NO EFFECT OF MARINE PROTECTED AREAS ON MANAGED REEF FISH SPECIES IN THE SOUTHEASTERN UNITED STATES ATLANTIC OCEAN

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Abstract:

[1] Abbreviations:
SEUS – southeast United States
SAFMC – South Atlantic Fishery Management Council
MARMAP – Marine Resources Monitoring Assessment and Prediction Program
SERFS – Southeast Reef Fish Survey
NSC – Northern South Carolina
ED - Edisto
NF – North Florida
LF – Length Frequency
LH – Life History
RFS – Reef Fish Species
GLP – General Linear Power Analyses

Marine protected areas (MPAs) have been recommended as an essential conservation tool for ecosystems and fisheries, with MPA coverage increasing four-fold globally since 2000. Despite the increased usage of MPAs, empirical results and scientists are divided on the effectiveness of MPAs to reach their conservation and management goals. In 2009, the South Atlantic Fishery Management Council established eight deep-water partially-protected MPAs off the southeast United States (SEUS) Atlantic coast with the goal of protecting long-lived, deep-water, reef-associated fishery species. Data collected during fish trapping from 2000 to 2018 as part of a fisheries-independent survey were used to evaluate the impacts of protection on a subset of fish species in three of these MPAs. There was a modest positive shift to larger fish observed in two of the MPAs and to older fish for one species, *Pagrus pagrus* (Linnaeus, 1758), in one of the MPAs relative to adjacent fished areas; however, there was either no change or a decrease in managed reef fish abundance in each MPA relative to adjacent fished areas. Based on these metrics, it does not appear that the SEUS MPAs have yet been effective at protecting managed reef fish species. Given that these MPAs have low enforcement, future assessments should examine compliance within the SEUS MPAs to determine if lack of success is due to illegal fishing, species examined, or MPA design before making a final determination if deep-water MPAs are an effective strategy for fisheries managers in the SEUS.

Keywords: Marine Protected Areas; Partially-Protected; Deep-Water; Reef Fish; Southeast United States; Atlantic Ocean

1. Introduction

Marine protected areas (MPAs) have become widely used by fisheries managers to increase abundance, biomass, biodiversity, and body sizes of previously targeted fish inside MPAs by limiting fishing mortality; in some cases, this has promoted spillover into adjacent regions (Russ & Alcala 1996; Babcock *et al*. 1999; Pomeroy *et al*. 2004; Russ, Stockwell & Alcala 2005; Di Lorenzo *et al*. 2016). Angulo-Valdés & Hatcher (2010) proposed many other potential benefits of MPAs that encompass a broad scope of ecological, social, and economic values. Because of these potential benefits, in 2016 the International Union for Conservation of Nature pushed to increase the establishment of MPAs, aiming to conserve at least 30% of the global ocean by 2030 (https://portals.iucn.org/library/node/46467).

In 2009, the South Atlantic Fishery Management Council (SAFMC) established eight deep-water MPAs along the continental shelf break off the southeast United States (SEUS) Atlantic coast. The establishment of the eight MPAs was a nearly two-decade long process, with the final placement and design of the MPAs representing a compromise between fishers and the SAFMC to meet fisheries management goals while minimizing economic and social impacts (SAFMC 2006). The intent of the designations of the SEUS MPAs was to protect a portion of long-lived, deep-water, reef-associated fishery species by prohibiting bottom fishing inside the MPAs. Many species of reef fish often share habitat preferences, and as a result it is common to catch and subsequently discard one species when another species is targeted. Release mortality in reef fish species is higher in deeper water due to increased barotrauma (Wilson & Burns 1996; Burns & Restrepo 2002; Burns *et al*. 2002; Rudershausen et al. 2007; Runde and Buckel 2018); thus, the establishment of MPAs in deep-water was pursued. As partially-protected MPAs, fishing for (bottom fishing), possessing, or retaining reef fish species is prohibited, but trolling and harvesting of other species, such as mackerel, marlin, or tuna, is allowed (SAFMC 2016). The MPAs also have a transit provision allowing for fishers with reef fish species onboard their vessels to traverse the MPA if their fishing gear is stowed (SAFMC 2016). It was believed that by solely prohibiting bottom fishing, these MPAs would, in turn, decrease catch and bycatch mortality and protect spawning areas for reef fish, ultimately promoting spillover into fishable areas (SAFMC 2016). Additionally, the placement of the SEUS MPAs along the shelf could provide potential sources of fish larvae as they are transported throughout the SEUS via the Gulf Stream and inner and mid shelf currents if enhanced spawning occurs in these MPAs (Hare & Walsh 2007; Lesher 2008; Govoni *et al*. 2013; SAFMC 2016).

Since the establishment of the SEUS MPAs, only one study has been published that examined the efficacy of these MPAs (Bacheler *et al*. 2016). Using underwater videos from manned and unmanned submersibles (2001-2014 time series), Bacheler et al. (2016) determined that there was no increase in the number of reef fish species or density of some managed reef fish species in SEUS MPAs regionally, and in two SEUS MPAs individually, six years after their implementation. At the time of that study, the MPAs were only six years old and thus changes to the fish community may have not had enough time to accrue. A meta-analysis of MPAs globally showed that MPA age (>10 years) was one of five key criteria influencing MPA effectiveness (Edgar *et al*. 2014). In addition, previous studies have shown that the recovery time for long-lived reef fish abundance and biomass within MPAs can be on the scale of decades (McClanahan & Mangi 2000; Russ *et al*. 2005; Russ & Alcala 2010). This suggests that continued evaluation of the SEUS MPAs is needed as their lifespans increase.

Another reason Bacheler *et al*. (2016) observed no MPA effect may be due to the biological indicators used to evaluate SEUS MPA effectiveness (species richness and individual density). Indicators used to evaluate protection effectiveness vary across MPAs and will depend on MPA goals and objectives (Pomeroy *et al*. 2004; Pelletier *et al*. 2005; Fox *et al*. 2014; Gallacher *et al*. 2016). One of the primary goals of the SEUS MPAs, as stated by the SAFMC, is to protect the size, age, and genetic structure of deep-water species susceptible to overfishing (SAFMC 2016). The Pelletier *et al*. (2005) review of MPA metrics showed that density and body size distributions were the most effective indicators of rehabilitation of population and age structure in fish. In addition, ecological and environmental benefits following MPA establishment occur over different timeframes, with increased size, age, abundance, and biomass expected shortly after MPA establishment with biodiversity and community composition benefits expected later (Ward *et al*. 2001; Stelzenmuller & Pinnegar 2011). As such, demographic (size and age) indicators, in addition to abundance, should be used to evaluate the effectiveness of the SEUS MPAs.

We evaluated the impact of protection in three of the eight SEUS MPAs using abundance, size, and age of managed reef fish species. We used trap catch data from fishery-independent surveys from the year 2000 (nine years pre-establishment) to 2018 (nine years post-establishment) from within the MPAs and adjacent fished areas. We focused on the commonly encountered managed reef fish species to provide an overall view of protection impacts and a more specific focus on Red Porgy, *Pagrus pagrus* (Linnaeus, 1758), a relatively short-lived but common reef fish species that is likely to benefit from protection due to its overfished status (SEDAR 2020).

2. Methods

This study used data collected by the Marine Resources Monitoring Assessment and Prediction (MARMAP) program from 2000 to 2008 and the Southeast Reef Fish Survey (SERFS) from 2010 to 2018 to examine changes in abundance, size, and age of managed reef fish species in response to the implementation of three deep-water MPAs off the southeast United States (SEUS) Atlantic coast. Initially, regional reef fish monitoring in the SEUS was conducted solely by the MARMAP program. MARMAP has since been joined by two other programs, the Southeast Area Monitoring and Assessment Program – South Atlantic (SEAMAP-SA) and the Southeast Fishery Independent Survey (SEFIS). This colloboration is now referred to as SERFS, with each collaborator using gear and methodologies consistent with historical MARMAP sampling (Bacheler *et al.* 2014; Smart *et al.* 2015). The SERFS sampling covers the continental shelf and shelf edge between Cape Hatteras, North Carolina, and St. Lucie Inlet, Florida. The survey is the main contributor of fishery-independent data to SEUS reef fish species stock assessments, collecting information on relative abundance, distribution and demographics for managed (and some unmanaged) reef fish species. Although this survey was not designed to explicitly test MPA effectiveness, its coverage of known reef habitat sites inside and outside the MPAs as well as sampling pre- and post-MPA establishment makes it one of few data sets available to assess reef fish response to SEUS MPA establishment. In addition, to the best of our knowledge, it is the only data set available that has monitored changes in abundance, size, and age of reef fish, important metrics to assess the effectiveness of the SEUS MPAs.

2.1 Study Sites

The size of the MPAs established by the SAFMC in 2009 range from 30 to 515 km^2, with water depths from 50 m to 300 m, and boundaries encompassing a variety of outer shelf, shelf-edge, and upper slope habitats. MARMAP and SERFS samples include five of the nine deep-water MPAs. Due to sampling characteristics such as the geographic scope of the survey, available funding, and survey priorities, three of the five MPAs sampled most consistently were analyzed in this study: Northern South Carolina (NSC), Edisto (ED), and North Florida (NF) (Figure 1; Table 1). Samples collected from 2000 to 2018, excluding 2009 (year of MPA implementation), were used for inside-outside and before-after comparison for the NSC and Edisto MPAs. Due to low sampling effort prior to the establishment of the NF MPA, only samples collected from 2010 to 2018 were used, and only for an inside-outside comparison.

Sites used for inside-outside MPA comparisons were selected from adjacent fished areas (<55 km from MPA boundary), with sufficient sample sizes and similar depth and distance to the continental shelf edge. Depth and distance to shelf edge were considered in the designation of adjacent fished areas as they have been shown to be dominating factors structuring fish assemblage in the SEUS (Glasgow 2017). Additionally, proximity to shelf edge ensured that MPAs and adjacent fished sites were approximately equidistant to the coastline and fishing ports. These adjacent fished comparison areas covered a larger spatial extent than their respective MPA comparison areas, as sampling outside the MPA was not as concentrated.

2.2 Data Collection

As part of SERFS standard sampling, chevron traps (see Collins 1990) were used to sample along the SEUS continental shelf in depths ranging from 9 to 115 m. Each year, a subset of stations was selected randomly from known reef stations identified for monitoring in a manner such that no station selected in a given year was closer than 200 m to any other selected station. Prior to deployment each chevron trap was baited with a combination of 40 whole or cut clupeids, with *Brevoortia* spp. most often used. Generally, chevron traps were deployed in sets of six and soaked for approximately 90 min, during which time a CTD cast was done. Gear deployments occurred during daylight hours (no earlier than 30 minutes after sunrise and retrieved no later than 30 minutes before sunset). Depth (m), latitude, longitude, bottom temperature (C), time of day, date, and soak time were recorded as part of the standard SERFS sampling protocol for each trap deployment.

Beginning in 2011, all chevron traps used by SERFS were equipped with a camera mounted above and facing away from the trap opening (trap mouth) and a camera mounted above and facing away from the back of the traps (trap back) to record habitat characteristics. All camera settings remained constant throughout a given sampling year and were set to record continuous video during the entire soak period of the chevron traps until memory cards filled or batteries ran out of power. Following gear retrieval, videos were uploaded to external hard drives, processed on shore, and used in this study for characterizing habitat type. Habitat characterization followed SERFS standard protocols (Bacheler *et al.* 2014). Habitat was coded from each video immediately upon the trap stabilizing on the sea floor, noting dominant surface geologic and biotic components: substrate density, size, and relief, and dominant biota height, type, and density. Prior to this study, habitat coding had been done by trained SEFIS personnel for 2011-2017 and was used for this study. Samples collected in 2018 were coded for habitat by trained MARMAP/SEAMAP-SA personnel following the same protocol.

Once a set of traps was fully retrieved, all fish caught in each trap underwent a Length Frequency work-up (LF). LF occurred shortly after retrieval and consisted of identifying and counting all fish in each trap to species level or the lowest possible taxon, then weighing all fish of a given species per trap as an aggregate (biomass in g wet weight) and measuring each individual fish. Abundance was calculated for each species per trap based on the number measured. Prior to 2012, lengths were measured as either total length or fork length in cm and since 2012 all lengths for all species were measured as total length in cm. Fork lengths were converted to total length for this study based on conversions developed by Bubley *et al.* (2019). During LF, specimens of priority species were retained for additional processing to collect biological samples (Life History or LH processing). Any fish not retained for the LH processing were degassed (vented) as necessary and released.

On-board, as part of LH processing, both sagittal otoliths were removed from Red Porgy, *Pagrus pagrus* (Linnaeus, 1758), the only species examined in this study for changes in age structure. Both sagittal otoliths were placed in dry coin envelopes until further processing on shore. The left sagitta (or right if the left was broken or unavailable) was used in age estimation. Otolith sectioning followed standard MARMAP protocols (Smart *et al.* 2015). Otolith increments were determined by the number of alternating translucent and opaque bands and were counted independently by two trained readers without knowledge of specimen length, mass, location, date of capture, or results of the other reader. Upon completion of independent reads, increment counts were compared and in cases where readers disagreed, readers simultaneously viewed the sections and attempted to reach a consensus. If consensus could not be reached, those specimens were eliminated from analyses.

2.3 Study Design

This study used a *post hoc* sampling design to control for differences in habitat structural complexity and uneven sample sizes between MPAs and their adjacent fished comparison areas. In many cases, more stations were available for analysis in the adjacent fished areas than in the MPA, leading to uneven sample sizes and a risk of comparing sites of dissimilar habitat complexity. Since the implementation of camera-mounted chevron traps in 2011, it was clear that among chevron stations in the SERFS sampling universe, there was considerable variation in reef habitat structural complexity. Camera data were not consistently available for habitat characterization for trap deployments before 2011, however chevron sites sampled 2000-2010 consisted of the same stations used for 2011-2018 sampling. Previous work done by MARMAP, using a series of repeated measures analyses of variance, showed that there were no significant changes in some habitat characteristics (relief, substrate density, and biota density) over time for traps deployed at the same station from 2011 to 2017 (Smart *et al.* 2020). These results supported *post hoc* assignment of habitat scores for samples collected 2000-2010 in MPA and adjacent fished areas based on station number. This was done by averaging substrate and biota density and taking the mode of vertical relief for station numbers that were sampled multiple times (≥ 3) from 2011 to 2018. For stations that did not have habitat codes assigned, habitat classification from the nearest station with habitat characterized was used. Nearby stations generally have a high degree of correlation in habitat type for the three characteristics included here based on spatial autocorrelation results (Moran's I for biota density = 0.697, substrate density = 0.717, and vertical relief = 0.709 and all p-values <0.001) and because the survey specifically targets hard bottom habitats. In addition, the average distance between stations with significantly different habitat types was >120 m while distance to the nearest station used as a proxy for habitat was on average 51 m.

Average station depth along with the three proxies for habitat complexity described above (vertical relief, substrate density, and biota density) were used to select adjacent fished area deployments with similar habitat characteristics to MPA deployments for analyses. These categories were selected as they have been shown to be some of the dominant habitat features structuring reef fish assemblage in the SEUS (Glasgow 2017). To avoid subjectivity in selecting deployments, habitat similarity was determined by cluster analysis in R using the cluster package (Maechler et al. 2019). Because depth, substrate density, and biota density are continuous and vertical relief is categorical, a Gower's Distance test was used to produce a distance metric for cluster analysis (Gower 1971; Borcard *et al.* 2011).

Gower's tests were done for each year of sampling and for each MPA and adjacent fished area pair as not every station was sampled in each year of the survey due to the random selection. Continuous variables (substrate and biota density) were square root transformed to meet normality assumptions. Partitioning around Medoids algorithm was then used to create clusters comprising MPA and adjacent fished area sites from each Gower's distance metric. The number of clusters in which to partition the distance metric was determined by the highest average silhouette width. Silhouette width is a measure of how similar an object (in this study the object is each deployment) is to its own cluster and how distinct it is from other clusters. This grouped deployments (MPA and fished) into clusters of low to high structural habitat complexity with similar depth. Deployments were then selected from the adjacent fished area based on their respective silhouette width, with deployments having the greatest silhouette width being selected. The number of adjacent fished deployments chosen from each cluster were based on the number of MPA deployments that occurred within that cluster to produce even sample sizes. If there were fewer adjacent fished deployments in a cluster than MPA deployments, then adjacent fished area deployments with the greatest silhouette width from the nearest neighbor cluster were selected. Essentially, this clustering approach provided a structured, reproducible, unbiased way of selecting comparative deployments outside of the MPAs and producing even samples sizes for MPAs and fished areas. The approach also ensured we compared sites of similar habitat complexity (and quality) by minimizing the possibility of comparing sites of high reef habitat complexity inside the MPA to sites of low habitat complexity in the adjacent fished area, or vice versa.

2.4 Data Analysis

The combined relative abundance of the ten most commonly caught managed reef fish species (RFS) in chevron traps for each MPA served as a proxy for the effects of MPAs on managed reef fish species in general, even though the exact composition of the RFS groups differed among MPAs (Table 2). Most common is defined in this paper as highest frequency of occurrence and abundance in catches. Changes in Red Porgy abundance in response to MPA implementation was chosen for species-specific analyses because they were commonly caught in all three MPAs. Also, due to Red Porgy's overfished status (SEDAR 2020), relatively short longevity (< 18 years), and early maturing life history patterns (~100% mature at age 4; Wyanski *et al*. 2019), Red Porgy was expected to respond more quickly to MPA implementation than other, longer lived SEUS managed reef fish species (Polacheck 1990; Hilborn *et al.* 2004; Rassweiler *et al.* 2014), such as the Speckled Hind (*Epinephelus drummondhayi,* Goode & Bean, 1878), which may live up to 80 years and reach maturity at 7 years (Andrews *et al*. 2013; Kobara *et al*. 2017). Using a trap catch data set permitted us to examine changes in abundance, while also examining changes in size and age. Despite these benefits, traps, like any survey gear type, are not able to efficiently collect all the information desired to monitor changes in an area, because some species are too large or less willing to enter traps or too small to be retained (Bacheler *et al*. 2013a). Thus, community-based parameters to assess the effects of MPA implementation, such as richness, evenness, or changes in community structure, were not examined in this study.

We used multiple regression models to examine changes in abundance of RFS and Red Porgy in response to protection while factoring out relevant covariates. Specifically, we fit the following linear model:

$$\log(\text{abundance} + 1) = \beta_0 + \beta_1(\textit{region}) + \beta_2(\textit{location}) + \beta_3(\textit{time}) + \beta_4(\textit{location} * \textit{time}) + \beta_4(\textit{temperature}) + \beta_5(\textit{depth}) + \beta_6(\textit{relief}) + \beta_7(\textit{substrate density}) + \beta_8(\textit{biota density}) + \text{offset}(\textit{trap soak time}) + \epsilon \,;\, \epsilon \sim \mathbf{N}(0, \sigma^2)$$

The primary variables of interest in this global model were: *region* which specified the Northern South Carolina, Edisto, or Northern Florida region, *location* which identified whether a given deployment was inside or outside of the MPA, *time* which denoted whether the deployment was before or after MPA implementation (year 2009), and the *location*-by-*time* interaction which was necessary to identify if deployments located within the MPA were different after protection was implemented. The other variables in the model were covariates that we wished to statistically control for including: *temperature* the bottom temperature (°C) from the paired CTD cast, *depth* the sampling depth (m) of the deployment, and *relief*, *substrate density*, and *biota density* were the average habitat characteristics for the station number where the deployment occurred. We included *trap soak time* as an offset term inside the model to account for variability in the sampling effort as some deviation from the targeted 90-minute soak time occurred which could affect abundance within the traps (Zuur *et al*. 2009; Bacheler *et al*. 2013b). An offset was used rather than dividing the abundance by soak time to allow variability to by captured in the model and allow us to investigate a wider range of error distributions appropriate for count data. Since geographic location (latitude and longitude) is specific to each MPA and adjacent fished comparison area, we did not include that as a predictor variable. We also fit this model to each region separately but dropped the region explanatory variable.

We compared the fit (i.e., negative log likelihood) of the Gaussian linear model on the log(x + 1) transformed abundance to General Linear Models with Poisson, negative binomial, and zero-inflated error structures. The negative binomial and Gaussian models consistently outperformed the other models. Diagnostic plots for assessing model assumptions (normality and variance) and model prediction, showed that Gaussian structure was the most appropriate with one fewer fitted parameter. We used Analysis of Variance (ANOVAs; Quinn and Keough 2002) (type 3) to test for significance of explanatory variables and overall model fit at the $\alpha = 0.05$ level.

It is possible that there may be a delayed effect in protection on abundance, which prompted an examination of trends of abundance over narrower time intervals. General linear power analyses (GLP) performed on RFS and Red Porgy abundance suggested that a sample size of 38 to 160 was needed to test for significance. These results prompted years to be grouped into three-year periods (2000-2002, 2003-2005, 2006-2008, 2010-2012, 2013-2015, 2016-2018) to ensure an adequate sample size for examining trends over time.

Changes in size were examined for RFS and Red Porgy. RFS for each MPA comparison were grouped into four periods to limit pair-wise comparisons: 2000-2004, 2005-2008, 2010-2014, and 2015-2018. Due to limited sample size prior to MPA establishment, Red Porgy total lengths were grouped for each MPA comparison into three periods: 2000-2008, 2010-2014, and 2015-2018. Changes in age were analyzed in response to MPA establishment for Red Porgy from 2000 to 2017 and were grouped into three periods based on sample size: 2000-2008, 2010-2013, and 2014-2017. To examine changes in Red Porgy age distributions, we compared changes in the percent of Red Porgy expected to be fully recruited to the fisheries as these would indicate a benefit to fisheries and a change in age structure. Red Porgy age at full recruitment to chevron trap (> age 3) was determined using length-age data collected from 2000 to 2017 and resulting catch curve and was consistent with Hood & Johnson (2000). To maintain an even sample size and habitat characteristics, the same deployments used in the abundance analyses for each of the

MPAs were used for size and age comparisons. Before-after and inside-outside changes in size distributions and percent of fully recruited fish were assessed for significance using a series of one-sided t-tests (assuming unequal variance) and chi-square tests, respectively. Because NF MPA samples were limited prior to MPA establishment, analyses of change in size and percent recruited were only examined post implementation.

3. Results

3.1 Reef Fish Species Abundance

Generally, the Reef Fish Species (RFS) linear models, both globally and for each MPA, were significant ($p<0.05$), but had low R^2 values (<0.13; Table 3). None of the models we examined were able to capture the degree of dispersion observed in fish abundance (Supplemental Figure 1). Across all three regions, the global models showed that RFS abundance was significantly ($p<0.05$) lower inside the MPAs than outside and that there was no significant ($p>0.05$) interaction effect (Figure 2; Table 3). In the North South Carolina (NSC) area, abundance was significantly ($p<0.05$) greater outside the MPA, pre- and post-MPA implementation, and exhibited a negative trend in abundance inside the MPA post establishment (Figure 3a). In the Edisto (ED) area, there was a significant ($p<0.05$) positive interaction effect, with greater abundance inside the MPA post-establishment relative to the adjacent fished area and pre-MPA establishment levels. From an examination of periods post-MPA implementation, it is apparent that the positive interaction was driven by a large increase in abundance in 2013-2015 (Figure 3b). In the most recent period of sampling, ED MPA abundance level was not significantly different ($p>0.05$) from abundance levels inside the MPA for any period pre-establishment or for 2010-2012. In the North Florida (NF) area, abundance inside the MPA was significantly lower ($p < 0.05$) than the adjacent fished area after MPA establishment (Figure 2; Figure 3c).

3.2 Red Porgy Abundance

Generally, the Red Porgy linear models, both globally and for each MPA, were significant ($p<0.05$), but had low R^2 values (<0.13; Table 3). Global models showed that Red Porgy abundance was significantly ($p<0.05$) greater inside than outside the MPAs post establishment, but there was no significant ($p>0.05$) interaction effect (Figure 2; Table 3). In the NSC area, there was no significant inside-outside, before-after or interaction effects. Red Porgy abundance for periods post-establishment show overlapping standard error bars and no significant ($p>0.05$) differences between the NSC MPA and adjacent fished area (Figure 4a). In the ED area, the ED MPA had significantly greater Red Porgy abundance than the adjacent fished area, both before and after MPA implementation, but showed no significant interaction effect (Figure 3; Figure 4b). In the NF area, there was no significant ($P>0.05$) difference in Red Porgy abundance inside or outside the MPA post establishment (Figure 3; Figure 4c).

3.3 Size-Distributions of RFS and Red Porgy

RFS mean total length (TL) inside the NSC MPA area was similar to the adjacent area for the period immediately prior to MPA implementation ($p = 1.0$) and in the most recent period post MPA implementation ($p = 0.99$; Figure 5a). Mean RFS TL was significantly greater inside the ED MPA compared to the adjacent fished area for all periods ($p < 0.001$) except 2005-2008 ($p = 1.0$, Figure 5b). In 2000-2004, RFS mean TL inside the ED MPA was 1.8 cm greater than the adjacent area. In 2015-2018, RFS mean TL inside the ED MPA was 4.7 cm greater than the adjacent fished site, suggesting an increase in the size difference over time. For both periods post NF MPA establishment, mean TL was significantly greater ($p < 0.001$) inside the MPA than the adjacent fished area, with difference in mean TL increasing over time from 2.8 cm to 7.1 cm (Figure 5c).

Red Porgy mean TL was similar inside the NSC MPA and in the adjacent area, regardless of the period ($p > 0.59$, Figure 6a). Red Porgy mean TL was significantly greater inside the ED MPA compared to the ED adjacent fished area for all periods (2000-2008, $p = 0.05$; 2010-2014 & 2014-2018, $p < 0.001$, Figure 6b). In both periods post MPA establishment, RFS mean TL inside the ED MPA was ~3 cm greater than the adjacent fished area. Finally, Red Porgy mean TL was significantly greater inside the NF MPA compared to the adjacent fished area by 4.1 cm during the final period of sampling ($p < 0.001$; Figure 6c).

3.4 Age Distributions of Red Porgy

Overall, percentage of fully recruited Red Porgy in 2014-2017 was significantly lower inside the NSC MPA, significantly greater inside the NF MPA, and not significantly different inside the ED MPA compared to their respective adjacent fished areas. Prior to NSC MPA establishment, percentage of fully recruited Red Porgy was significantly greater inside the NSC MPA than outside ($p < 0.001$; Figure 7a). For the period immediately following NSC MPA establishment, there was no significant difference in percentage of fully recruited Red Porgy inside or outside the MPA. During the most recent period (2014-2017), percent of fully recruited Red Porgy was significantly greater outside the NSC MPA than inside (67.7% and 50.0% respectively, $p < 0.01$), a reversal of the pre-establishment pattern. Prior to ED MPA establishment, there was no significant difference in percentage of fully recruited Red Porgy inside and outside the ED MPA (Figure 7b). For the period immediately following ED MPA establishment, percentage of fully recruited Red Porgy was greater inside the MPA than in the adjacent fished area (45.7% and 18.6%, respectively; $p=0.002$). During the most recent period

(2014-2017) both areas experienced an increase to ~80% fully recruited with no difference between the protected and adjacent fished area. For the period immediately following NF MPA establishment, percentage of fully recruited Red Porgy was lower inside the MPA than outside (46.8% and 68%, respectively; $p < 0.001$; Figure 7c). The most recent period (2014-2017), percentage of fully recruited Red Porgy was greater inside the NF MPA than the adjacent fished area (75.6% and 61.5%, respectively; $p = 0.02$), a reversal of the immediate post-establishment pattern.

4. Discussion

Our results suggest that the southeast United States (SEUS) MPAs examined here have not had a positive effect on exploited reef fish species, with a few exceptions. We did not observe fish abundances (Reef Fish Species (RFS) or Red Porgy) increasing inside of the MPAs after protection was implemented. Linear models showed no change, or in some cases appeared to exhibit a negative trend, in abundance of RFS and Red Porgy, both globally and for each of the three MPAs and adjacent fished area comparisons. The only exception to this was the Edisto MPA, which displayed a significant interaction effect, with RFS increasing inside the MPA over time relative to the adjacent fished area. However, upon further examination, trends in RFS abundances post-establishment showed that in the most recent sampling period there was no significant difference in RFS abundance inside and outside the MPA or before and after MPA implementation. The extraordinarily high catches in the ED MPA from 2013-2015 most likely drove the ED MPA positive interaction effect and the nearly significant ($p \sim 0.07$) interaction term for the global model. These results suggest that as of 2018, the SEUS MPAs have not (yet) been (or no longer are) effective in increasing abundances of managed reef fish species.
Unfortunately, this is not uncommon among MPAs, with many partially-protected MPAs such as

these being deemed ineffective and underperforming relative to no-take MPAs (Burke *et al.* 2011; Denny & Babcock 2004; Lester & Halpern 2008; Edgar *et al.* 2014).

Further examination of some biological indicators did show a positive response to MPA implementation. A significant positive before-after and inside-outside response was observed for the size of RFS and Red Porgy in ED MPA. A significant positive inside-outside response was also observed for the size of RFS and Red Porgy and age of Red Porgy in the NF MPA. While fish length comparisons between protected and adjacent fished areas may only differ by a few centimeters, this could be the difference between a legal- and sublegal-sized fish. Some of the more commonly caught reef fish in the SEUS, Vermilion Snapper (*Rhomboplites aurorubens,* Cuvier, 1829), Gray Triggerfish (*Balistes capriscus,* Gmelin, 1789), Black Sea Bass (*Centropristis striata,* Linnaeus, 1758), and Red Porgy have TL minimum limits between 30.5 and 35.5 cm, which falls withing the range of lengths observed in this study. When TLs of Red Porgy were examined (TL minimum limit = 35.5 cm), ED and NF MPAs both showed a significantly higher proportion (72% & 88%, respectively) of TLs over the minimum size limit post MPA establishment compared to adjacent fished area (62% & 64.5%, respectively; Figure 7). Additionally, the proportion of Red Porgy over the minimum size limit for ED MPA increased from 58% just prior to MPA establishment to 72% for the most recent period post MPA establishment. From a management perspective, this could be an important result increasing the availability of legally-sized fish in the region if spillover occurs. These size increases within the NF and ED MPA support previous findings on both the benefits of protected areas and the moderate size gains exhibited in partially protected MPAs relative to no-take areas (Babcock *et al.* 1999; Unsworth *et al.* 2007; Malcolm *et al.* 2015; Harasti *et al.* 2018).

Three of the reef fish species used in the RFS analysis had changes to their minimum size limit between 2000 and 2018: Black Sea Bass, Grey Triggerfish, and Red Snapper, (*Lutjanus campechanus*, Poey, 1860). The Black Sea Bass size limit increased by 2.54 cm in 2012, while a minimum size limit of 30.5 cm was imposed for Gray Triggerfish in 2016 and the size limit for Red Snapper was removed in 2011. While we do not expect these modest changes in size limit to affect our results, it is possible that is could provide a bias for the before-after comparisons, where observations are driven by size limit changes rather than the implementation of the MPA. However, since the data used in this study was collected as part of a fisheries-independent survey, which is not subjected to size restrictions, inside-outside comparisons for the RFS analysis should be able to identify changes in size related to MPA establishment rather than fishing mortality.

One possible reason why no positive effect was observed for abundance was the short span of time since the MPAs were implemented (Russ *et al.* 2005; Russ & Alcala 2010; Edgar *et al.* 2014). Age of MPA typically is recognized as one of the most important criteria influencing MPA effectiveness (Claudet *et al.* 2008; Molloy *et al.* 2009; Edgar *et al.* 2014). Yet, studies differ on the minimum time needed to be effective, from only a few years (Halpern & Warner 2002; Unsworth *et al.* 2007), to a decade (Edgar *et al.* 2014), to several decades (MacNeil *et al.* 2015). This difference can be attributed to differing life-history strategies of protected fish species, with a greater delay in protection response for slow-growing and long-lived species (Molloy *et al.* 2009; Claudet *et al.* 2010; Starr *et al.* 2015). Catches here were generally dominated by faster maturing and shorter-lived reef fish species, such as Vermilion Snapper and Red Porgy (Potts *et al.* 1998; Hood & Johnson 2000). Based on the relatively early age of maturity and faster growth of most species encountered, the MPAs appear to have been established long enough for an increase in abundance to be observed within the boundaries of MPA sampled, provided that there is indeed reduced fishing pressure and sufficient habitat in these areas.

Another major driver of MPA effectiveness is overall size (Claudet *et al.* 2008; Fenberg *et al.* 2012; Edgar *et al.* 2014). In order to be effective, MPAs must be large enough to ensure that fish are spending enough time inside the protected area to reduce fishing mortality and meet management goals. The three MPAs studied range in size from 170 to 340 km^2. Unfortunately, few movement pattern studies have been conducted on deeper reef fish in the SEUS to better understand their home ranges because of the difficulty of tagging these fish. Studies of reef fish species in shallower regions have shown that daily home ranges are well within the size limits of these MPAs, with some grouper, such as Red Grouper (*Epinephelus morio,* Valenciennes, 1828), Black Grouper (*Mycteroperca bonaci*, Poey, 1860), and Gag (*Mycteroperca microlepis*, Goode and Bean, 1879) (Coleman *et al.* 2011; Farmer & Ault 2011), and snapper, such as Mutton Snapper (*Lutjanus analis*, Cuvier, 1828) and Yellowtail Snapper (*Ocyurus chrysurus*, Bloch, 1791) (Farmer & Ault 2011), and Red Porgy (Afonso *et al.* 2009) exhibiting home ranges of less than 8 km^2. However, some of the managed reef fish species undergo ontogenetic migrations, moving from coastal to offshore habitats, as well as migrating great distances to spawning aggregations potentially taking them well outside the protection of these MPAs (Ross & Moser 1995; Coleman *et al.* 2000). Given the variability of movement patterns of studied managed reef fish species and general lack of information for deep reef fish species it is unclear what MPA size is needed to ensure that SEUS managed reef fish species remain inside the MPA to benefit from protection.

MPA placement and design could also have been a factor affecting MPA effectiveness. The SEUS MPAs were established as a result of a nearly two-decade long process and reflect a compromise between fishers and fisheries managers (SAFMC 2006). This compromise resulted in the MPAs being placed in locations to “lessen social and economic impacts”, which explains why they were designed perpendicular to the shelf contours rather than parallel (SAFMC 2006), which would have encompassed larger areas of reef habitat. This effectively limits the availability of on-shelf and shelf edge reef habitat in theses SEUS MPAs and concentrated reef habitat to the western boundaries of the MPAs. This is particularly evident with the NSC MPA where shelf reef habitat is concentrated in the northwestern corner of the MPA, resulting in the smallest on-shelf sampling area of the three MPAs studied (NSC ~ 72 km^2, ED ~ 170 km^2, and NF ~ 110 km^2). This limitation in sampling coverage and habitat may explain why the NSC MPA showed no positive effect for any metrics examined, and in some cases exhibited a negative response. Numerous studies have shown that the amount of available habitat and spatial distribution of habitat contribute significantly to MPA effectiveness, helping to maintain species diversity and provide shelter/refuge for species across the MPA (Foley et al. 2010; Gaines et al. 2010; Heyns-Veale et al. 2019). Additionally, studies have shown that fishing pressure typically increases at the margins of MPAs as fishers expect a spillover of larger/older individuals or more fish moving out of a protected area, known as the edge effect or “fishing the line” (Carr *et al.* 2003; McLeod *et al.* 2009; Green *et al.* 2014). This possible increased fishing pressure on the edge of the MPA, coupled with the fact that reef fish habitat is concentrated near the MPA boundary suggests that fish in the NSC MPA area may have been experiencing greater fishing pressure than the other two MPAs studied.

Based on age, size, and design of MPAs alone it is still unclear why no positive response in abundance was found in the North Florida and Edisto MPAs. This may be attributed partially to the lack of effective enforcement and compliance, a major factor affecting MPA success (Lundquist & Granek 2005; Guidetti *et al.* 2008; Edgar *et al.* 2014; Di Franco *et al.* 2016). In the most recent deep-water MPA management plan by the South Atlantic Fisheries Management Council (SAFMC), seven of the eight MPAs were given a rating of "low" for enforceability by the US Coast Guard (SAFMC 2016). This is driven by two factors: (1) distances from shore to MPAs and (2) the partial protection status of the MPAs allowing certain fishing activities to take place, making on-site enforcement, rather than flyovers, a necessity to determine if fishing is unlawful or not (SAFMC 2016). Since the MPAs have been established, not a single citation has been issued for illegal fishing (USCG, personal communication). This is not necessarily an indication of the level of infractions but may reflect the limited patrolling and difficulty associated with enforcing regulations. The consequences of instituting partially protected areas instead of full no-take reserves have been shown widely in other regions, with no take reserves outperforming partially protected areas (Francour 1994; Denny & Babcock 2004; Sciberras *et al.* 2013; Edgar *et al.* 2014; Ballantine 2014). Because of the low enforceability of the SEUS MPAs, it is nearly impossible to assess compliance within the protected areas, which is a major problem moving forward with evaluations of SEUS MPAs as a management strategy in SEUS Atlantic region.

Sampling design could have influenced our results and explain why metrics did not support that SEUS MPAs provide effective protection for reef fish. Because our samples were collected as part of a regional survey, they may be limited relative to a study designed to specifically test MPA effectiveness. However, it is the only standardized sampling available before and after MPA establishment that provides information on reef fish size and age compositions, in addition to abundance. Chevron trap sampling by MARMAP and SERFS was limited to previously established sites with known reef habitat <115 m depth. This restricted sampling to on-shelf, shallower regions of the MPAs relative to the full spatial scope of the MPAs. Reef fish species assemblages' change with depth in the SEUS (Glasgow 2017), and the results of this study therefore may not be as applicable to reef fish distributed in deeper, off-shelf portions of the MPAs. It should be noted that limited high-resolution mapping of the MPAs has shown much less reef habitat in the deeper regions of the MPAs than where sampling was conducted (SAFMC 2016), and the effects of protection provided to deeper reef fish may be inconsequential due to the limited availability of deep reef habitat. Additionally, reef fish distributed in off-shelf waters tend to be slower-growing and longer-lived (Coleman *et al.* 2000; Sabetian 2003; Costa *et al.* 2012; Bubley *et al.* 2019), thus one would expect these species, and subsequently deeper regions of the MPAs, to respond more slowly to protection (Molloy *et al.* 2009; Starr *et al.* 2015). Here we focused on species expected to be more responsive due to their shorter life spans and times to maturity and still found limited evidence of MPA effectiveness. Lastly, although our samples were collected as part of a larger survey, our novel *post hoc* stratification approach did mitigate at least some uncertainty that results were driven by differences in habitat complexity or sampling effort.

The SEUS MPAs were implemented as a fisheries management tool. The desired goal was that by protecting suitable reef fish habitat in the MPAs, this would result in higher abundance and biomass of exploited reef fish and increase the number of individuals reaching reproductive maturity within the MPA, promoting the spillover of fish out of the protected boundaries into the surrounding areas. From size and age metrics, our study indicates that the

SEUS MPAs are protecting reef fish, permitting more fish to reach larger sizes and older ages which may relate to their reproductive output; however, none of the MPAs exhibited an increase in abundance and, in some cases, abundance showed a decline. We believe this may negate the modest gains in size and age observed and would not result in a significant MPA effect on reproductive potential or population recovery. In addition, patterns of effectiveness were not consistent across MPAs. For example, the NSC MPA showed no positive fish size responses to protection, while only the NF MPA showed increases in fish age relative to its adjacent fished area. Unfortunately, until compliance within MPAs has been assessed, it will be difficult to determine if deep-water MPAs, or the current deep-water MPA orientations and protection level, are an effective strategy for protecting reef fish over the long term. If fisheries managers in the SEUS Atlantic region wish to use MPAs as a management tool, it is important to continue to understand why an increase in abundance has not been observed and what is driving the differences among the MPAs responses post-establishment.

CRediT author statement

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Literature Cited

Andrews, A.H., B.K. Barnett, R.J. Allman, R.P. Moyer and H.D. Trowbridge, 2013. Great longevity of speckled hind (Epinephelus drummondhayi), a deep-water grouper, with novel use of postbomb radiocarbon dating in the Gulf of Mexico. Can. J. Fish. Aquat. Sci. 70: 1131-1140.

Afonso, P., Fontes, J., Guedes R., Tempera, F., Holland, K.N., Santos, R.S., 2009. Tagging and Tracking of Marine Animals with Electronic Devices. Rev Methods Technol Fish Biol Fish 9:423–443.

Angulo-Valdés, J.A., Hatcher, B.G. 2010. A new typology of benefits derived from marine protected areas. Mar Policy 34:635–644.

Babcock, R.C., Kelly, S., Shears, N,T., Walker, J.W., Willis, T.J., 1999. Changes in community structure in temperate marine reserves. Mar Ecol Prog Ser 189:125–134.

Bacheler, N.M., Schobernd, C.M, Schobernd, Z.H., Mitchell, W.A., Berrane, D.J., Kellison, G.T., Recihert, M.J.M, 2013a. Comparison of trap and underwater video gears for indexing reef fish presence and abundance in the southeast United States. Fish. Res. 143: 81-88.

Bacheler, N. M., Bartolino, V., and Reichert, M. J. M. 2013b. Influence of soak time and fish accumulation on catches of reef fishes in a multispecies trap survey. Fishery Bulletin 111:218-232.

Bacheler, N.M., Berrane, D.J., Mitchell, W.A., Schobernd, C.M., Schobernd, Z.H., Teer, B.Z., Ballenger, J.C., 2014. Environmental conditions and habitat characteristics influence trap and video detection probabilities for reef fish species. Mar Ecol Prog Ser 517:1–14.

Bacheler, N.M., Schobernd, C.M., Harter, S.L., David, A.W., Sedberry, G.R., Kellison, G.T., 2016. No evidence of increased demersal fish abundance six years after creation of marine protected areas along the southeast United States Atlantic coast. Bull Mar Sci 92:447–471.

Ballantine, B., 2014. Fifty years on: Lessons from marine reserves in New Zealand and principles for a worldwide network. Biol Conserv 176:297–307.

Boonzaier, L., Pauly, D., 2016. Marine protection targets: An updated assessment of global progress. ORYX 50.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer New York: New York, NY.

Bubley, W.J., Smart, T.I., Reichert, M.J.M., 2019. Trends in relative abundance of reef fishes in fishery-independent surveys in waters off the SE US. SCDNR Reef Fish Survey Technical Report 2019-03.

Burke, L., Reytar, K., Spalding, M., Perry, A., 2011. Reefs at Risk: Revisited. Washington, DC.

Burns, K., Koenig, C., Coleman, F., 2002. Evaluation of multiple factors involved in release mortality of undersized Red Grouper, Gag, Red Snapper and Vermilion Snapper. Mote Marine Laboratory.

Burns, K., Restrepo, V., 2002. Survival of reef fish after depressurization: field and laboratory studies. Am Fish Soc Symp 30:148–151.

Carr, M.H., Neigel, J.E., Estes, J.A., Andelman, S., Warner, R.R., Largier, J.L., 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. Ecol Appl 13:90–107.

Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J-A., Pérez-Ruzafa, Á., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., Culioli, J-M., Dimech, M., Falcón, J.M., Guala, I., Milazzo, M., Sánchez-Meca, J., Somerfield, P.J., Stobart, B., Vandeperre, F., Valle, C., Planes, S. 2008. Marine reserves: size and age do matter. Ecol Lett 11:481–489.

Claudet, J., Osenberg, C.W., Domenici, P., Badalamenti, F., Milazzo, M., Falcón, J.M., Bertocci, I., Benedetti-Cecchi, L., García-Charton, J-A., Goñi, R., Borg, J.A., Forcada, A., de Lucia, G.A., Pérez-Ruzafa, Á., Afonso, P., Brito, A., Guala, I., Diréach, L., Sanchez-Jerez, P., Somerfield, P.J., Planes, S., 2010. Marine reserves: Fish life history and ecological traits matter. Ecol Appl 20:830–839.

Coleman, F.C., Koenig, C.C., Huntsman, G.R., Musick, J.A., Eklund, A.M., McGovern, J.C., Sedberry, G.R., Chapman, R.W., Grimes, C.B., 2000. Long-lived Reef Fishes : The Grouper-Snapper Complex. AFS Policy Statement 25:14–21.

Coleman, F.C., Scanlon, K.M., Koenig, C.C., 2011. The Professional Geographer Groupers on the Edge: Shelf Edge Spawning Habitat in and Around Marine Reserves of the Northeastern Gulf of Mexico. Prof Geogr 63:456–474.

Collins, M.R., 1990. A comparison of three fish trap designs. Fish Res 9:325–332.

Costa, P.A.S, Braga, A.C., Rubinich, J.P., Ávila-da-Silva, A.O., Neto, C.M., 2012. Age and growth of the snowy grouper, Epinephelus niveatus , off the Brazilian coast . J Mar Biol Assoc United Kingdom 92:633–641.

Denny, C.M., Babcock, R.C., 2004. Do partial marine reserves protect reef fish assemblages? Biol Conserv 116:119–129.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A., Thomson, R.J. 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature 506:216–229.

Farmer, N.A., Ault, J.S. 2011. Grouper and snapper movements and habitat use in Dry Tortugas, Florida. Mar Ecol Prog Ser 433:169–184.

Fenberg, P.B., Caselle, J.E., Claudet, J., Clemence. M., Gaines, S.D., Antonio García-Charton, J., Gonçalves, E.J., Grorud-Colvert, K., Guidetti, P., Jenkins, S.R., Jones, P.J.S., Lester, S.E., McAllen, R., Moland, E., Planes, S., Sørensen, T.K., 2012. The science of European marine reserves: Status, efficacy, and future needs. Mar Policy 36:1012–1021.

Foley, M.M, Halpern, B.S., Micheli, F., Armsby, M.H., and others 2010. Guiding ecological principles for marine spatial planning. Mar Policy 34:955-966.

Fox, H.E., Holtzman, J.L., Haisfield, K.M., Mcnally, C.G., Cid, G.A., Mascia, M.B., Parks, J.E. Pomeroy, R.S. 2014. How Are Our MPAs Doing? Challenges in Assessing Global Patterns in Marine Protected Area Performance. Coast Manag 42:207–226.

Di Franco, A., Thiriet, P., Di Carlo, G., Dimitriadis, C., Francour, P., Gutiérrez, NL., Jeudy De Grissac, A., Koutsoubas, D., Milazzo, M., Otero, M.D.M., Piante, C., Plass-Johnson, J., Sainz-Trapaga, S., Santarossa, L., Tudela, S., Guidetti, P., 2016. Five key attributes can increase marine protected areas performance for small-scale fisheries management. Sci Rep 6.

Francour, P., 1994. Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola natural reserve (Corsica, Northwestern Mediterranean). Oceanologica 17:309–317.

Gaines, S. D., White, C., Carr, M.H. and Palumbi, S.R. 2010. Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences USA 107:18286–18293.Gallacher, J., Simmonds, N., Fellowes, H., Brown, N., Gill, N., Clark, W., Biggs, C. Rodwell, L.D. 2016. Evaluating the success of a marine protected area: A systematic review approach. J Environ Manage 183:280–293.

Geraldi, N.R., Kellison, G.T., Bacheler, N.M., 2019. Climate indices, water temperature, and fishing predict broad scale variation in fishes on temperate reefs. Frontiers in Marine Science 6:1-13.

Glasgow, D.M., 2017. Environmental Relationships And Predator-Prey Interactions Within The Snapper-Grouper Complex In The Southeastern U.S. Atlantic – Implications For Fisheries

Management. (Doctoral dissertation).

Govoni, J.J., Hare, J.A., Davenport, E.D., 2013. The Distribution of Larval Fishes of the Charleston Gyre Region off the Southeastern United States in Winter Shaped by Mesoscale, Cyclonic Eddies. Mar Coast Fish 5:246–259.

Gower, J.C., 1971. A General Coefficient of Similarity and Some of Its Properties. Biometrics 27:857.

Green, A.L., Fernandes, L., Almany, G., Abesamis, R., Mcleod, E., Alino, P.M., White, A.T., Salm, R., Tanzer, J., Pressey, R.L. 2014. Designing Marine Reserves for Fisheries Management, Biodiversity Conservation, and Climate Change Adaptation. Coast Manag 42:143–159.

Guidetti, P., Milazzo, M., Bussotti, S., Molinari, A., Murenu, M., Pais, A., Spanò, N., Balzano, R., Agardy, T., Boero, F., Carrada, G., Cattaneo-Vietti, R., Cau, A., Chemello, R., Greco, S., Manganaro, A., Notarbartolo di Sciara, G., Russo, G.F., Tunesi, L., 2008. Italian marine reserve effectiveness: Does enforcement matter? Biol Conserv 141:699–709.

Halpern, B.S., Warner, R.R., 2002. Marine reserves have rapid and lasting effects. Ecol Lett 5:361–366.

Harasti, D., Williams, J., Mitchell, E., Lindfield, S., Jordan, A., 2018. Increase in Relative Abundance and Size of Snapper Chrysophrys auratus Within Partially-Protected and No-Take Areas in a Temperate Marine Protected Area. Front Mar Sci 5:1–12.

Hare, J.A., Walsh, H.J., 2007. Planktonic linkages among marine protected areas on the south Florida and southeast United States continental shelves. Can J Fish Aquat Sci 64:1234–1247.

Heyns-Veale, E.R., Bernard, A.T.F., Götz, A., Mann, B.Q., Maggs, J.Q., Smith, M.K.S. 2019. Community-wide effects of protection reveal insights into marine protected area effectiveness for reef fish. Mar Ecol Prog Ser 620:99-117. https://doi.org/10.3354/meps12970

Hilborn, R., Stokes, K., Maguire, J.J., Smith, T., Botsford, L.W., Mangel, M., Orensanz, J. Al, E., 2004. When can marine reserves improve fisheries management? Ocean Coast Manag 47:197–205.

Hood, P.B., Johnson, A.K., 2000. Age, growth, mortality, and reproduction of red porgy, *Pagrus pagrus*, from the eastern Gulf of Mexico. Fish Bull 98:723–735.

Jost, L., 2006. Entropy and diversity. Oikos 113:363–375.

Kobara, S., B. Erisman, W. Heyman, C. Biggs, N. Farmer, S. Lowerre-Barbieri, M. Karnauskas, and J. Brenner. 2017. Cooperative monitoring program for spawning aggregations in the Gulf of Mexico: data portal. Version 1.0 GCOOS, USA.

Lesher, A., 2008. An analysis of larval dispersal and retention within the South Atlantic Bight using satellite-tracked drifters released on reef fish spawning grounds. M. Sc. 87pp.

Lester, S., Halpern, B., 2008. Biological responses in marine no-take reserves versus partially protected areas. Mar Ecol Prog Ser 367:49–56.

Lorenzo, M. Di., Claudet, J., Guidetti, P., 2016. Spillover from marine protected areas to adjacent fisheries has an ecological and a fishery component. J Nat Conserv 32:62–66.

Lundquist, C.J., Granek, E.F., 2005. Strategies for Successful Marine Conservation: Integrating Socioeconomic, Political, and Scientific Factors. Conserv Biol 19:1771–1778.

MacNeil, M.A., Graham, N.A.J., Cinner, J.E., Wilson, S.K., Williams, I.D., Maina, J., Newman, S., Friedlander, A.M., Jupiter, S., Polunin, N.V.C., McClanahan, T.R., 2015. Recovery potential of the world's coral reef fishes. Nature 520:341–344.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2019. cluster: Cluster Analysis Basics and Extensions. R package version 2.1.0.

Malcolm, H.A., Schultz, A.L., Sachs, P., Johnstone, N., Jordan, A., 2015. Decadal changes in the abundance and length of snapper (Chrysophrys auratus) in subtropical marine sanctuaries. PLoS One 10:1–19.

McClanahan, T.R., Mangi, S., 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. Ecol Appl 10:1792–1805.

McLeod, E., Salm, R., Green, A., Almany, J., 2009. Designing marine protected area networks to address the impacts of climate change. Front Ecol Environ 7:362–370.

Molloy, P.P., McLean, I.B., Côté, I.M., 2009. Effects of marine reserve age on fish populations: a global meta-analysis. J Appl Ecol 46:743–751.

NOAA, 2019. Fishery Stock Status Updates: 2019 Q1. Available at: https://www.fisheries.noaa.gov/national/population-assessments/fishery-stock-status-updates#2019-quarterly-updates. (accessed 11 May 2019).

Pelletier, D., García-Charton, J.A., Ferraris, J., David, G., Thébaud, O., Letourneur, Y., Claudet, J., Amand, M., Kulbicki, M., Galzin, R., 2005. Aquatic Living Resources Designing indicators for assessing the effects of marine protected areas on coral reef ecosystems: A multidisciplinary standpoint. Aquat Living Resour 18:15–33.

Polacheck, T., 1990. Year round closed areas as a management tool. Nat Resour Model 4:327–

353.

Pomeroy, R.S., Watson, L., Parks, J., 2004. How is your MPA doing? a methodology for evaluating the management effectiveness of marine protected areas. Ocean Coast Manag 48:485–502.

Potts, J.C., Manooch, C.S., Vaughan, D.S., 1998. Age and Growth of Vermilion Snapper from the Southeastern United States. Trans Am Fish Soc 127:787–795.

Quinn G.P., Keough M.J. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge: 1–511.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rassweiler, A., Costello, C., Hilborn, R., Siegel, D., 2014. Integrating scientific guidance into marine spatial planning. R Soc B-Biological Sci 281:20132252.

Ross, S., Moser, M., 1995. Life History of Juvenile Gag, Mycteroperca Microlepis, in North Carolina Estuaries. Circulation 56:222–237.

Rudershausen, P.J., Buckel, J.A., and Williams, E.H., 2007. Discard composition and release fate in the snapper grouper commercial hook-and-line fishery in North Carolina, USA. Fish Manage. Ecol. 14: 103-113.

Runde, B.J., Buckel, J.A., 2018. Descender devices are promising tools for increasing survival in deepwater. Mar Coast Fish 10: 100-117.

Russ, G., Stockwell, B., Alcala, A., 2005. Inferring versus measuring rates of recovery in no-take marine reserves. Mar Ecol Prog Ser 292:1–12.

Russ, G.R., Alcala, A.C., 2010. Decadal-scale rebuilding of predator biomass in Philippine marine reserves. Oecologia 163:1103–1106.

Russ, G.R., Alcala, A.C., 1996. Marine Reserves: Rates and Patterns of Recovery and Decline of Large Predatory Fish. Ecol Appl 6:947–961.

Sabetian, A., 2003. The association of physical and environmental factors with abundance and distribution patterns of groupers around Kolombangara Island, Solomon Islands. Environ Biol Fishes 68:93–99.

SAFMC, 2006. Historical Overview of the South Atlantic Fishery Management Council's Marine Protected Areas Related Activites: 1990-2206. https://safmc.net/wp-content/uploads/2016/06/MPAHist_Overview.pdfSAFMC, 2016. System Management Plan for Deepwater Marine Protected Areas A Blueprint for Research, Monitoring, Outreach, Administration, and Evaluation of Deepwater Marine Protected Areas Created in Amendment 14 to the Snapper Grouper Fishery Management Plan.

SEDAR, 2020. South Atlantic Red Porgy Stock Assessment Report, SEDAR, North Charleston, South Carolina.Available online at: http://sedarweb.org/sedar-60

Sciberras, M., Jenkins, S.R., Kaiser, M.J., Hawkins, S.J., Pullin, A.S., 2013. Evaluating the biological effectiveness of fully and partially protected marine areas. Environ Evid 2:4.

Smart, T.I., Reichert, M.J.M., Ballenger, J.C., Bubley, W.J., Wyanski, D.M., Reichert, M.J.M., Ballenger, J.C., Walter, J., Wyanski, D.M., 2015. Overview of sampling gears and standard protocols used by the Southeast Reef Fish Survey and its partners SEDAR50-RD20. MARMAP Techincal Report # 2015-005.

Smart, T.I., Glasgow, D.M., Bubley, W.J., Reichert, M.J.M., 2020 In review. Spatial Distribution Changes and Habitat Use in Red Porgy off the Southeast U.S. Atlantic Coast. Marine and Coastal Fisheries.: Dynamics, Management, and Ecosystem Science 12:381-394.

Starr, R.M., Wendt, D.E., Barnes, C.L., Marks, C.I., Malone, D., Waltz, G., Schmidt, K.T., Chiu J., Launer, A.L., Hall, N.C., Yochum, N., 2015. Variation in Responses of Fishes across Multiple Reserves within a Network of Marine Protected Areas in Temperate Waters. PLoS One 10:e0118502.

Stelzenmuller, V., Pinnegar, J., 2011. Monitoring fisheries effects of marine protected areas: current approaches and the need for integrated assessments. In: *Marine Protected Areas: A Multidisciplinary Approach*. J. Claudet (ed). Cambridge University Press. pp. 168–189.

United Nations, 1992. Convention on Biological Diversity. https://www.cbd.int/convention/text/

Underwood A.J. 1996. Spatial patterns of variance in density of intertidal populations. In: Floyd R.B., Sheppard A.W., De Barro P.J. (Eds), Frontiers of Population Ecology. CSIRO, Victoria: 369–389.

Unsworth, R.K.F., Powell, A., Hukom, F., Smith, J., 2007. The ecology of Indo-Pacific grouper (Serranidae) species and the effects of a small scale no take area on grouper assemblage, abundance and size frequency distribution.

Ward, T.J., Heinemann, D., Evans, N., 2001. The role of marine reserves as fisheries management tools. Australia Bureau of Rural Sciences.

Wilson, R.R., Burns, K.M., 1996. Potential Survival of Released Groupers Caught Deeper than

40 m based on Shipboard and in-situ Observations, and Tag-Recapture Data. Bull Mar Sci 58:237–247.

Wyanski, D.M., Kolmos, K.J., and Bubley,W.J. 2019. Update of Red Porgy, Pagrus pagrus, Reproductive Life History from the MARMAP/SERFS program. SEDAR60-WP02. SEDAR, North Charleston, SC. 21 pp.

Zuur A.F., Ieno E.N., Walker N.J., et al. 2009. Mixed effects models and extension in ecology with R. Springer-Verlag, New York, 574 pp. http://dx.doi.org/10.1007/978-0-387-87458-6

Tables

Table 1. Sampling distributions of three southeast United States (SEUS) marine protected areas (MPAs): Northern South Carolina (NSC), Edisto (ED), and North Florida (NF). Provided are the area and depths sampled as compared to the total area and depth range of the MPAs.

MPA	**Sampling Area (km^2)**	**Boundary Area (km^2)**	**Sampling Depth Range (m)**	**Boundary Depth Range (m)**
NSC	72	170	45-68	45-170
ED	170	170	45-60	45-140
NF	110	340	45-64	45-380

Table 2. Most commonly caught managed reef fish species in Northern South Carolina (NSC), Edisto (ED), and North Florida (NF) marine protected areas and adjacent fished areas. x = ten most common reef fish species for each MPA and comparison.

Species Name	**NSC**	**ED**	**NF**
Balistes capriscus (Gmelin, 1789)	x	x	x
Calamus nodosus (Randwall & Caldwell, 1966)	x	x	
Centropristis striata (Linnaeus, 1758)	x		x
Cephalopholis cruentata (Lacepède, 1802)		x	
Cephalopholis fulva (Linnaeus, 1758)	x		
Epinephelus adscensionis (Osbeck, 1765)	x		
Epinephelus drummondhayi Goode & Bean, 1878			x
Epinephelus morio (Valenciennes, 1828)	x	x	x
Haemulon plumierii (Lacepède, 1801)	x	x	
Lutjanus campechanus (Poey, 1860)		x	x
Mycteroperca phenax Jordan & Swain, 1884	x	x	x
Pagrus pagrus (Linnaeus, 1758)	x	x	x
Rhomboplites aurorubens (Cuvier, 1829)	x	x	x
Seriola dumerili (Risso, 1810)			x
Seriola rivoliana (Valenciennes, 1833)		x	x

Table 3. ANOVA (type 3) results (F-statistics unless otherwise noted) on abundance (log(x + 1) transformed) for the top ten most abundant reef fish species (RFS) and for Red Porgy (RP). Global models include all MPA regions ("All"), as well as the results of sub-models for each MPA region: Northern South Carolina (NSC), Edisto (ED), North Florida (NF). F-statistics greater than 3.87 are significant ($p<0.05$) and in bold. Coefficient-Estimate (β) is provided for the location by time interaction term.

Model Type	Region	Location (Inside|Outside)	Time (Before|After)	Location by Time		Temperature	Depth	Relief	Substrate Density	Biota Density	Degrees of Freedom	Adjusted R^2	F-statistic
				F	β								
RFS													
All	**4.90**	**12.5**	**4.0**	3.2	0.25	**24.3**	0.40	**10.4**	1.83	1.05	1185	0.06	**9.13**
NSC	-	**17.8**	3.21	0.76	0.16	**9.29**	**7.09**	2.00	0.13	0.21	505	0.12	**10.0**
ED	-	0.73	2.24	**4.86**	0.56	**16.6**	0.63	1.69	2.35	1.76	325	0.07	**43.92**
NF	-	**5.22**	-	-	-	**4.53**	0.21	2.55	0.26	0.31	341	0.05	**3.23**
RP													
All	**7.97**	1.5	**5.98**	0.23	-0.06	0.76	**4.10**	**18.1**	**4.03**	**6.3**	1185	0.08	**11.1**
NSC	-	0.19	3.47	0.55	-0.11	1.95	0.04	**12.4**	0.68	1.70	505	0.09	**7.07**
ED	-	**5.11**	0.69	0.66	0.19	0.05	1.88	0.42	3.40	**9.45**	325	0.12	**6.71**
NF	-	0.03	-	-		0.18	0.05	2.77	0.01	0.33	341	0.03	**2.55**

Figures

Figure 1. Sampling Locations. Southeast Reef Fish Survey (SERFS) chevron trap sampling locations in the southeast United States (SEUS) Atlantic Ocean with the three Marine Protected Areas (MPA) and adjacent fished comparison areas analyzed in this study: Northern South Carolina, Edisto, and North Florida.

Figure 2. MPA Global Analysis of Changes in Reef Fish Abundances. Mean (log(x + 1)) +/- standard error (se) and linear model predicted values +/- se (red) for abundance of the ten most commonly caught managed reef fish species (upper panel) and Red Porgy (lower panel) inside/outside of three SEUS MPAs and before/after MPA implementation. Refer to Table 3 for summary of ANOVA (type 3) results. Values are based on trap data collected by the Southeast Reef Fish Survey 2000-2018, excluding samples collected in 2009 when MPAs were established.

Figure 3. MPA Analysis of Changes in Reef Fish Abundances. Mean (log(x + 1)) +/- standard error of the ten most commonly caught managed reef fish species inside and outside of three SEUS MPAs Northern South Carolina (a), Edisto (b) and North Florida (c). Values are based on trap data collected by the Southeast Reef Fish Survey 2000-2018, excluding samples collected in 2009 (vertical dashed line) when MPAs were established. Sample sizes (N) for each three-year period are reported below each graph (inside|outside).

Figure 4. MPA Analysis of Changes in Red Porgy Abundances. Mean (log(x+1)) +/- standard error of the ten most commonly caught managed reef fish species inside and outside of three SEUS MPAs Northern South Carolina (a), Edisto (b) and North Florida (c). Values are based on trap data collected by the Southeast Reef Fish Survey 2000-2018, excluding samples collected in 2009 (vertical dashed line) when MPAs were established. Sample sizes (N) for each three-year period are reported below each graph (inside|outside).

Figure 5. MPA Analysis of Changes in Reef Fish Sizes. Total length distributions (cm) of the ten most commonly caught managed reef fish species inside and outside three MPAs: Northern South Carolina (a), Edisto (b), North Florida (c). Values are based on trap data collected by the Southeast Reef Fish Survey 2000-2018, excluding samples collected in 2009 (vertical dashed line) when MPAs were established. One-sided t-test (assuming unequal variance) of inside-outside comparison used to assess significance. ($p<0.05$ = *, $p<0.01$ = **, $p<0.001$ = ***). Sample sizes (N) for each four-year period are reported below each graph (inside|outside).

Figure 6. MPA Analysis of Changes in Red Porgy Sizes. Total length distributions (cm) of Red Porgy inside and outside three MPAs: Northern South Carolina (a), Edisto (b), North Florida (c). Values are based on trap data collected by the Southeast Reef Fish Survey 2000-2018, excluding samples collected in 2009 (vertical dashed line) when MPAs were established. One-sided Wilcoxon rank sum test of inside-outside comparison used to assess significance. ($p<0.05$ = *,

p<0.01 = **, p<0.001 = ***). Sample sizes (N) for each four-year period are reported below each graph (inside|outside).

Figure 7. MPA Analysis of Changes in Percent of Fully-Recruited Red Porgy. Percent of fully-recruited Red Porgy (age 4 and above), three MPAs: Northern South Carolina (a), Edisto (b), North Florida (c). Values are based on trap data collected by the Southeast Reef Fish Survey 2000-2018, excluding samples collected in 2009 (vertical dashed line) when MPAs were established. Significance tested for inside-outside comparisons using chi-square test (p<0.05 = *, p<0.01 = **, p<0.001 = ***). Sample sizes (N) for each four-year period are reported below each graph (inside|outside).