Fish use of reef structures and adjacent sand flats: implications for selecting minimum buffer zones between new artificial reefs and existing reefs

R. Claire Rosemond[1], Avery B. Paxton[1,2,*], Hayley R. Lemoine[1], Stephen R. Fegley[1,3], Charles H. Peterson[1,2]

[1]**Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, NC 28557, USA**
[2]**Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599, USA**
[3]**Coastal Environmental Consulting and Planning, Morehead City, NC 28557, USA**

ABSTRACT: Artificial reefs are deployed worldwide to enhance fisheries. Placement of artificial reefs relative to nearby existing artificial and natural reefs can influence fish use of these structures, yet no quantitative guidelines exist for selecting optimal distances between new and existing reefs. Here, we documented fish abundance, biomass, species richness, community composition, and key environmental variables on 24 artificial and natural reefs with adjacent sand flats to infer minimum buffer distances around existing reefs where placement of new artificial reefs should be avoided. At each site, we surveyed 4 transects: one 30 m transect across reef structure and 3 consecutive 30 m transects of increasing distance from the reef across sand bottom. Fish abundance, biomass, and species richness were highest on reefs and progressively decreased across adjacent sand flats. Environmental variables influenced these community metrics, but patterns of fish habitat use persisted. Fish community composition shifted gradually from reefs across adjacent sand flats, with fish communities on reefs most dissimilar to communities on sand bottom farthest from the reefs. A minimum buffer of 60 m (30 m around existing reefs plus 30 m around new reefs) or 120 m (60 m plus 60 m) between reefs would encompass 77 and 97 %, respectively, of fishes utilizing sand-bottom habitat around each reef. Future artificial reef deployment should maintain these minimum buffer zones between reefs to more effectively enhance fisheries by minimizing attraction of fishes from existing reefs, while also maximizing food resource availability for reef fishes and area for routine reef fish behaviors.

KEY WORDS: Fish communities · Fisheries · Fisheries management · Artificial reef deployment · Natural reefs

INTRODUCTION

Artificial reefs are human-made materials deployed on the seafloor, often intended to mimic natural reefs (Baine 2001) and influence physical, biological, and socioeconomic processes related to living marine resources (Seaman 2000). Resource managers incorporate artificial reefs into management plans as a method to enhance fisheries in many parts of the world, such as the USA and Japan (McGurrin et al. 1989, Yamane 1989, Seaman & Sprague 2013). Artificial reef productivity varies with controllable factors, such as reef design and placement, and environmental variables (Strelcheck et al. 2005). To maximize fish production, greater emphasis should be placed on determining optimal location, design, and spatial arrangement of artificial reefs (Bohnsack & Sutherland 1985, Bortone 1998, Strelcheck et al. 2005).

Reef placement can substantially influence fish communities even at relatively small scales (m) (Walsh

1985). For example, on artificial reefs separated from other artificial reefs by distances of 5, 10, 25, and >35 m, total fish abundance and species richness increases with greater isolation distance from other reefs (Jordan et al. 2005). On artificial reefs spaced 60 m apart and artificial reefs spaced 2 m apart, the more widely spaced reefs support higher numbers of fishes (Frazer & Lindberg 1994). In addition, as spacing between artificial reefs increases, fish biomass increases (Strelcheck et al. 2005). These observed trends in fish distribution among increasingly isolated reefs likely result from density-dependent interactions related to prey resources and foraging opportunity (Lindberg et al. 1990, Vanderklift et al. 2007). Fishes may have access to greater proportion of prey with less risk of predation around reefs with enough uninterrupted area to support maximum foraging activity (Lindberg et al. 1990). Some studies have found an opposite result, with less isolated reefs supporting higher fish species richness (Molles 1978, Gascon & Miller 1981).

Reef fish behavior is not confined to reef structures; some fishes that rely on reefs for refuge also rely on prey resources found in surrounding sand habitats (Lindquist et al. 1994, Posey & Ambrose 1994). Home ranges of reef fishes include areas within which fishes exhibit patterns of space utilization for foraging, reproduction, and caring for young (Burt 1943, Jennrich & Turner 1969, Anderson 1982). On artificial reefs, heightened reef fish (red snapper *Lutjanus campechanus*) activity occurs within 100 m of reefs, and 75% of fish (*L. campechanus*) movement from reefs occurs within 30 m of reefs (Topping & Szedlmayer 2011). However, home ranges of reef fishes tend to expand at night and with fish size (Kramer & Chapman 1999, Meyer et al. 2000, Topping & Szedlmayer 2011). In general, resident fishes consume prey items closer to reefs more rapidly than those located further from reefs, creating halos of decreasing benthic prey density approaching reefs (Randall 1965, Frazer & Lindberg 1994, Johnson et al. 1994, Pondella et al. 2006, Galván et al. 2008). For this reason, sand habitats around reefs that are located farther from other reefs provide a greater density of prey items than sand habitat around reefs in closer proximity to other reefs (Jordan et al. 2005). With prey available closer to reefs, reef fishes can feed more efficiently and reduce their risk of predation (Milinski 1986), thus potentially contributing to increased abundance, biomass, and species richness on isolated reefs (Lindberg et al. 1990). Where prey halos around reefs do not overlap, it is the distance from reefs where foraging activity diminishes that

reef separation will have its maximum benefit. To optimize potential fisheries production from artificial reefs, managers should recognize the contribution of adjacent habitats, such as sand bottom, in sustaining viable fish communities on artificial reefs (Bortone et al. 1998).

Reefs and adjacent sand habitats may be managed conjointly by establishing buffer zones around reefs that encompass adjacent sand habitats. Buffer zones delineate habitats and adjacent areas for protection from development, resource extraction, or area-use change in order to enhance the conservation value of the protected areas (Burke & Gibbons 1995, Rodgers & Smith 1997, Semlitsch 1998). They may also serve to augment populations of certain species by allocating core habitat inclusive of all species' life stages (Rodgers & Smith 1997, Semlitsch 1998). Buffer zones around reefs that encompass the full range of resident fish activities should minimize resource exploitation (Grossman et al. 1997). They may be established in support of particular management objectives, such as where to place other artificial reefs relative to existing reefs to most effectively augment fisheries. Buffer zones could be defined as spaces between reefs where no additional reefs should be placed, yet no empirical recommendations exist for buffer zones around reefs to guide placement of new artificial reefs.

Artificial and natural reefs of North Carolina (NC), USA, provide ideal study sites to determine where to place artificial reefs relative to other reefs to ensure optimal enhancement of fish habitat. The inner continental shelf of NC features both artificial reefs and naturally occurring, rocky reefs that support diverse assemblages of benthic flora and fauna (Peckol & Searles 1984) and both recreationally and commercially important fish species (Chester et al. 1984, Whitfield et al. 2014). Forty-two ocean artificial reef plots, which reflect the locations of intentionally scuttled and now sunken structures, such as concrete pipes and metal ships, occur along the NC continental shelf (NC DMF 1988). Natural, rocky reefs ranging from flat pavements to extensive ledges also occur in high concentrations along the southern NC continental shelf. Some of these natural reefs occur within artificial reef plots. This matrix of co-occurring reef types provides an opportunity to determine how fishes differentially use reefs and areas of sand located between reefs.

The goal of this study was to determine where to place new artificial reefs relative to existing reefs to optimize enhancement of fish habitat as judged by observing differential fish habitat use. Specifically, we intended to (1) compare patterns of fish use of

reef structures to fish use of adjacent sand bottom extending away from reefs, (2) quantify how environmental variables influence fish occupation of reefs and adjacent sand-bottom habitats, and (3) use our findings to recommend quantitative minimum buffer zones around existing reefs where placement of new reefs should be avoided. Our results should guide management decisions regarding artificial reef deployment relative to pre-existing reefs to ensure that newly deployed artificial reefs enhance fisheries.

MATERIALS AND METHODS

Survey sites

We conducted SCUBA-diver surveys of 24 natural and artificial reefs located on the inner continental shelf of NC in Onslow Bay (Fig. 1; Table S1 in the Supplement at www.int-res.com/articles/suppl/m587 p187_suppl.pdf). All selected reefs fell within boundaries of ocean artificial reef plots designated and managed by the NC Division of Marine Fisheries. These artificial reef plots contained multiple submerged structures, including intentionally deployed artificial reef structures, such as concrete pipes and metal ships. Some artificial reef plots also contained

naturally occurring rocky reefs. To infer how reef structure influences abundance, biomass, species richness, and community composition of co-occurring fishes, we selected 6 artificial reef plots for sampling. Three were selected because they also included naturally occurring rocky reefs, allowing us to compare the fish communities utilizing natural versus artificial reefs. Two of the selected artificial reef plots are located in northern Onslow Bay, whereas the remaining 4 are approximately 110 km to the south in southern Onslow Bay. Within each of these 6 artificial reef plots, we sampled 3 to 6 natural or artificial reef structures, totaling 24 reefs. These reefs occurred at relatively shallow depths (10.7–18.8 m) and were located 1.8–14.6 km from shore.

At each reef, divers established 4 survey transects: 1 across reef structure (reef transect) and 3 consecutive collinear transects (i.e. no space between each transect) of increasing distance radiating away from the reef and across adjacent sand bottom (off-reef transects). Each transect was treated as a separate treatment, for a total of 4 treatments (on-reef, and 0–30, 30–60, and 60–90 m from reef). For the reef transect, divers routed the survey along the most prominent reef features for a total distance of 30 m. For the consecutive off-reef transects, divers routed the survey following a pre-selected heading, chosen
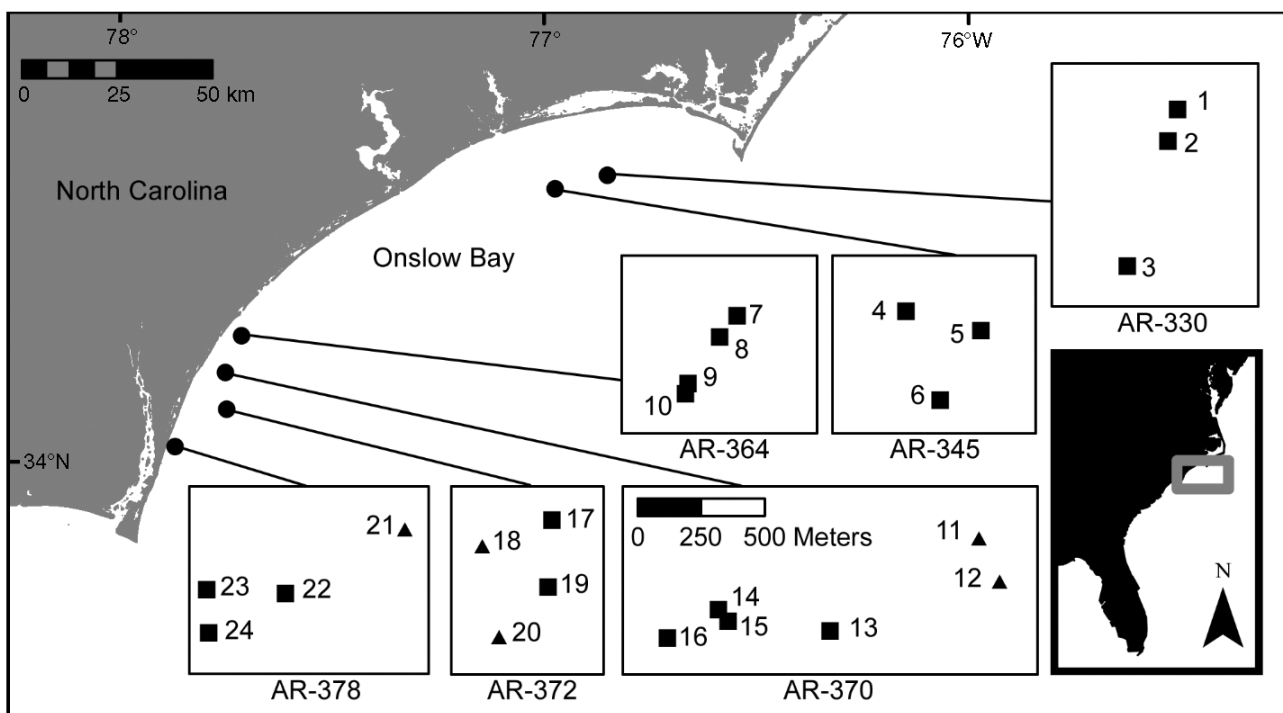

Fig. 1. Survey sites in Onslow Bay, North Carolina, USA. Black circles represent the selected subset of 6 out of 42 possible artificial reef plots. Equally magnified insets of each artificial reef plot, labeled as AR-#, contain multiple sites, numbered 1 through 24. Black squares represent artificial reefs. Black triangles represent natural reefs. Details of each site are shown in Table S1 in the Supplement

from archived side-scan sonar data, such that off-reef transects traversed sand bottom and avoided reef structures. Occasionally, the off-reef transect surveys included minor reef structures that were accounted for in complexity measurements. The first of the 3 off-reef transects began at the edge of the reef and traversed the adjacent sand flat for 30 m (0–30 m from reef). The second and third off-reef transects continued across sand bottom, at increasing distances from the reef for 30 m each (30–60 and 60–90 m from reef, respectively). Divers surveyed the fish community, habitat complexity, and water temperatures along all 4 transects. Each site was sampled once during each of 3 sampling periods (August–October 2015, November 2015–February 2016, and March–April 2016) to test for seasonal variability in fish communities (Whitfield et al. 2014). On occasion, diving conditions prohibited completion of all 4 transects at a particular site and missing transects were then not sampled during that sampling period.

Fish surveys

On each transect, divers conducted a fish survey constituting a 30 × 4 m (120 m^2) belt transect (V. E. Brock 1954, R. E. Brock 1982, Samoilys & Carlos 2000). Divers laid the 30 m transect tape along the reef and surveyed fishes simultaneously to avoid disturbing fishes via multiple swim-overs. Divers avoided double counting fishes by continuously moving, looking forward, and noting when any particular school of fish crossed from one 30 m transect to another. Along each belt transect, divers identified every fish present throughout the water column to the lowest taxonomic level possible. Divers also recorded fish abundance and fish total length (cm). Total length was estimated visually by trained divers. Biomass was calculated using the length–weight power function as:

$$W = aL^b \tag{1}$$

where L is length (cm) recorded on the fish survey and W is weight (g). When a school of fish spanned multiple sizes, L was calculated as the midpoint of the recorded size range. Species-specific morphometric values for a and b were obtained from FishBase (Froese & Pauly 2016). For species identifiable only to genus or family, we substituted average morphometric values of local congeners or confamiliars. We also computed species richness (S, no. of species) for fish communities on each transect. Species richness was computed using those fishes identified to species

level. For fishes identified only to the family level, the family was used for our calculation of species richness (e.g. scad *Decapterus* sp.). We characterized fish as either demersal or pelagic (Froese & Pauly 2016). We distinguished species of management concern, specifically those identified as members of the snapper-grouper complex (South Atlantic Fisheries Management Council 1983). These include commercially and recreationally important species, many of which have reef affinities (Parker & Dixon 1998, Whitfield et al. 2014).

Habitat complexity

To measure habitat complexity of reef structures and adjacent sand flats, we followed methods developed by Dustan et al. (2013) to establish a digital reef rugosity (DRR) metric along each 30 m transect. We collected measurements of the contour of the benthic substrate using an Onset HOBO U20 titanium water level logger (U20-001-02-Ti) containing a pressure-transducer that records fine-scale variations in depth, from which bottom elevations were inferred. We swam about 10 cm s^{-1} over the length of each transect, while suspending the logger from a line in a position as close as possible to the substrate. We raised the logger 1 m above and rapidly lowered the logger back down to the substrate surface in a spike motion 5 times at the start and end of each transect and 3 times every 5 m between these endpoints. Because the logger records continuously during each dive, these spikes were used to identify the beginning and end points of each transect within the data stream and to calibrate the distance surveyed. During post-dive processing, we removed the distance calibration spikes from each transect and converted the raw pressure recorded by the pressure-transducer from units of pounds per square inch (psi) to m, corresponding to the water depth. Atmospheric pressure at the surface was assumed to be 1 atm. If the sampling rate differed from the target rate of 10 cm s^{-1}, then the transect length was scaled for comparison. For each transect, the mean, minimum, and maximum depths were determined. DRR (Dustan et al. 2013) was calculated as the standard deviation of depths (m) along each transect.

Water temperature

We measured water temperature on each 30 m transect using the same Onset HOBO U20 titanium

water level logger (U20-001-02-Ti) that we used to measure habitat complexity. The water level logger recorded temperature every second over the duration of each transect. These raw temperature values were used to calculate mean temperature (°C) over each transect.

Statistical analyses

Data analyses were conducted using R version 3.2.2 (R Development Core Team 2015). Alpha levels for all statistical tests were 0.05 unless otherwise stated.

On- and off-reef fish communities

To investigate patterns of habitat use by fish communities on and off reefs, we regressed power-transformed fish abundance, biomass, and species richness data separately against the fixed effects of transect number and reef type with linear mixed-effects models fit in the 'nlme' package (Pinheiro et al. 2016), utilizing the log-likelihood maximized (ML) method. The linear mixed-effects models also incorporated the random effects of reef site nested within reef plot. We retained only significant factors in the regression models. Initial results revealed that reef type was non-significant (ANOVA, $F_{(abundance: reef type)}$ = 0.04, $F_{(biomass: reef type)}$ = 0.003, $F_{(species richness: reef type)}$ = 0.3; p > 0.05), so artificial and natural reefs were analyzed conjointly. Fish abundance, biomass, and species richness data were transformed with Box-Cox power transformations (Box & Cox 1964, Osborne 2010) as:

$$y' = (y + c)^{\lambda} \qquad (2)$$

All power transformations (λ) were computed with the 'boxcox' function in the 'MASS' package (Venables & Ripley 2002). Power transformations (λ) for abundance, biomass, and species richness data were $\lambda = -0.14$, $\lambda = -0.67$, and $\lambda = 0.02$, respectively. The frame shifts (c) within the Box-Cox transformations for abundance, biomass, and species richness data were $c = 1.00$, $c = 0.09$, and $c = 2.00$, respectively, and were included to improve normality of model residuals. Using the Shapiro-Wilk normality test (Shapiro & Wilk 1965), we tested the normality of the residuals from the linear mixed-effects models. The residuals of linear mixed-effects models were normal (Shapiro-Wilk, $p_{(abundance)} > 0.05$; $p_{(species richness)} > 0.05$) or approached normality

(Shapiro-Wilk, $p_{(biomass)} = 0.01$), so we tested for differences in fish community metrics (abundance, biomass, and species richness) on- and off-reef (0–30, 30–60, and 60–90 m from reef) using ANOVA. The linear mixed-effects model of fish biomass violated the assumption of normality; however, the magnitude of the effect of non-normality was minimal compared to the factor effects because of the low calculated alphas. Consequently, we interpreted the results as significant (p < 0.05), although we did not know actual alpha values. To examine how patterns in fish occupancy of reefs and adjacent sand habitats may have been influenced by a complete absence of fish, we quantified the proportion of transects (on-reef and 0–30, 30–60, and 60–90 m from reef) on which we observed zero fishes (fish abundance = 0) out of the total number of transects per distance from reef. This analysis highlights the difference between transects occupied by zero fish versus transects occupied by low numbers of fish.

To determine whether fish community composition varied among transects (on-reef and 0–30, 30–60, and 60–90 m from reef), we used analysis of multivariate homogeneity of group dispersions (PERMDISP), permutational ANOVA (PERMANOVA), nonmetric multidimensional scaling (NMS) analysis, and similarity percentages (SIMPER) analyses. These tests were applied to transformed fish abundance at the species taxonomic level. We transformed fish abundance data with a Box-Cox power transformation as in Eq. (2), where $\lambda = 0.5$ and $c = 0.001$ (Osborne 2010). The power transformation (λ) reduced the effects of high abundances due to fish schooling, while still including rare species in the analyses (Clarke & Warwick 2001). The frame shift (c) preserved the differences between low abundances. Transects with recorded fish abundance of zero were excluded from multivariate analyses.

To test how robust our transformed data were for statistical analyses, we examined the homogeneity of dispersion among our sample groups (on-reef and 0–30, 30–60, and 60–90 m from reef) using PERMDISP analysis in the 'vegan' package (Oksanen et al. 2016). To test for differences in variability among on- and off-reef (0–30, 30–60, and 60–90 m from reef) fish communities, we performed an ANOVA of the distances to the centroid of each group. To explicitly test whether fish community composition differed by distance from reef, we analyzed our data with PERMANOVA in the 'vegan' package (Oksanen et al. 2016) with 1000 iterations. For the PERMANOVA analysis, we used Bray-Curtis dissimilarities between power-transformed fish species

abundances among on- and off-reef communities. NMS was performed on the fish community data in the 'vegan' package (Oksanen et al. 2016) with 1000 iterations. Samples were mapped into the ordination space using the ecological distances between samples ordered by rank terms. Bray-Curtis distances calculated on power-transformed data summarized pairwise distances among samples and helped overcome the problem of joint absences in species data (Oksanen et al. 2016). A Shepard diagram ensured linearity between the ordination distance and Bray-Curtis distance. Fish species mainly responsible for the Bray-Curtis dissimilarity of power-transformed data among on- and off-reef groups were determined using SIMPER analysis. SIMPER, run with 1000 iterations, identified species that contributed to the Bray-Curtis dissimilarity between on-reef and off-reef (0–30, 30–60, and 60–90 m from reef) fish communities (Clarke 1993).

Influence of environmental variables

To examine the influence of environmental variables on fish use of reefs and adjacent sand-bottom habitats, we used regression tree analyses (Breiman et al. 1984). We developed separate regression tree models for fish abundance, biomass, and species richness using the ANOVA method of recursive partitioning of untransformed community metric data conducted in the 'rpart' package (Therneau et al. 2015). The environmental factors included in these analyses were depth, habitat complexity, water temperature, and reef type. We pruned over-fitted trees using kfold cross-validation and visualized the regression trees using the 'rpart.plot' package (Milborrow 2015).

RESULTS

A total of 37 220 fishes belonging to 70 species and 27 families were observed across 230 transects on 24 temperate reefs located on the continental shelf of NC (Table S2 in the Supplement). The most abundant genus was scad *Decapterus* sp., with 11 182 observed fishes. The most abundant species was tomtate *Haemulon aurolineatum*, with 8982 observed fish. The total biomass of fishes surveyed across the study was 2732 kg. Fishes belonging to the snapper-grouper management complex contributed to 53% of the total fishes observed (19 745 fishes).

On- and off-reef fish communities

Abundance of fishes declined with increasing distance across adjacent sand-bottom habitats (Fig. 2). Results of the linear mixed-effects model of power-transformed fish abundance indicated that mean fish
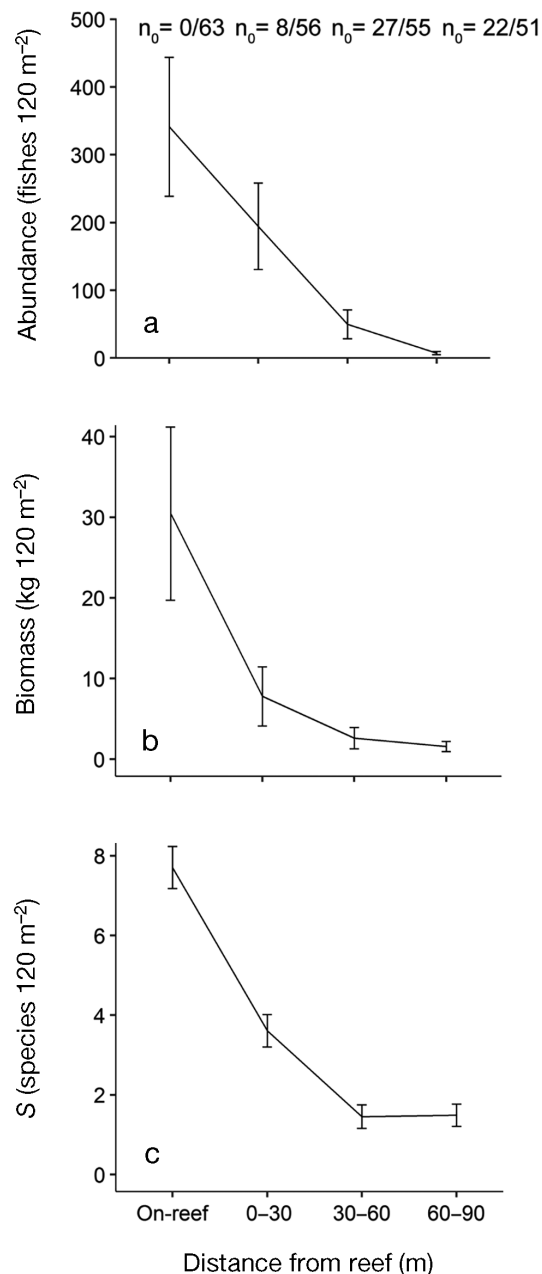

Fig. 2. Fish community metrics (mean ± SE). (a) Untransformed fish abundance per distance from reef. Numbers (n_0) represent the proportions of transects with zero observed fish (abundance = 0) out of the total number of transects per distance from reef. (b) Untransformed fish biomass per distance from reef. (c) Untransformed species richness (*S*) per distance from reef

abundance was highest on reefs (pooled artificial and natural; see 'Materials and methods') and decreased significantly across 0–30, 30–60, and 60–90 m from reefs (Fig. 2a; ANOVA, $F_{(distance)}$ = 73.13, p < 0.0001, random effects: reef plot and reef site). Mean untransformed fish abundance on reefs decreased by 43% across 0–30 m from reefs, another 42% across 30–60 m from reefs, and another 13% to 90 m from reefs. Mean (untransformed) fish abundance on sand bottom across 60–90 m from reefs was 2% of mean (untransformed) abundance observed on reef structures.

For surveys 30–60 and 60–90 m from reefs, we observed zero fish on almost half of the total transects at each of these distances (Fig. 2a). The proportion of transects with zero recorded fish (fish abundance = 0) was the greatest 30–60 m from reefs (n_0 = 27/55), followed by transects 60–90 m from reefs (n_0 = 22/51). Transects with zero observed fish 0–30 m from reefs accounted for less of a proportion of the total (n_0 = 8/56), and there were no transects with zero observed fish across on-reef transects (n_0 = 0/63).

Results from the linear mixed-effects model of power-transformed fish biomass revealed that fish biomass decreased in a pattern similar to fish abundance (Fig. 2b; ANOVA, $F_{(distance)}$ = 65.88, p < 0.0001, random effects: reef plot and reef site). Fish biomass, like fish abundance, was highest on reefs, decreasing with increased distance from reefs. Fish biomass decreased significantly across 0–30, 30–60, and 60–90 m from reefs. Across 0–30 m from reefs, fish biomass decreased by 74%, the greatest percent change across transects. Fish biomass across 60–90 m from reefs was 5% of on-reef mean (untransformed) fish abundance. Similarly, fish species richness also decreased with increased distance from reefs (Fig. 2c). Results from the linear mixed-effects model of transformed species richness indicated that species richness was highest on reefs, decreased significantly across 0–30 and 30–60 m from reefs, and remained low 60–90 m from reefs (ANOVA, $F_{(distance)}$ = 64.70, p < 0.0001, random effects: reef plot and reef site). Across 60–90 m from reefs, fish species richness was 19% of (untransformed) on-reef species richness.

Fish communities (fish species and their relative abundances) on and off reefs were dispersed similarly among groups (on-reef and 0–30, 30–60, and 60–90 m from reef) (ANOVA/PERMDISP, $F_{3,172}$ = 2.51, p > 0.05). Consequently, fish community data did not violate the assumptions of further multivariate testing. Fish communities on reefs were most similar to those found 0–30 m from reefs, whereas fish communities 30–60 and 60–90 m from reefs were
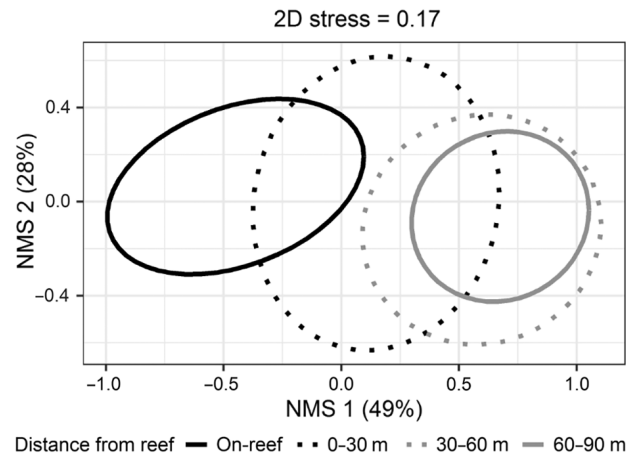

Fig. 3. Nonmetric multidimensional scaling (NMS) ordination of fish community at the species level based on the Bray-Curtis dissimilarity matrix of Box-Cox transformed abundance of fishes. Ellipses are 50% confidence intervals for samples classified by distance from reef

similar to each other and most dissimilar to reef communities (Fig. 3; PERMANOVA, $F_{3,172}$ = 11.11, p < 0.001). Fish communities changed gradually across adjacent sand habitats, with the communities found 0–30 m from reefs overlapping with both reef communities and communities occupying the farthest distances from reefs. Results from SIMPER analysis indicated that the dissimilarity between on-reef and off-reef transects was driven by (1) a decrease, from the reefs across adjacent sand flats, of highly abundant planktivores that were likely feeding on plankton in the water column around and above reefs, and (2) an increase, across contiguous sand flats, of transient pelagic predators that were likely moving between reefs (Table 1; Table S3 in the Supplement). Demersal reef fish species were present on reef structures and across adjacent sand habitats and also contributed to differences in community composition among transects (Table 1; Table S3).

Influence of environmental variables

Of the environmental variables included in the regression tree analyses, reef type did not influence fish community metrics on or off reefs. Depth and habitat complexity influenced fish abundance on reefs and 0–30 m from reefs but did not drive fish abundance 30–60 m from reefs or 60–90 m from reefs (Fig. 4a). On reefs and 0–30 m from reefs, habitats at depths ≥19 m supported higher mean fish abundance (931 fishes) than habitats at depths <19 m (198 fishes). At shallower depths (<19 m), the habitats

Table 1. SIMPER analysis for on- and off-reef fish communities. Species that most influenced dissimilarity were more abundant on reefs. Percentages are mean percentage contribution to dissimilarity per species for off-reef communities compared to on-reef communities. Asterisks indicate permutation p-values (probability of getting larger or equal mean contribution in random permutation of the group factor) with significance level of *p < 0.05, **p < 0.01, or ***p < 0.001

Scientific name	Common name	Demersal or pelagic	Functional group	Contribution to dissimilarity to on-reef communities (%)		
				0–30 m from reefs	30–60 m from reefs	60–90 m from reefs
Stenotomus sp.	Longspine porgy/scup	Demersal	Benthic carnivore	16.8	14.4	14.2
Haemulon aurolineatum	Tomtate	Demersal	Planktivore/ omnivore	14.2*	11.6	11.5
Diplodus holbrookii	Spottail pinfish	Demersal	Omnivore	12.6	13.8**	14.8**
Centropristis striata	Black sea bass	Demersal	Benthic carnivore	10.7	14.8***	16.5***
Decapterus sp.	Scad sp.	Pelagic	Planktivore/ invertivore	7.6	8.9	3.8
Halichoeres bivittatus	Slippery dick	Demersal	Benthic carnivore	4.6	5.3	5.8*
Serranus subligarius	Belted sandfish	Demersal	Invertivore	3.5*	3.6*	4.0***
Cumulative contribution (%)				70.0	72.4	70.6
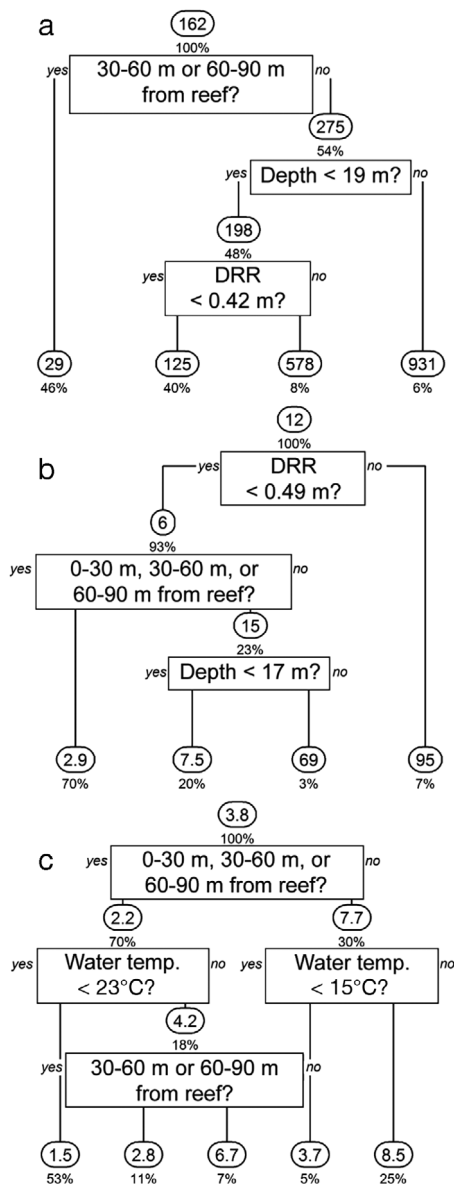
with DRR >0.42 m supported higher mean fish abundance (578 fishes) than habitats with DRR <0.42 m (125 fishes). Sand-bottom habitats farthest away from reefs supported lower mean abundances, regardless of the influence of environmental variables. The splitting criterion that influenced fish abundance 30–60 and 60–90 m from reefs was simply the categorical distance from reef.

Depth and complexity also influenced fish biomass on and off reefs; complexity most greatly influenced the distribution of fish biomass (Fig. 4b). DRR ≥0.49 m supported higher mean fish biomass (95 kg m^{-2}) than DRR <0.49 m (6 kg m^{-2}). Of habitats that were less complex (DRR <0.49 m), reefs supported higher mean fish biomass (15 kg m^{-2}) than off-reef habitats (2.9 kg m^{-2}). Reefs located at depths ≥17 m supported higher mean fish biomass (69 kg m^{-2}) than those located at more shallow depths (<17 m) (7.5 kg m^{-2}). Regardless of the influences of depth and complexity, off-reef habitats supported less fish biomass than reefs.

Water temperature was the main driver of species richness on and off reefs (Fig. 4c). Mean water temperature ≥15°C supported higher mean species richness on reefs (S = 8.5) than temperature <15°C (S =

Fig. 4. Regression model results. (a) Untransformed fish abundance (fishes per 120 m^2), (b) untransformed fish biomass (kg per 120 m^2), (c) untransformed species richness (S per 120 m^2). Rectangular nodes include splitting criteria determined by environmental variable conditions. The values in the ellipsoidal nodes represent mean fish abundance of all samples satisfying the splitting criteria before (above) and after (below) nodes. Percentages represent the percentage of samples included before (above) and after (below) each node. Depth is mean depth (m) per transect, DRR is mean digital reef rugosity (m) per transect, and water temp. is mean water temperature (°C) per transect

3.7). Along sand-bottom habitats, mean water temperature >23°C supported higher mean species richness ($S = 4.2$) than temperature <23°C ($S = 1.5$). Regardless of the influence of mean water temperature on species richness, reef habitats supported higher mean species richness than sand-bottom habitats.

DISCUSSION

We estimated minimum buffer zones around existing reefs, in which the placement of new artificial reefs should be avoided, by identifying distance ranges from reefs where reef fishes utilized adjacent sand-bottom habitats. Our study revealed that fish abundance, biomass, and species richness were highest on reefs and decreased significantly across adjacent sand bottom, with the greatest magnitude decrease occurring across 0–30 m from reefs. Environmental variables influenced fish community metrics, with greater depth, habitat complexity, and water temperature supporting higher fish abundance, biomass, and species richness; however, the pattern of decreasing fish community metrics with distance from reefs remained, despite the influence of environmental variables. Fish community composition shifted gradually across adjacent sand flats, with reef communities most dissimilar to communities occupying sand bottom 30–60 and 60–90 m from reefs.

To explicitly estimate minimum buffer zones, we incorporated findings from analyses of on- and off-reef fish communities. We calculated the percent of the mean number of fishes occupying each off-reef transect (0–30, 30–60, and 60–90 m from reef) out of the total mean number of fishes occupying all 3 off-reef transects. We then identified 2 specific buffer zone distances around reefs and estimated the percentages of fishes utilizing off-reef habitats within the respective buffers. Our buffer zone recommendations are based on realistic management objectives to enhance fisheries by introducing artificial reefs.

A buffer zone of 60 m (30 m around existing reefs plus 30 m around new reefs) would include 77% of the mean number of fishes occupying adjacent sand flats and 90% of the total mean numbers of fishes observed on reefs and across adjacent sand-bottom habitats (Fig. 5). A buffer zone of 120 m (60 m plus 60 m) would include 97% of the mean number of fishes occupying sand flats and 99% of total mean numbers of fishes observed on and off reefs.

We found a significant decrease in fish abundance, biomass, and species richness across sand flats up to
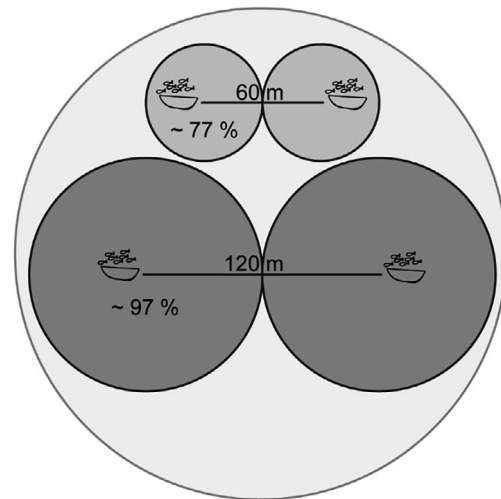

Fig. 5. Buffer zones and percentages of fishes occupying respective habitat areas. Buffer zones of 60 m and 120 m between reefs delineate areas around reefs (shaded circles) that encompass percentages of mean untransformed abundance of fishes observed occupying sand habitat

90 m from reefs. Trends of decreased fish abundance and species richness with increased distance from reefs exist in other locations and reef habitats (Stanley & Wilson 1997, Lokkeborg et al. 2002, Vanderklift et al. 2007, dos Santos et al. 2010). On the southeastern Brazilian coast, fishes travel from artificial reefs to 100 m from reefs, with a sharp decrease in total fish abundance and species richness at 50 m or less from reefs; however, ranges of movement are species-specific (dos Santos et al. 2010). A similar trend exists on natural reefs on the coast of Australia: reef fish density is highest immediately adjacent to reefs and decreases to 30 m from reefs (Vanderklift et al. 2007). For each study, including ours, the extent of fish habitat utilization should be considered relative to the constraints of the sampling design (distance bin sizes) and analyses.

Our results on fish community composition are consistent with previously recorded observations of the influence of distance from reefs on fish communities (Jordan et al. 2005, dos Santos et al. 2010). Few studies have directly studied fish community composition across a gradient of increasing distance from reefs; of those that have, studies note species-specific responses to such a gradient (Jordan et al. 2005, dos Santos et al. 2010). We found that fish community composition shifted gradually across adjacent sand-bottom habitat, with communities located 30–60 and 60–90 m from reefs most dissimilar to reef communities. This shift was, in part, due to higher abundances of tomtate *Haemulon aurolineatum* on reef

structures than on sand bottom farthest from reefs, which contributed to the dissimilarity between on- and off-reef communities. High numbers of *H. aurolineatum* can occur as recruits on artificial reef structures (Simon et al. 2011), and adult *H. aurolineatum* can drive decreases in fish abundance with increased distance from reefs (dos Santos et al. 2010). The *H. aurolineatum* that we documented at high abundances on reefs may be recruits or adults seeking refuge. The shift in fish community composition across sand-bottom habitats may also be driven by species-specific foraging patterns. Foraging ranges are species-specific and vary greatly (Ogden & Ehrlich 1977, Burke 1995, Kurz 1995); therefore, our results of fish distribution include effects of species-specific foraging ranges.

Influences of environmental variables on fish communities are well documented. The influences of depth, habitat complexity, and water temperature on fish community metrics (abundance, biomass, and species richness) found in this study are similar to previously recorded observations (McGehee 1994, Rilov & Benayahu 2000, Whitfield et al. 2014). For example, reef depth influences fish distribution and abundance on natural reefs off the coast of Puerto Rico (McGehee 1994). In the northern Red Sea, vertical relief and habitat complexity drive fish communities on artificial reefs, with more complex structures supporting higher abundance and species richness (Rilov & Benayahu 2000). A study of natural and artificial reefs in Onslow Bay, NC (also the location of our study sites) showed that depth and water temperature influence the structure of fish communities on reefs (Whitfield et al. 2014), which is consistent with our results. Many studies compare fish communities on natural and artificial reefs, highlighting differences (Thanner et al. 2006) and similarities (Matthews 1985, Recasens et al. 2006). Differences in fish communities on natural and artificial reefs are likely driven by habitat complexity (Rilov & Benayahu 2000, Hackradt et al. 2011). In the present study, reef type did not drive fish community metrics. The lack of influence of reef type may be a result of similar habitat complexities between the natural and artificial reefs that we studied; many of the artificial reefs that we surveyed were low-lying concrete structures that mimic the substrate and relief of naturally occurring, rocky reefs. Reef size can also influence fish community structure on natural and artificial reefs (Bohnsack et al. 1994, Jordan et al. 2005). The scope of the present study did not include reef size, as we did not have a relevant metric to describe this variable. From archived side-scan sonar, we could deter-

mine an approximate 'footprint' area of each reef, but we were not confident that this metric would accurately portray the influence of reef size. For example, the 'footprint' of an artificial reef constructed of concrete pipes included some areas of sand between pipes, resulting in a greater 'footprint' area than the 'footprint' of a scuttled ship, even though the ship had a greater volume and was composed of more materials. Future studies should examine the influence of reef size on fish utilization of sand flats adjacent to reefs using relevant reef size metrics.

Due to limited survey time underwater, we did not assess the movement of fishes beyond 90 m from reefs. Because fish abundance across 60–90 m from reefs reached such a low percentage of on-reef abundances, we postulate that a buffer of 90 m would encompass the majority (>97%) of reef fishes utilizing sand flats around reefs. We acknowledge that reef fishes may be utilizing sand habitat past 90 m from reefs; therefore, a buffer zone of 180 m (90 m plus 90 m) between reefs may not include the full community of reef fishes utilizing sand habitat around reefs. We were unable to survey at night due to limited suitable survey conditions. From our daytime data, we estimated the extent of fish use of reefs and adjacent sand flats during the daytime but could not extrapolate activity to address nocturnal activity. Some reef fish species are known to forage greater distances from reefs at night than during the day (Burke 1995, Meyer et al. 2000, Topping & Szedlmayer 2011); therefore, patterns of fish habitat use that we observed during the day may not encompass the full extent of fish movement from reefs nocturnally due to foraging behavior. The buffer zones discussed in the present paper should be interpreted as minimum buffer zones because actual habitat use by reef fishes may extend past our survey range and may also extend nocturnally, as fishes may travel greater distances from reefs to forage at night.

Our buffer zone recommendations were determined based on habitat use by reef fishes. This method for determining buffer zones was employed in other studies (Burke & Gibbons 1995, Semlitsch 1998); however, these other studies focused on terrestrial or freshwater habitats rather than marine habitats. One study of habitat use by reef fishes found similar trends of decreased community metrics with distance from reefs, but researchers chose to recommend a maximum buffer zone based on that information, not a minimum buffer zone (dos Santos et al. 2010). The distinction between the study by dos Santos et al. (2010) and ours is important because their study focused on 'reef fishability' and did not

take into account the positive effects of reef isolation as described by Jordan et al. (2005), as our study did. The goal of the dos Santos el al. (2010) study was to maximize inshore catch by fishermen by placing reefs in close proximity to each other, whereas our goal and the goal of Jordan et al. (2005) was to maximize prey resources available to reef fishes and to subsequently increase fish abundance with increased reef isolation. Our study did not directly test the influence of reef isolation on reef fish communities. In many cases, increased reef isolation supports greater fish abundance, biomass, and species richness (Walsh 1985, Frazer & Lindberg 1994, Jordan et al. 2005, Strelcheck et al. 2005); however, when reef size or depth co-vary with isolation, fish species richness decreases with increased reef isolation (Molles 1978, Gascon & Miller 1981).

We recommend minimum buffer zones to optimize the enhancement of fish habitat by (1) minimizing attraction from existing reefs, (2) maximizing food resource availability in off-reef habitats, and (3) maximizing area for routine fish behaviors, including reproducing and foraging. Our recommended buffer zones would minimize attraction from existing reefs by allowing access to sand habitats that support reef fish communities. With access to adequate food resources, fishes would not need to colonize new reefs for additional prey but, arguably, could still randomly move between reefs. Our recommended buffer zones take into account habitat utilization by reef fishes and are delineated based on significant decreases in fish abundance across sand habitats and an increased proportion of surveys with zero recorded fish at farthest distances from reefs. We recorded multiple species identified as benthic carnivores that were more abundant off-reef than on-reef and some that are known foragers (Meyer et al. 2000). Maximizing buffer zones between reefs would optimize the foraging habitat available to these fishes. We also found higher numbers of pelagic predators, which were likely moving between reefs. The gradual change of fish communities across sand habitat adjacent to reefs, as observed in this study, suggests that as distance increases from reefs, fewer reef-associated fishes utilize the habitat and more mobile predators utilize sand flats as they move between reefs.

In summary, this study of 24 natural and artificial reefs on the southeastern US continental shelf revealed that fish abundance, biomass, and species richness decreased with increased distance from reefs across adjacent sand bottom, despite the influence of environmental variables. Fish community composition shifted gradually with increased dis-

tance from reefs: on-reef fish communities were most dissimilar to fish communities occupying sand habitat farthest from reefs. Based on these results, we argue for establishing minimum buffer zones between reefs based on areas of high habitat use by reef fishes. Although other research has focused on fish community use of reefs and adjacent sand bottom, none has suggested minimum buffer zones between reefs to encompass adjacent sand flats utilized by reef fishes. Resource managers should avoid the placement of artificial reefs within our recommended minimum buffer zones around existing reefs to allow fishes to have maximum access to food resources, thus optimizing the enhancement of fish habitat and potential fisheries production.

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