	–	–	–	–	–	–	–
Calamus calamus^{P-}	954	28.6	5	<0.001	63%	**−0.42**	**0.62**	**0.68**	**0.72**	0.11	−0.08	**−0.85**
Caranx crysos^{CR+}	311	9.3	25	<0.001	65%	**−0.23**	**0.29**	**0.69**	**0.77**	**0.87**	**0.37**	**−0.35**
Caranx latus	7	0.2	25	–	–	–	–	–	–	–	–	–
Caranx ruber^{P-}	1194	35.7	25	<0.001	58%	**−0.2**	**0.58**	**0.7**	**0.73**	**0.36**	**0.49**	**−0.89**
Carcharhinus leucas	7	0.2	25	–	–	–	–	–	–	–	–	–
Carcharhinus limbatus	0	0.0	25	–	–	–	–	–	–	–	–	–
Centropomus undecimalis	8	0.2	5	–	–	–	–	–	–	–	–	–
Chaetodipterus faber^{CR+}	109	3.3	5	<0.001	57%	**−0.58**	**0.52**	**0.55**	**0.47**	**0.59**	0.18	**−0.42**
Chaetodon capistratus^{DM+}	982	29.4	0.5	<0.001	68%	0.15	**0.67**	**0.57**	**0.28**	**0.54**	−0.16	**−0.62**
Chaetodon striatus^{DM+}	299	8.9	0.5	<0.001	66%	−0.15	**0.83**	**0.51**	**0.27**	**0.42**	−0.14	**−0.67**
Chilomycterus schoepfii	7	0.2	5	–	–	–	–	–	–	–	–	–
Chriodorus atherinoides	0	0.0	5	–	–	–	–	–	–	–	–	–
Cryptotomus roseus^{M-}	514	15.4	5	<0.001	61%	**0.38**	**−0.22**	**−0.77**	**−0.7**	**−0.28**	**0.32**	**0.61**
Dasyatis americana	34	1.0	5	0.14	–	ns	ns	ns	ns	ns	ns	ns
Diodon hystrix	33	1.0	0.5	0.035	–	ns	ns	ns	ns	ns	ns	ns
Diplectrum formosum^{P-}	80	2.4	5	<0.001	62%	0.16	**0.46**	**0.54**	**0.72**	**0.21**	**−0.37**	**−0.87**
Diplodus holbrookii^{DM+}	78	2.3	5	<0.001	94%	−0.09	**0.48**	0.1	**0.43**	**0.38**	0.18	−0.14
Echeneis naucrates	82	2.5	25	0.08	–	ns	ns	ns	ns	ns	ns	ns
Elops saurus	0	0.0	25	–	–	–	–	–	–	–	–	–
Epinephelus itajara^{CR+}	22	0.7	5	<0.001	76%	0.05	**−0.48**	0.12	**0.31**	**0.52**	**0.32**	0.19
Epinephelus morio^{Y+}	379	11.3	5	<0.001	61%	**0.78**	**0.2**	**−0.23**	**−0.44**	−0.19	<0.01	0.09
Epinephelus striatus^{S+}	20	0.6	5	<0.001	75%	**0.4**	0.04	**0.67**	**0.79**	–0.09	0.02	**–0.65**
Eucinostomus argenteus	2	0.1	5	–	–	–	–	–	–	–	–	–
Eucinostomus gula	0	0.0	5	–	–	–	–	–	–	–	–	–
Eucinostomus lefroyi	1	0.0	5	–	–	–	–	–	–	–	–	–
Gerres cinereus^{DM+}	37	1.1	5	<0.001	75%	−0.01	**0.79**	−0.01	0.1	**0.31**	−0.01	−0.14
Ginglymostoma cirratum	67	2.0	25	0.02	–	ns	ns	ns	ns	ns	ns	ns
Gymnothorax funebris^{S+}	61	1.8	0.5	<0.001	61%	−0.08	−0.09	**0.31**	**0.35**	**−0.28**	0.04	**0.33**
Haemulon album	70	2.1	5	0.12	–	ns	ns	ns	ns	ns	ns	ns
Haemulon aurolineatum^{CR+}	554	16.6	5	<0.001	61%	−0.11	**0.3**	**−0.22**	**−0.25**	**0.72**	0.17	**0.36**
Haemulon carbonarium^{S+}	247	7.4	0.5	<0.001	62%	**0.46**	0.04	**0.52**	**0.66**	0.01	0.11	−0.17
Haemulon chrysargyreum^{M+}	108	3.2	0.5	<0.001	64%	0.01	**0.27**	**0.59**	**0.7**	**0.24**	0.16	**−0.56**
Haemulon flavolineatum^{S+}	970	29.0	5	<0.001	64%	0.05	**0.21**	**0.86**	**0.89**	**0.41**	−0.1	**−0.53**
Haemulon macrostomum	120	3.6	5	0.025	–	ns	ns	ns	ns	ns	ns	ns
Haemulon melanurum	200	6.0	5	0.08	–	ns	ns	ns	ns	ns	ns	ns

(Table 2. *Continued*)

Species	No.	Dives present (%)	HR (km)	*P*	CC	Year	Dist	Habitat extent				HP
								M	S	CR	H	
Haemulon parra^{P+}	216	6.5	5	0.002	58.40%	−0.02	0.19	−0.02	−0.1	**0.59**	0.09	**0.61**
Haemulon plumierii^{S+}	1952	58.4	5	<0.001	66.20%	−0.25	**0.24**	**0.85**	**0.93**	**0.29**	0.09	**−0.52**
Haemulon sciurus^{S+}	859	25.7	5	<0.001	62.40%	**−0.23**	0.14	**0.71**	**0.91**	**0.36**	−0.04	**−0.48**
Halichoeres bivittatus^{S+}	2288	68.5	0.5	<0.001	69%	−0.09	0.03	**0.61**	**0.76**	**−0.33**	**0.24**	**−0.32**
Hippocampus erectus	0	0.0	0.5	–	–	–	–	–	–	–	–	–
Hypoplectrus puella^{S+}	124	3.7	5	<0.001	55%	−0.14	**0.35**	**0.82**	**0.9**	**0.24**	−0.06	**−0.84**
Lachnolaimus maximus^{M+}	1548	46.3	0.5	<0.001	68%	−0.14	**0.59**	**0.89**	**0.66**	**0.22**	**−0.46**	**−0.57**
Lactophrys trigonus	34	1.0	5	0.03	–	ns	ns	ns	ns	ns	ns	ns
Lactophrys triqueter^{H+}	398	11.9	5	<0.001	56%	0.15	0.04	**0.23**	**0.31**	−0.13	**0.86**	−0.03
Lagodon rhomboides	2	0.1	5	–	–	–	–	–	–	–	–	–
Lutjanus analis^{H+}	775	23.2	5	<0.001	58.80%	**0.31**	**0.48**	0.05	**−0.23**	−0.08	**0.52**	−0.06
Lutjanus apodus^{S+}	249	7.5	5	<0.001	65.30%	−0.02	**0.26**	**0.86**	**0.93**	**0.25**	0.14	**−0.73**
Lutjanus cyanopterus	4	0.1	5	–	–	–	–	–	–	–	–	–
Lutjanus griseus^{S+}	582	17.4	5	<0.001	60.90%	−0.1	**0.29**	**0.79**	**0.91**	−0.18	−0.01	**−0.78**
Lutjanus jocu^{M+}	24	0.7	5	0.003	73%	**0.41**	**0.44**	**0.48**	**0.21**	**−0.31**	**−0.24**	**−0.43**
Lutjanus synagris^{CR+}	248	7.4	5	<0.001	67%	−0.02	**0.51**	0.18	**0.34**	**0.63**	**0.35**	−0.03
Megalops atlanticus	11	0.3	25	0.21	–	ns	ns	ns	ns	ns	ns	ns
Monacanthus ciliatus	8	0.2	0.5	–	–	–	–	–	–	–	–	–
Mycteroperca bonaci^{P-}	283	8.5	5	<0.001	67%	**−0.41**	**0.61**	**0.69**	**0.72**	0.01	−0.14	**−0.87**
Negaprion brevirostris	2	0.1	5	–	–	–	–	–	–	–	–	–
Nes longus	0	0.0	0.5	–	–	–	–	–	–	–	–	–
Nicholsina usta^{CR+}	27	0.8	0.5	<0.001	72%	−0.04	**0.27**	**−0.29**	**−0.7**	**0.57**	**0.23**	**0.43**
Oligoplites saurus	4	0.1	25	–	–	–	–	–	–	–	–	–
Orthopristis chrysoptera	4	0.1	5	–	–	–	–	–	–	–	–	–
Paraclinus marmoratus^{CR+}	255	7.6	0.5	<0.001	67%	0.19	**0.64**	**0.42**	**0.33**	**0.68**	**−0.57**	**−0.4**
Paralichthys albigutta	1	0.0	0.5	–	–	–	–	–	–	–	–	–
Pomacanthus arcuatus^{H-}	1735	51.9	0.5	<0.001	59%	**−0.28**	0.03	**0.54**	**0.58**	**0.26**	**−0.79**	**−0.22**
Pristis pectinata	0	0.0	5	–	–	–	–	–	–	–	–	–
Pterois volitans^{M+}	364	10.9	0.5	<0.001	63%	−0.02	0.11	**0.8**	**0.75**	−0.19	0.17	**−0.41**
Remora remora^{CR+}	25	0.7	25	0.004	69%	**0.47**	−0.19	**0.31**	**0.35**	**0.61**	**−0.26**	0.04
Rhinesomus triqueter^{H+}	398	11.9	5	<0.001	56%	0.15	0.04	**0.23**	**0.31**	−0.13	**0.86**	−0.03
Scarus coelestinus^{S+}	179	5.4	5	<0.001	63%	0.06	**0.35**	**0.88**	**0.95**	**0.21**	−0.08	**−0.79**
Scarus coeruleus^{M+}	401	12.0	0.5	<0.001	67.00%	0.19	**0.42**	**0.89**	**0.76**	0.03	**−0.32**	**−0.79**
Scarus guacamaia^{S+}	396	11.9	0.5	<0.001	69%	−0.05	0.15	**0.52**	**0.9**	0.05	**−0.21**	**−0.77**
Scarus iseri^{M+}	2010	60.2	0.5	<0.001	72.40%	**−0.21**	**0.44**	**0.86**	0.69	**0.36**	**−0.37**	**−0.65**
Scarus taeniopterus^{S+}	898	26.9	5	<0.001	61%	0.04	0.04	**0.45**	**0.59**	**−0.5**	**0.4**	**−0.55**
Scarus vetula^{M+}	207	6.2	0.5	<0.001	68%	−0.04	**0.59**	**0.65**	**0.38**	**0.52**	0.06	**−0.51**
Scomberomorus cavalla	5	0.1	25	–	–	–	–	–	–	–	–	–
Scomberomorus maculatus^{H+}	32	1.0	25	<0.001	76%	**0.49**	**0.32**	**0.57**	**0.64**	**0.28**	**0.75**	**−0.43**
Selene vomer	0	0.0	25	–	–	–	–	–	–	–	–	–
Seriola dumerili	22	0.7	25	0.01	–	ns	ns	ns	ns	ns	ns	ns
Sparisoma atomarium$^{Y+, DM+}$	1376	41.2	0.5	<0.001	58%	**0.56**	**0.56**	−0.05	**−0.25**	0.16	0.12	**−0.33**
Sparisoma aurofrenatum^{CR+}	2728	81.7	0.5	<0.001	75%	<0.01	**0.49**	**0.6**	**0.46**	**0.73**	**−0.48**	**−0.29**
Sparisoma chrysopterum^{P-}	682	20.4	0.5	<0.001	63%	−0.04	**0.66**	**0.77**	**0.8**	0.14	−0.16	**−0.83**
Sparisoma radians^{Y+}	305	9.1	0.5	<0.001	55%	**0.77**	0.1	**0.39**	**0.6**	−0.11	−0.16	**−0.34**
Sparisoma rubripinne^{S+}	695	20.8	0.5	<0.001	67%	−0.09	**0.29**	**0.69**	**0.91**	**0.28**	**−0.34**	**−0.48**
Sparisoma viride^{M+}	1744	52.2	0.5	<0.001	65%	−0.02	**0.39**	**0.76**	**0.73**	**0.5**	**−0.37**	**−0.52**
Sphoeroides nephelus	1	0.0	5	–	–	–	–	–	–	–	–	–
Sphoeroides spengleri^{P-}	268	8.0	5	<0.001	59%	−0.19	**0.36**	**0.75**	**0.8**	−0.08	−0.04	**−0.93**
Sphoeroides testudineus	11	0.3	5	0.01	–	ns	ns	ns	ns	ns	ns	ns

(Table 2. *Continued*)

Species	No.	Dives present (%)	HR (km)	*P*	CC	Year	Dist	Habitat extent				HP
								M	S	CR	H	
Sphyraena barracuda^{M+}	217	6.5	25	<0.001	58.20%	−0.08	**0.57**	**0.9**	**0.83**	**0.5**	**0.75**	**−0.82**
Sphyrna tiburo	1	0.0	25	–	–	–	–	–	–	–	–	–
Stegastes leucostictus^{S-}	847	25.4	0.5	<0.001	62%	**0.26**	**0.39**	**−0.52**	**−0.56**	0.19	0.08	0.05
Stegastes variabilis^{S+}	1693	50.7	0.5	<0.001	62%	**−0.32**	−0.17	**0.67**	**0.73**	−0.15	−0.14	**−0.33**
Strongylura notata	2	0.1	5	–	–	–	–	–	–	–	–	–
Syngnathus scovelli	0	0.0	0.5	–	–	–	–	–	–	–	–	–
Synodus foetens	25	0.7	0.5	0.036	–	ns	ns	ns	ns	ns	ns	ns
Synodus intermedius	58	1.7	0.5	0.463	–	ns	ns	ns	ns	ns	ns	ns
Trachinotus falcatus	11	0.3	25	0.21	–	ns	ns	ns	ns	ns	ns	ns

Notes: No., number of dives present; HR, home range used in analysis; CC, correctly classified; Dist, distance from mangroves; M, mangroves; S, seagrass; CR, coral reef; H, hardbottom; HP, human population density. Each species' home range was used in the analysis, inferred from Green et al. (2015). Provided predicted classifications (correctly classified) are the percent correctly classified as a measure of LDA performance. Positive coefficients indicate that higher values of a variable were associated with the presence of a species, and a negative coefficient suggested that lower values of a variable were associated with species presence. Also shown are the number of sightings for each species and the percentage of dives that the fish was observed (of the total 3341 dives). Superscript code next to species name indicates strongest discriminant variable for the species. Y = year; M = mangrove extent; DM = distance from mangroves; S = seagrass extent; CR = coral reef extent; H = hardbottom extent; P = human population. A plus (+) or minus (−) sign signals direction of the relationship. Significance was determined using a family-wise alpha of 0.1 and a Hochberg correction to account for false discovery rate associated with multiple hypothesis testing (Benjamini and Hochberg 1995). Boldface values indicate "significance" for coefficients >0.20 following Jones et al. (1995).

four had higher occurrence with higher hardbottom extent and one with lower hardbottom extent (Table 2).

Human population.—The occurrence of most reef fishes was negatively related to the presence of nearby human population density: 44 reef fishes (71%) were more likely to occur at sites with low levels of nearby human population, while six (7%) were more likely to be present at sites with high levels of human population (Table 2, Fig. 3C). Eight reef fish species had human population as the strongest discriminating variable, with seven species having higher occurrence with lower human population density and one with higher human population (Table 2).

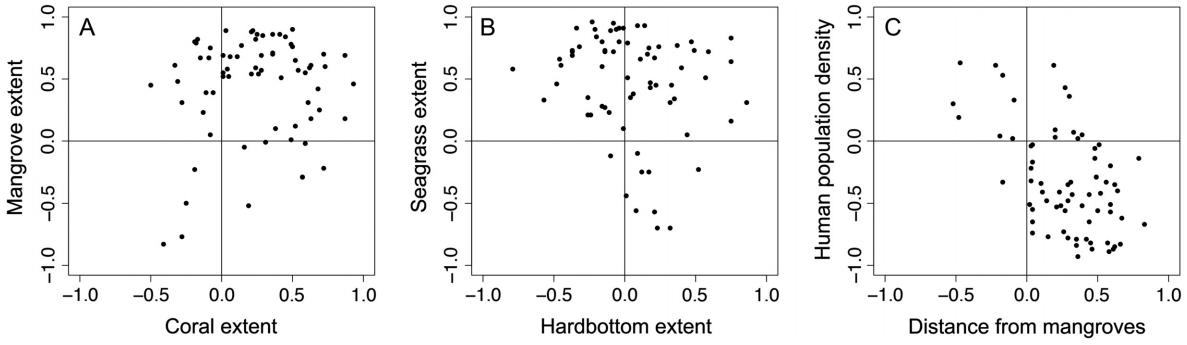

Fig. 3. Graphic representation of species-specific linear discriminant analysis (LDA) coefficients examining whether there was a significant difference between those habitats that had reef fish presences and absences on the Florida Reef Tract from 2012 to 2014, and identifying which variables were involved in the discrimination. Habitat attributes are on each axis, and all fish for which there were significant differences are plotted. Positive coefficients indicate that higher values of a variable were associated with the presence of a species, and a negative coefficient suggested that lower values of a variable were associated with species presence. For exact coefficient values and full LDA results, see Table 2.

Discussion

Here, we examined the potential effect of mangrove habitat on 106 reef fish species, while accounting for the effects of other submerged habitat and human population pressures. Further, for the first time, we investigated the relationship between mangrove-associated reef fish richness and mangrove habitat in non-linear fashion. If these mangrove-associated species show a dependence on mangroves—or their numbers are enhanced by them—their occurrence on the coral reef should be a function of the quantity of nearby mangrove forest (Nagelkerken et al. 2002). Our GAM results revealed that the relationship between mangrove forest extent and reef fishes is not linear and that there are apparent thresholds in community response to mangrove quantity (i.e., 20 and 80 km^2 of mangrove extent within 25 km of a reef site). This is consistent with decades of research on habitat thresholds in various ecosystems (Fahrig 2001), but to our knowledge, ours is the first study to examine this for mangrove fish. In a previous study, Serafy et al. (2015) found that the majority of their focal species were significantly enhanced (i.e., higher indices of abundance) by the presence of increased mangrove forest extent, which was largely consistent with findings of previous studies conducted at far smaller scales (i.e., see Table 3 in Serafy et al. 2015 for synthesis). In fact, Serafy et al. (2015) found that for all Lutjanidae, Haemulidae, and Scaridae, mangrove extent was the primary abundance-limiting factor (with the exception of *Scarus iseri,* which was limited by latitude, a result that might be related to our differing spatial scales). In the present study, reef sites nearer to low extents of mangrove forest (<20 km^2 within 25 km^2) had significantly lower focal species richness, and sites nearer larger forest extents (>80 km^2) had significantly higher focal species richness. The majority of species driving these differences were comprised of parrotfishes (Scaridae) and grunts (Haemulidae), followed by some snappers (Lutjanidae) and an assortment of other fish families (Table 3; Appendix S1: Table S2). Some species, such as *Scarus coeruleus, Scarus coelestinus, Sphyraena barracuda,* and *Lutjanus apodus,* were nearly absent at reef sites with <20 km^2 of nearby mangrove habitat (present at 5%, 2%, 3%, and 2% of sites, respectively) and were observed much more frequently with high levels of mangrove habitat (present at 32%, 16%, 18%, and 16% of sites, respectively; Appendix S1: Table S2). Other fish species had lower occurrences near low mangrove extent and were substantially increased by greater extent of mangroves. For example, French grunt, *Haemulon flavolineatum,* increased from 20% to 49% and the striped parrotfish, *S. iseri,* from 44% to 88% (see Appendix S1 for complete list of species and results). This might be expected because these families have several species that have been shown to be substantially enhanced by the presence of mangroves (Nagelkerken et al. 2002, Mumby et al. 2004, Igulu et al. 2014, Serafy et al. 2015).

Results of the LDA suggested that at least 49 of these reef fish species were associated with higher levels of mangrove forest extent. Previous studies examining the relationship between mangrove extent and reef fish species (e.g., abundance, biomass, occurrence) have been limited to examining a smaller number of species (e.g., 17 in Nagelkerken et al. 2002, 2 in Halpern 2004, 6 in Mumby et al. 2004, 12 in Serafy et al. 2015). Further, they have not been able to quantitatively account for confounding factors, such as anthropogenic influences (Mumby et al. 2004), and have examined this relationship by comparing means or analyzing linear relationships. To our knowledge, we are the first to examine the relationship between species occurrence and extent of mangrove forest for a large number of species, and to account for the effects of seagrasses, corals, hardbottom, and anthropogenic pressures. We found that for the majority of reef fish species, occurrence was positively related to seagrass and coral extent and negatively related to human population density and had a weak but negative relationship with hardbottom extent. Our study also serves as additional evidence for the long-held belief that mangroves do play a role in enhancing reef fishes (here occurrence, and to the extent that increasing occurrence reflects greater density/abundance) in neritic waters in the Caribbean region. This concept has been prevalent at least since the onset of mangrove–energy flux studies (Heald 1971, Odum and Heald 1972), but elusive in terms of empirical evidence (Manson et al. 2005, Aguilar-Perera and Hernández-Landa 2016).

Table 3. List of occurrence rate differences between survey sites with high (>80 km^2), moderate (≥20 to ≤80 km^2), and low (<20 km^2) levels of mangrove forest extent based on generalized additive model results examining effect of habitat quantity on reef fish species richness.

High mangroves vs. low mangroves		Intermediate mangroves vs. low mangroves		High mangroves vs. intermediate mangroves	
Species	Difference (%)	Species	Difference (%)	Species	Difference (%)
Scarus iseri	44	*Scarus iseri*	41	*Lutjanus analis*	21
Sparisoma viride	39	*Sparisoma viride*	30	*Scarus coeruleus*	11
Haemulon flavolineatum	29	*Chaetodon capistratus*	27	*Caranx ruber*	11
Haemulon plumierii	28	*Haemulon plumierii*	25	*Sparisoma atomarium*	10
Lachnolaimus maximus	28	*Acanthurus coeruleus*	25	*Epinephelus morio*	10
Scarus coeruleus	27	*Lachnolaimus maximus*	24	*Pomacanthus arcuatus*	10
Acanthurus coeruleus	27	*Haemulon flavolineatum*	23	*Chaetodon capistratus*	−21
Sparisoma aurofrenatum	24	*Sparisoma aurofrenatum*	21		
Caranx ruber	22	*Calamus calamus*	17		
Haemulon sciurus	21	*Haemulon sciurus*	16		
Abudefduf saxatilis	20	*Sparisoma chrysopterum*	16		
Halichoeres bivittatus	19	*Scarus coeruleus*	16		
Pomacanthus arcuatus	17	*Lutjanus apodus*	13		
Sparisoma rubripinne	17	*Stegastes variabilis*	13		
Sphyraena barracuda	15	*Halichoeres bivittatus*	13		
Lutjanus analis	15	*Sparisoma rubripinne*	12		
Scarus coelestinus	15	*Abudefduf saxatilis*	11		
Lutjanus apodus	14	*Caranx ruber*	11		
Sparisoma chrysopterum	13	*Lutjanus griseus*	10		
Stegastes variabilis	12	*Scarus guacamaia*	10		
Sparisoma atomarium	12	*Sphoeroides spengleri*	−10		
Mycteroperca bonaci	11	*Cryptotomus roseus*	−11		
Calamus calamus	11	*Acanthurus chirurgus*	−20		
Stegastes leucostictus	10	*Balistes capriscus*	−27		
Caranx crysos	−10				
Sphoeroides spengleri	−10				
Cryptotomus roseus	−10				
Pterois volitans	−11				
Acanthurus chirurgus	−13				
Balistes capriscus	−29				

Notes: Shown are the difference rates between the left comparison over the right comparison (higher over lower of each mangrove extent comparison) in each instance for all comparisons with >10% difference between mangrove levels. Negative values indicate that the lower mangrove extent had higher occurrences. See Appendix S1 for full species list for each level of mangrove forest extent.

It has long been understood that seagrass meadows harbor higher densities and richer assemblages of both vertebrates and invertebrates compared to nearby unvegetated areas (see Orth et al. 1984, Serrano et al. 2017). Specifically, seagrass provides not only feeding grounds for many reef fish species (Zieman 1982), but also refuge from predators (Orth et al. 1984, Serrano et al. 2017). Results of our study are consistent with the hypothesis that reefs nearby to higher seagrass extent are associated with higher occurrences of the majority (85%) of focal reef fish species. However, it is important to point out that seagrass and mangroves are known to co-occur spatially, and teasing apart their relationship with reef fishes is difficult (Serafy et al. 2015). While we believe that our GAM was the most appropriate approach to investigating these two habitats in a single model, we are unable to say with absolute certainty that we were able to tease apart the mangrove extent and the seagrass extent relationships. Most correlative observational studies have great difficulty accomplishing this. In contrast to other habitat attributes, the GAM reduced the seagrass effect to a linear relationship, which suggests that there are no thresholds in the response of reef fishes to this habitat. Regardless, it is clear from previous research that

both mangroves (Nagelkerken 2007, Serafy et al. 2015) and seagrass (Serrano et al. 2017) play important roles for species of reef fish, and results of our study highlight the need for both to be considered as important for conservation and management.

One potentially counterintuitive result of our study was that most reef fish species were associated with survey sites farther from mangroves, especially given that a recent study found distance from juvenile fish habitats to have a negative effect on offshore fish densities (Nagelkerken et al. 2017). However, we did not find this result entirely surprising given that several studies have found increased distance from shore to be correlated with increased fish metrics. In a global analysis of marine protected areas (MPAs), Gill et al. (2017) found that close proximity to shore had a significant and negative impact on MPA success, attributed to potential land-based stressors (i.e., water quality, fishing pressure). Increased fish abundance has been attributed to increased distance from the pressures of fishing in the Red Sea (Advani et al. 2015); and Angeloni et al. (2013) found that on Cottesloe Reef off Western Australia, there was an increase in fish abundance and diversity with distance from shore. Perhaps the most obvious explanation for our results would be the positive relationship between topographic complexity and species richness in this region. In this previous examination by Walker et al. (2009), in situ rugosity measurements yielded the best explanation of fish assemblage patterns, a pattern that is consistent with several other studies in the tropical western Atlantic region (e.g., Gratwicke and Speight 2005, Kuffner et al. 2007, Medeiros et al. 2011). We would like to point out that our GAM analysis found no significant relationship between distance from mangroves and species richness. However, our LDA results revealed that approximately 68% of the reef fish species examined had higher occurrences with increasing distance from mangroves. Because portions of the outer reef (farther from shore) have higher relief and complexity (Banks et al. 2007), it is possible that the patterns we found here could be related to benthic topographic relief, not distance from mangroves. Future studies would need to control for topographic relief to determine whether distance from mangroves plays a role in coral reef fish richness or species-level occurrence.

Several studies have documented the effects of anthropogenic impacts on reef fish, which can come in many forms, including habitat degradation (Lotze et al. 2006), water quality declines (Shideler et al. 2015), or fishing pressure (Stallings 2009, Advani et al. 2015, Serafy et al. 2015). Stallings (2009) used publicly available citizen science data to examine human impacts on predatory reef fish communities across the Greater Caribbean region. Generally, as human population density increased, the presence of large-bodied fishes decreased, and fish communities nearer to higher human population were dominated by smaller fish species. Specifically, Stallings (2009) found that most focal species in Lutjanidae, Serranidae, and Sphyraenidae had negative relationships with human population density (see Table 3 in Stallings 2009), similar to our study (see Table 2). Moreover, in the Solomon Islands, Brewer et al. (2013) found that market proximity and local human population density explained the effects of fishing on fish biomass distributions. Results of studies such as these suggest that local human population is a good indicator of the effects that anthropogenic impacts may have on offshore reef fish communities, and that it is important to account for them (Mumby et al. 2004, Serafy et al. 2015).

Previous to our study, research has suggested a mangrove enhancement effect applying to reef fishes on a wide geographical region (Serafy et al. 2015) or to local fisheries at a global scale (Carrasquilla-Henao and Juanes 2017). We are aware that these ecosystem relationships are complex and, according to Pittman et al. (2004), can be more fully understood by taking a landscape approach to these heterogeneous environments at a large scale. However, this approach requires a body of data on ecosystem attributes (e.g., topographic complexity, mangrove forest structure or prop root complexity, regional data on seagrasses, measures of anthropogenic impact) that are largely absent for most regions where these ecosystems co-occur. Florida's highly mapped seascape has afforded the opportunity to examine the effects of these habitats on reef fish occurrence in a way that has not been achievable previously. However, our deviance explained value of 18.5% for the species richness GAM suggests that additional explanatory variables would improve the predictive power of our

model. For example, we could not incorporate other factors that are known to affect reef fish distributions, such as the quality of the available nearby habitat or topographic complexity (Walker et al. 2009, Fisco 2016). Also, we are unable to rule out the possibility that the patterns that have emerged in our study are covariates of another factor that the species are responding to, such as latitude. Lastly, though our decisions for circle sizes and scale were determined based on a literature review based on fish movements (for MPA size recommendations), it is unclear how our results may have differed had we selected different scales. Future studies should investigate scale and its impact on results and interpretation. Still, that almost one-fifth of fish occurrence data were explained by a model examining only nearby habitat extent and human population densities, without accounting for the many different aspects that might influence fish occurrence on a particular reef (e.g., topography, oceanographic data, predator–prey relationships and high-resolution fishing mortality, mangrove structure or prop root complexity), is consistent with the conclusion that the availability of nearby habitat plays a role in reef fish occurrence and species richness, especially in relation to the present study's detected thresholds.

There have been several species singled out in the literature that has reported dependencies on mangrove habitat. In particular, *S. iseri, Scarus guacamaia, Haemulon sciurus,* and *L. apodus* were previously noted as "highly dependent" on mangrove habitat (Nagelkerken et al. 2002, Mumby et al. 2004). Using a quantile regression approach, Serafy et al. (2015) found evidence that low mangrove extent was a limiting factor for these species at the Caribbean-wide scale and that the mean relative abundance of *L. apodus* and *H. sciurus* was positively related to mangrove extent. Our results add to the growing evidence that in the tropical western Atlantic region, mangroves serve as important habitat for several species of commercial importance. Not only were all these species among those with the highest mangrove coefficients in our species-by-species analyses, but also they were present in the species richness comparisons among sites with low, intermediate, and high mangrove forest extents (see Table 3). In fact, our results suggest that there could be more fish considered "dependent" on mangroves that warrant further study, especially among the Lutjanidae, Haemulidae, and Scaridae families. The apparent mangrove extent thresholds we found could also be incorporated into fisheries management, as such information may be crucial for U.S. managers to comply with the Essential Fish Habitat component of the Magnuson-Stevens Act.

Results of our study at the regional scale (Florida Reef Tract), taken together with the other Caribbean-region studies conducted at the island- and Caribbean-wide levels, suggest that for this region of the world, mangroves play a role in the richness of reef fish communities, as well as for the occurrence of valuable species. Our results suggest that generalizations or syntheses evaluating the impact of mangroves be taken with the caveat that they are based on linear analyses and comparisons of means, when we have shown here and elsewhere (Serafy et al. 2015) that there are thresholds and limiting functions in the contribution of this habitat to reef fishes. Future studies seeking to examine the relationship that coral reef fishes have with mangrove habitat should account for the relationships found here.

Acknowledgments

We are grateful to the many people involved in the collection of fish survey data for the Reef Visual Census (RVC) program, especially to National Marine Fisheries Service and the Coral Reef Conservation Program, who support the RVC initiative. This study could not have been performed without benthic mapping data by NOAA, FWC, Nova Southeastern University, and Biscayne National Park; the spatial census data from the U.S. Census Bureau and the Florida Department of Transportation; and the mangrove cover data from the Southwest Florida and South Florida water management districts. Funding for the benthic mapping data was provided in part by a Coastal Services Center grant from the U.S. Department of Commerce, NOAA National Ocean Service Award No. NA11N0S4820003, and by the Florida Department of Environmental Protection, through its Office of Coastal and Aquatic Managed Areas. The views, statements, findings, conclusions, and recommendations expressed herein are those of the author(s) and do not necessarily reflect the views of the State of Florida, U.S. Department of Commerce, NOAA, or any of its subagencies. We are thankful to A. Chester (NOAA) for his helpful comments to improve the manuscript.

We are very thankful to M. Carr for his very helpful comments on our manuscript, as well as those of two anonymous reviewers.

Literature Cited

Advani, S., L. N. Rix, D. M. Aherne, M. A. Alwany, and D. M. Bailey. 2015. Distance from a fishing community explains fish abundance in a no-take zone with weak compliance. PLoS ONE 10: e0126098.

Agresti, A. 2007. An introduction to categorical data analysis. Second edition. John Wiley & Sons, Hoboken, New Jersey, USA.

Aguilar-Perera, A., and R. C. Hernández-Landa. 2016. The rainbow parrotfish (*Scarus guacamaia*) does not depend on mangroves as nursery habitat in the Parque Nacional Arrecife Alacranes, southern Gulf of Mexico. Marine Biodiversity 47:13–14.

Angeloni, T., L. Campbell, H. Davis, O. Fredriksson, C. Patrick, N. Prinz, J. Schaefer, and K. Werndly. 2013. The marine habitat gradient of Cottesloe Reef: increasing fish abundance and diversity towards outer reef. Marine Systems:SCIE2204. https://cottesloeecosystem.files.wordpress.com/2013/08/fish-abundance-and-diversity-increases-towards-outer-reef.pdf

Banks, K. W., B. M. Riegl, E. A. Shinn, W. E. Piller, and R. E. Dodge. 2007. Geomorphology of the southeast Florida continental reef tract (Miami-Dade, Broward, Palm Beach Counties, USA). Coral Reefs 26:617–633.

Barbier, E. B., et al. 2008. Coastal ecosystem-based management with nonlinear ecological functions and values. Science 319:321–323.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B 57:289–300.

Brewer, T. D., J. E. Cinner, A. Green, and R. L. Pressey. 2013. Effects of human population density and proximity to markets on coral reef fishes vulnerable to extinction by fishing. Conservation Biology 27:443–452.

Carrasquilla-Henao, M., and F. Juanes. 2017. Mangroves enhance local fisheries catches: a global meta-analysis. Fish and Fisheries 18:79–93.

Chittaro, P. M., B. J. Fryer, and P. F. Sale. 2004. Discrimination of French grunts (*Haemulon flavolineatum*, Desmarest, 1823) from mangrove and coral reef habitats using otolith microchemistry. Journal of Experimental Marine Biology and Ecology 308: 169–183.

Coghlan, A. 2014. A little book of R for multivariate analysis. Release 0.1. Wellcome Trust Sanger Institute, Cambridge, UK.

Conover, W. J. 2012. The rank transformation—an easy and intuitive way to connect many nonparametric methods to their parametric counterparts for seamless teaching introductory statistics courses. Wiley Interdisciplinary Reviews: Computational Statistics 4:432–438.

Dorenbosch, M., M. C. van Riel, I. Nagelkerken, and G. van der Velde. 2004. The relationship of reef fish to the proximity of mangrove and seagrass nurseries. Estuarine, Coastal and Shelf Science 60:37–48.

Dray, S., and A. B. Dufour. 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22:1–20.

Fahrig, L. 2001. How much habitat is enough? Biological Conservation 100:65–74.

Faunce, C. H., and J. E. Serafy. 2006. Mangroves as fish habitat: 50 years of field studies. Marine Ecology Progress Series 318:1–18.

FDEP (Florida Department of Environmental Protection). 2016. Information about coastal habitats. http://www.dep.state.fl.us/coastal/habitats/

Fisco, D. 2016. Reef fish spatial distribution and benthic habitat associations on the southeast Florida Reef Tract. Thesis. Nova Southeastern University. http://nsuworks.nova.edu/occ_stuetd/408

Ganz, H. 2015. rvc: a statistical package for the Reef Visual Census. R package version 0.3.1. https://github.com/jeremiaheb/rvc

Gerard, T., E. Malca, B. A. Muhling, I. Mateo, and J. T. Lamkin. 2015. Isotopic signatures in the otoliths of reef-associated fishes of southern Florida: linkages between nursery grounds and coral reefs. Regional Studies in Marine Science 2:95–104.

Gill, D. A., et al. 2017. Capacity shortfalls hinder the performance of marine protected areas globally. Nature, *in press*. https://doi.org/10.1038/nature21708

Gratwicke, B., and M. R. Speight. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66:650–667.

Green, A. L., A. P. Maypa, G. R. Almany, K. L. Rhodes, R. Weeks, R. A. Abesamis, M. G. Gleason, P. J. Mumby, and A. T. White. 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biological Reviews 90:1215–1247.

Green, E. P., and F. T. Short. 2003. The world atlas of seagrasses. University of California Press, Berkley, California, USA.

Halpern, B. 2004. Are mangroves a limiting resource for two coral reef fishes? Marine Ecology Progress Series 272:93–98.

Hamilton, S. 2013. Assessing the role of commercial aquaculture in displacing mangrove forest. Bulletin of Marine Science 89:585–601.

Heald, E. J. 1971. The production of organic detritus in a south Florida estuary. Sea Grant Technical Bulletin No. 6. University of Miami Sea Grant Program, Miami, Florida, USA.

Igulu, M. M., I. Nagelkerken, M. Dorenbosch, M. G. G. Grol, A. R. Harborne, I. A. Kimirei, P. J. Mumby, A. D. Olds, and Y. D. Mgaya. 2014. Mangrove habitat use by juvenile reef fish: Meta-analysis reveals that tidal regime matters more than biogeographic region. PLoS ONE 9:e114715.

Jones, M. J., M. D. Linsley, and S. J. Marsden. 1995. Population sizes, status, and habitat associations of the restricted-range bird species of Sumba, Indonesia. Bird Conservation International 5:21–52.

Jones, D. L., J. F. Walter, E. N. Brooks, and J. E. Serafy. 2010. Connectivity through ontogeny: fish population linkages among mangrove and coral reef habitats. Marine Ecology Progress Series 401:245–258.

Kilfoyle, K., B. Walker, D. Fisco, S. Smith, and R. Spieler. 2015. Southeast Florida coral reef fishery-independent baseline assessment 2012–2014 summary report. Florida Department of Environmental Protection, Miami, Florida, USA. http://nsuworks.nova.edu/occ_facreports/86

Koch, E. W., et al. 2009. Non-linearity in ecosystem services: temporal and spatial variability in coastal protection. Frontiers in Ecology and the Environment 7:29–37.

Koenig, C. C., F. C. Coleman, A. M. Eklund, J. Schull, and J. Ueland. 2007. Mangroves as essential nursery habitat for goliath grouper (*Epinephelus itajara*). Bulletin of Marine Science 80:567–586.

Kuffner, I. B., J. C. Brock, R. Grober-Dunsmore, V. E. Bonito, T. D. Hickey, and C. W. Write. 2007. Relationships between reef fish communities and remotely sensed rugosity measurements in Biscayne National Park, Florida, USA. Environmental Biology of Fishes 78:71–82.

Lidz, B. H., A. C. Hine, E. A. Shinn, and J. L. Kindinger. 1991. Multiple outer-reef tracts along the south Florida bank margin; outlier reefs, a new windward-margin model. Geology 19:115–118.

Lirman, D., and P. Fong. 2007. Is proximity to land-based sources of coral stressors an appropriate measure of risk to coral reefs? An example from the Florida Reef Tract. Marine Pollution Bulletin 54:779–791.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809.

Manson, E. J., N. R. Loneragan, B. D. Harch, G. A. Skilleter, and L. Williams. 2005. A broad-scale analysis of links between coastal fisheries production and mangrove extent: a case-study for northeastern Australia. Fisheries Research 74:69–85.

Medeiros, P. R., R. S. Rosa, and R. B. Francini-Filho. 2011. Dynamics of fish assemblages on a continuous rocky reef and adjacent unconsolidated habitats at Fernando de Noronha Archipelago, tropical western Atlantic. Neotropical Ichthyology 9:869–879.

Mumby, P. J., et al. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427:533–536.

Nagelkerken, I. 2007. Are non-estuarine mangroves connected to coral reefs through fish migration? Bulletin of Marine Science 80:595–607.

Nagelkerken, I., M. G. G. Groll, and P. J. Mumby. 2012. Effects of marine reserves vs nursery habitat availability on structure of reef fish communities. PLoS ONE 7:e36906.

Nagelkerken, I., K. B. Huebert, J. E. Serafy, M. G. G. Grol, M. Dorenbosch, and C. J. A. Bradshaw. 2017. Highly localized replenishment of coral reef fish populations near nursery habitats. Marine Ecology Progress Series 568:137–150.

Nagelkerken, I., S. Kleijnen, T. Klop, R. A. C. J. van den Brand, E. Cocheret de la Morinière, and G. van der Velde. 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Marine Ecology Progress Series 214:225–235.

Nagelkerken, I., C. M. Roberts, G. van der Velde, M. Dorenbosch, M. C. van Riel, E. Cocheret de la Morinière, and P. H. Nienhuis. 2002. How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. Marine Ecology Progress Series 244:299–305.

Nagelkerken, I., and G. van der Velde. 2002. Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curacao (Netherlands Antilles)? Marine Ecology Progress Series 245:191–204.

Odum, W. E., and E. J. Heald. 1972. Trophic analyses of an estuarine mangrove community. Bulletin of Marine Science 22:671–738.

Orth, R. J., R. L. Heck Jr., and J. van Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. Estuaries 7: 339–350.

Parrish, J. D. 1989. Fish communities of interacting shallow water habitats in tropical oceanic regions. Marine Ecology Progress Series 58:143–160.

Peduzzi, P., J. Concato, E. Kemper, T. R. Holford, and A. R. Feinstein. 1996. A simulation study of the number of events per variable in logistic regression

analysis. Journal of Clinical Epidemiology 49:1373–1379.

Pittman, S. J., C. A. McAlpine, and K. M. Pittman. 2004. Linking fish and prawns to their environment: a hierarchical landscape approach. Marine Ecology Progress Series 283:233–254.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rohmann, S., J. Hayes, R. Newhall, M. Monaco, and R. Grigg. 2005. The area of potential shallow-water tropical and subtropical coral ecosystems in the United States. Coral Reefs 24:370–383.

Saenger, P., D. Gartside, and S. Funge-Smith. 2013. A review of mangrove and seagrass ecosystems and their linkage to fisheries and fisheries management. RAP Publication 2013/09. FAO Regional Office for Asia and the Pacific, Bangkok, Thailand.

Sagarese, S. R., M. G. Frisk, T. J. Miller, K. A. Sosebee, J. A. Musick, and P. J. Rago. 2014. Application of generalized additive models to examine ontogenetic and seasonal distributions of spiny dogfish (*Squalus acanthias*) in the Northeast (US) shelf large marine ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 71:847–877.

Serafy, J. E., C. H. Faunce, and J. J. Lorenz. 2003. Mangrove shorelines fishes of Biscayne Bay, Florida. Bulletin of Marine Science 72:161–180.

Serafy, J. E., G. S. Shideler, R. J. Araújo, and I. Nagelkerken. 2015. Mangroves enhance reef fish abundance at the Caribbean regional scale. PLoS ONE 10:e0142022.

Serrano, O., E. Serrano, K. Inostroza, P. L. Lavery, M. A. Mateo, and E. Ballesteros. 2017. Seagrass meadows provide 3D habitat for reef fish. Frontiers in Marine Science 4:54.

Shideler, G. S., S. R. Sagarese, W. J. Harford, J. Schull, and J. E. Serafy. 2015. Assessing the suitability of mangrove habitats for juvenile Atlantic goliath grouper. Environmental Biology of Fishes 98:2067–2082.

Smith, S. G., J. S. Ault, J. A. Bohnsack, D. E. Harper, J. Luo, and D. B. McClellan. 2011. Multispecies survey design for assessing reef-fish stocks, spatially-explicit management performance, and ecosystem condition. Fisheries Research 109:25–41.

Stallings, C. D. 2009. Fishery-independent data reveal negative effect of human population density on Caribbean predatory fish communities. PLoS ONE 4:e5333.

UNEP-WCMC (United Nations Environment Programme's World Conservation Monitoring Centre), and F. T. Short. 2016. Global distribution of seagrasses. Version 4.0. Fourth update to the data layer used in Green and Short (2003). UNEP World Conservation Monitoring Centre, Cambridge, UK. http://data.unep-wcmc.org/datasets/7

Verweij, M. C., I. Nagelkerken, S. L. J. Wartenbergh, I. R. Pen, and G. van der Velde. 2006. Caribbean mangroves and seagrass beds as daytime feeding habitats for juvenile French grunts, *Haemulon flavolineatum*. Marine Biology 149:1290–1299.

Verweij, M. C., I. Nakelkerken, I. Hans, S. M. Ruseler, and P. R. D. Mason. 2008. Seagrass nurseries contribute to coral reef fish populations. Limnology and Oceanography 53:1540–1547.

Walker, B. K. 2012. Spatial analyses of benthic habitats to define coral reef ecosystem regions and potential biogeographic boundaries along a latitudinal gradient. PLoS ONE 7:e30466.

Walker, B. K., L. K. B. Jordan, and R. E. Spieler. 2009. Relationship of reef fish assemblages and topographic complexity on southeastern Florida Coral Reef Habitats. Journal of Coastal Research 53:39–48.

Welsh, J. Q., C. H. R. Goatley, and D. R. Bellwood. 2013. The ontogeny of home ranges: evidence from coral reef fishes. Proceedings of the Royal Society B 280:20132066.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semi-parametric generalized linear models. Journal of the Royal Statistical Society Series B (Statistical Methodology) 73:3–36.

Zieman, J. C. 1982. The ecology of the seagrasses of south Florida: a community profile. FWS/OBS-82/25. FUS Fish and Wildlife Services, Office of Biological Services, Washington, D.C., USA.

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1943/full