Juvenile Density, Fishing Mortality, and Habitat use of Red Snapper, *Lutjanus campechanus*, on Artificial and Natural Reefs in the Northern Gulf of Mexico.

by

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Abstract

The Red Snapper, *Lutjanus campechanus,* fishery in the Gulf of Mexico has been intensively regulated as managers attempt to rebuild the fishery. This has led to a need for improved data collection, and a better understanding of Red Snapper biology. This study examined three aspects of the biology and fishery of Red Snapper. First, patch-reefs were examined as a novel method for estimating Red Snapper juvenile density as an index of year-class strength, which could improve fishery management efforts if years of strong or weak year classes can be measured before they enter the directed fishery. The timeframe examined also included years before and after the 2010 Deepwater Horizon oil spill, allowing for an evaluation of the spill's effects on juvenile Red Snapper. Second, the present study estimated tagging mortality, natural mortality and fisher nonreporting from acoustic telemetry of Red Snapper to calibrate a conventional mark-recapture study to improve fishing mortality estimates, which can increase the accuracy of management efforts. Finally, while many artificial reefs have been deployed in the northern Gulf of Mexico to improve fishing opportunities, it is unclear if these artificial reefs function differently than natural reefs. Fine scale telemetry methods were used to compare Red Snapper home range, diel and seasonal behaviors, site fidelity, and mortality on natural reefs and artificial reefs to help improve our understanding of how Red Snapper use these different habitats.

High densities of age-0 Red Snapper in 2009, 2011, and 2013 on patch-reefs indicated years of higher potential year classes of Red Snapper. The density of age-0 Red Snapper in 2010 was low at an offshore location, but similarly low densities were also observed in other years. The density of age-0 Red Snapper in 2010 at an inshore

location, and the density of age-1 Red Snapper in June 2011 were similar to other years. Thus, the present study detected little effect of the 2010 Deepwater Horizon oil spill on the density of age-0 Red Snapper on patch-reefs.

Mean fishing mortality for Red Snapper greater than 406 mm total length was $F = 0.22$ in 2015 and 2016, with an estimated annual harvest of 212,237 fish per year. These results were based on estimates of tagging mortality, natural mortality, tag shedding, and fisher nonreporting from telemetry that were applied to the conventional tagging effort, and accounting for Red Snapper distributions on different reef types. Red Snapper living on both natural and artificial reefs had similar mortality rates, site fidelity and movement patterns, and similar relations to changing seasons and temperature on these two reef types. These observed similarities indicated that these two reef types have similar ecological functions for Red Snapper. Importantly, fishing mortality rates were nearly identical on both reef types and provided little evidence that artificial reefs disproportionally concentrate Red Snapper and increase exploitation compared to natural reefs.

Red Snapper are closely tied to reef structure, even at the youngest ages. The present study used this association to measure year-class strength, and to estimate fishing mortality in this valuable fishery. Importantly, this study indicated little difference in Red Snapper behavior and exploitation between natural and artificial reefs. This supports the idea that artificial reefs benefit, rather than harm, Red Snapper populations. Thus, further artificial reef deployments have the potential to increase Red Snapper habitat, even at early life stages.

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Table of Contents

Abstract 2

Acknowledgments 4

List of Tables 7

List of Figures 8

Chapter 1: Juvenile Red Snapper *Lutjanus campechanus*, densities on small artificial reefs to estimate year-class strength. 9

Abstract 9

Introduction 10

Methods 12

Results 18

Discussion 20

References 28

Chapter 2: Fishing mortality estimates for Red Snapper *Lutjanus campechanus*, based on acoustic telemetry and conventional mark-recapture 43

Abstract 43

Introduction 44

Methods 46

Results 55

Discussion 60

References 66

Chapter 3: A comparison of home range, site fidelity, and mortality of Red Snapper, *Lutjanus campechaus*, on artificial and natural reefs in the northern Gulf of

Mexico 77
Abstract 77
Introduction 78
Methods 80
Results 88
Discussion 92
References 102

List of Tables

Chapter 1:

Table 1-1: Environmental conditions associated with visual surveys 32

Table 1-2: Location, deployment and survey date for patch-reef sets 33

Table 1-3: Mean SEAMAP CPUE of age-0 and age-1 Red Snapper 34

Chapter 2:

Table 2-1: The number of Red Snapper released each year 70

Table 2-2: The number of conventionally-tagged Red Snapper harvested and reported 71

Table 2-3: Instantaneous fishing mortality (*F*) for conventionally-tagged Red Snapper 72

Table 2-4: The number of conventionally-tagged Red Snapper reported by reef type 73

Chapter 3:

Table 3-1: Summary of VPS site attributes 108

Table 3-2: Differences in diel KDE area with VPS sites sorted by depth 109

List of Figures

Chapter 1:

Figure 1-1: Small patch-reef deployed in the present study 35

Figure 1-2: Locations of artificial patch-reefs 36

Figure 1-3: Mean density of Red Snapper on patch-reefs deployed each year 37

Figure 1-4: Mean densities of Red Snapper on patch-reefs in August each year 38

Figure 1-5: Mean densities of Red Snapper on patch-reefs in September each year. 39

Figure 1-6: Mean densities of Red Snapper on patch-reefs in October each year...................... 40

Figure 1-7: Mean densities of Red Snapper on patch-reefs in June each year 41

Figure 1-8: Comparison of patch-reefs to CPUE from SEAMAP summer trawl surveys 42

Chapter 2:

Figure 2-1: Location of the telemetry receiver array 74

Figure 2-2: Locations of reefs where conventionally-tagged Red Snapper were released......... 75

Figure 2-3: Survival (*S*) of transmitter-tagged Red Snapper from fishing mortality by year..... 76

Chapter 3:

Figure 3-1: Locations of telemetry receivers in the northern Gulf of Mexico.......................... 110

Figure 3-2: Mean 95% KDE ± SE (m^2) for fish residing on each VPS site 111

Figure 3-3: All fish positions on R6 and N1.. 112

Figure 3-4: Diel period and depth effects on Red Snapper home range 113

Figure 3-5: Mean 95% KDE ± SE by season and reef type... 114

Chapter 1:

Juvenile Red Snapper *Lutjanus campechanus*, densities on small artificial reefs to estimate year-class strength.

Abstract

Densities of age-0 and age-1 Red Snapper, *Lutjanus campechanus*, were compared over a nine-year period (2007 to 2015), based on SCUBA visual estimates on small (1.42 m^3) artificial patch reefs (patch-reefs) in the northern Gulf of Mexico. This time period included years both before and after the Deepwater Horizon oil spill in 2010 and provided a robust evaluation of the effect of the oil spill on initial density on patch-reefs of this species. Densities of juvenile Red Snapper on patch-reefs were also compared with catch (number caught/H) of juvenile Red Snapper from trawl surveys by the Southeast Area Monitoring and Assessment Program (SEAMAP) that has been used as an index of juvenile density in the Gulf of Mexico. High densities of age-0 Red Snapper in 2009, 2011, and 2013 on patch-reefs indicated years of higher potential year classes of Red Snapper. The density of age-0 Red Snapper in 2010 was low at an offshore location, but similarly low densities were also observed in 2014 and 2015. The density of age-0 Red Snapper in 2010 at an inshore location was higher than the offshore location and similar to densities in other years. Also, the density of age-1 Red Snapper in June 2011 was similar to that in other years. Thus, the present study detected little effect of the 2010 Deepwater Horizon oil spill on the density of age-0 Red Snapper on patch-reefs. There was an inverse relation between the natural log density of age-0 and the

density of age-1 Red Snapper in August, September, and October, indicating that older conspecifics interfered with age-0 Red Snapper movements to patch-reefs. There was no significant correlation between the density of age-0 Red Snapper on patch-reefs in October and catch per unit effort (CPUE = catch/H) of Red Snapper from the SEAMAP fall trawl surveys. However, in June the density of age-1 Red Snapper on patch-reefs was significantly correlated with CPUE from SEAMAP summer trawl surveys, after a 2015 outlier was removed. In the present study, visual surveys of small patch-reefs were effective in estimating the density of juvenile age-0 and age-1 Red Snapper. This survey method, if applied throughout the northern Gulf of Mexico may substantially enhance present management efforts to reliably determine initial densities on reef structure and potentially help management in predictions of year class strength.

Introduction

Accurate stock assessment and management of marine reef fishes requires an understanding of juvenile settlement and movement to reef habitats. Management efforts are more effective if year class strength can be estimated before juveniles enter the fishery, rather than back-calculating year class strength after a year class moves into the exploited portion of the fishery. The open nature and large size of marine habitats make accurate measurement of juvenile fish density difficult. Red Snapper, *Lutjanus campechanus*, is a valuable reef fish that is intensively managed in the northern Gulf of Mexico (SEDAR 2018). Accurately predicting year class strength could allow quotas to be increased when it can be anticipated that large year classes will enter the fishery.

Jointly, stocks could be protected from overfishing by decreasing quotas as less abundant year classes enter the fishery. Historically, density estimates of juvenile Red Snapper in stock assessments were based on trawl surveys (Pollack et al. 2012; SEDAR 2018). However, such estimates are inherently unsuitable for Red Snapper, as juveniles quickly move to structured habitat within their first year of life (Szedlmayer and Lee 2004; Szedlmayer 2011). With these known difficulties in trawl surveys, other survey methods may be more accurate for determining the density of juvenile Red Snapper, especially after they settle to benthic habitats and quickly move to reef structure (Bailey et al. 2001; Gallaway et al. 2009; Szedlmayer 2011; Mudrak and Szedlmayer 2012).

Small isolated reefs (patch-reefs) have long been used to experimentally manipulate reef fish communities (Sale 1980; Doherty 1982; Steele 1998). Patch-reefs can be constructed of natural or man-made materials, and because they are easily manipulated, can facilitate experimental designs that address specific questions. Studies that used patch-reefs have examined several factors that may affect Red Snapper density in the northern Gulf of Mexico, including reef complexity (Workman et al. 2002; Lingo and Szedlmayer 2006; Piko and Szedlmayer 2007), predator exclusion (Piko and Szedlmayer 2007), large reef habitat proximity (Workman et al. 2002; Mudrak and Szedlmayer 2012), epibenthic faunal exclusion (Redman and Szedlmayer 2009; Szedlmayer and Miller 2018) and reef location (Szedlmayer and Mudrak 2014). Also, a previous study suggested that juvenile Red Snapper density on artificial patch-reefs could be used as a population attribute to estimate potential Red Snapper recruitment to the fishery (Szedlmayer 2011). Szedlmayer and Mudrak (2014) applied this approach and detected little effect of the Deepwater Horizon oil spill on Red Snapper densities on patch-reefs. However, comparisons to surveys prior to the spill were from patch-reefs of various materials and designs, different deployment times, or different locations. All of these features of patch-reefs can affect juvenile Red Snapper density (Szedlmayer and Mudrak 2014). Also, in the previous study, densities of Red Snapper were only compared with pre-spill densities one year after the oil spill (Szedlmayer and Mudrak 2014).

The present study estimated the density of juvenile Red Snapper on artificial patch-reefs deployed at similar times and locations from 2007 to 2015. All patch-reefs had the same dimensions and design, and were deployed in the same general area from 2007 to 2011 as part of other studies that examined densities of Red Snapper and Gray Triggerfish, *Balistes capriscus*, over shorter times (Simmons and Szedlmayer 2011; Mudrak and Szedlmayer 2012; Szedlmayer and Mudrak 2014). The present study estimated Red Snapper density from these previous studies, along with Red Snapper densities from patch-reefs built between 2012 and 2015. Combined, all surveys allowed comparisons of densities of juvenile Red Snapper on the same patch-reef structure over a nine-year period. Importantly, the present study provided a robust evaluation of the effect of the 2010 Deepwater Horizon oil spill, because identical survey methods were used before and after the spill.

Methods

Reef design and surveys

Each patch-reef had a total volume of 1.42 m^3 and consisted of a polyethylene plastic pallet (1.22 × 1.02 × 0.14 m), 10 concrete blocks (41 × 20 × 10 cm) and a plastic crate (65 × 35 × 28 cm; Figure 1-1). Patch-reefs were assembled with 122-cm plastic cable ties with a breaking strength of 79 kg. A small plastic float (5.1 × 12.7 cm) was attached to each reef corner and floated 1 m above the reef. A larger float (15.2-cm in diameter) was attached at the patch-reef center and also floated 1 m above the patch-reef. The floats added vertical structure to the patch-reef and facilitated patch-reef relocations with sonar. The patch-reefs were anchored by attachment to a 1.2 m ground anchor with a 3 m length of 1.3 cm diameter nylon rope. All patch-reefs were placed at least 500 m apart and 500 m distant from any known reefs in the area (Mudrak and Szedlmayer 2012).

Patch-reefs were visually surveyed by SCUBA divers. Divers identified fish to species, counted all fish present on the patch-reef, and estimated their size in 25 mm total length (TL) intervals. Divers took up stationary positions 2 m from the patch-reef and counted all fish within visible range of the patch-reef over an approximate 15 min survey period. Fish distance varied and was not measured; thus, all densities were calculated as density per m^3 reef size. However, diver visibility typically exceeded maximum fish distances from the reef due to the small size of the patch-reefs. If diver visibility was determined to be less than the 3 m distance to the far side of the reef (i.e., divers could not count all fish on the far side of the reef), the reef surveys were discontinued. Some of the patch-reefs became partially buried after storms. If more than 50% of a patch-reef was buried, the estimate of fish density from that patch-reef was not included in the analysis. The age of Red Snapper observed was estimated based on TL as determined from previous studies. All Red Snapper greater than 305 mm TL were considered age 2 or older. Red Snapper were considered age-0 in May, June and July when less than 76 mm TL, in August when less than 102 mm TL, in September when less than 127 mm TL, in October when less than 152 mm TL, in November when less than 178 mm TL and in December when less than 203 mm TL (Szedlmayer and Conti 1999; Szedlmayer and Lee 2004). No surveys were conducted in January, February, March or April. At the time of the diver surveys, temperature, salinity and dissolved oxygen were measured within 1 m of the bottom with a remote YSI 6920 meter. If more than one water condition reading was taken at a reef site during a survey, temperature, salinity and dissolved oxygen were presented as a mean of the measurements. Temperature ranged from 22.9 to 30.0 °C, salinity from 29.0 to 36.2 ppt and dissolved oxygen (DO) from 2.0 to 6.5 ppm (Table 1-1).

Interannual comparisons

The densities (number of fish/m^3 patch-reef size) of age-0 and age-1 Red Snapper were compared among deployment dates, locations and survey dates (Table 1-2). Patch-reefs deployed at the same time and location were referred to as a reef set (Table 1-2; Figure 1-2). The patch-reefs (described above) were deployed with 10 to 30 patch-reefs per set. One set of patch-reefs was deployed each year, with the exception of 2010 when three patch-reef sets (N = 10 patch-reefs for each set, N = 30 total patch-reefs) were deployed to evaluate the effect of the Deepwater Horizon oil spill on reef-associated fish assemblages (Table 1-2). The offshore location was 19 – 23 km from shore and ranged in depth from 17 – 24 m (Figure 1-2). The inshore location was 12 – 16 km from shore and ranged in depth from 14 – 18 m (Figure 1-2). If there was more than one survey conducted in the same month, the highest mean density of age-0 Red Snapper per survey was used for interannual comparisons of juvenile fish density. In 2008, not all patch-reefs could be located after Hurricane Gustav (1 September 2008). In 2009, patch-reefs could not be located or were damaged after Hurricane Ida (10 November 2009). In 2011, one patch-reef could not be located after tropical storm Lee (4 September 2011), and in 2012 four patch-reefs could not be located after Hurricane Isaac (28 August 2012).

Patch-reefs were deployed as part of manipulative experiments aimed at estimating reef fish densities and quantifying fish assemblage characters associated with various independent factors such the proximity of the patch-reef to a larger reef, reef spatial distribution, and the addition or removal of potential predators and competitors (Simmons and Szedlmayer 2011, Mudrak and Szedlmayer 2012, Szedlmayer and Mudrak 2014). Only fish densities recorded from patch-reefs that were deployed in July or August, placed at least 500 m from other known reefs and without fish artificially added or removed from the assemblage were used for comparing densities among years.

Diver visual data allowed comparisons of Red Snapper densities among years in four months (Table 1-2). The density of Red Snapper observed in August included data from eight years (2008 to 2015), in September from five years (2007, 2009, 2010, 2012, and 2014), in October from six years (2007, 2010, 2011, 2013, 2014, and 2015) and in June from six years (these patch-reefs were deployed in the previous years in 2007, 2010, 2011, 2013, 2014, and 2015). These data were also used to compare the relation between the density of age-0 and age-1 Red Snapper observed in August, September, and October.

Densities of age-0 to age-1 Red Snapper were not compared in June, because few age-0 Red Snapper were present on the patch-reefs.

The Deepwater Horizon oil spill occurred from April 20 to July 15, 2010 (NOAA 2010; Allan et al. 2012), and it was predicted to affect local fish populations (Rooker et al. 2013). In 2010, patch-reefs were deployed in July (Off-Jul2010) at the same location examined in an earlier study (Mudrak and Szedlmayer 2012; Figure 1-2). The initial survey conducted in August 2010 indicated that there was a lower density of age-0 Red Snapper and a higher density of age-1 Red Snapper relative to 2008 and 2009 (Szedlmayer and Mudrak 2014). To determine whether the reduced densities of age-0 Red Snapper observed on the patch-reefs were associated with the oil spill (or associated with increased density of age-1 Red Snapper), two additional patch-reef sets were deployed in August 2010. The Off-Aug2010 reef set was deployed at the same offshore location as the Off-Jul2010 reef set, and the In-Aug2010 reef set was placed closer to shore in an area where past studies had indicated the presence of high densities of age-0 Red Snapper (Szedlmayer and Conti 1999; Figure 1-2). The purpose of deploying more patch-reefs in August 2010 was to provide unoccupied habitat so that the density of age-0 Red Snapper could be determined in the absence of age-1 Red Snapper, which are potential competitors and predators to age-0 fish (Mudrak and Szedlmayer 2012). Red Snapper densities from the three reef sets in 2010 were analyzed separately when comparing the effect of interannual differences in density, because differences in location and deployment date were associated with differences in the density of Red Snapper (Szedlmayer and Mudrak 2014). All reef sets after 2010 were deployed at the inshore study location (Figure 1-2).

Trawl surveys

The densities of Red Snapper as determined from diver visual data were compared with the catch per unit effort (CPUE = catch/H) of Red Snapper estimated from trawl surveys (SEAMAP; Gulf States Marine Fisheries Commission 2018). SEAMAP summer trawl surveys were conducted in June and July each year, and SEAMAP fall trawl surveys were conducted in October and November each year. Only CPUE data obtained from trawl surveys conducted by the State of Alabama (therefore located proximate to the present study sites) were compared with densities from diver visual data from patch-reefs. Most Red Snapper collected by trawl were measured to fork length (mm FL). These lengths were converted to TL with the equation $TL = 1.073 \times FL + 3.56$ (Wilson et al. 2001). The same TL–age relation used to estimate age for the fish size data from the diver visual surveys of patch-reefs was applied to Red Snapper size (TL) collected by trawl. The CPUE of age-0 Red Snapper from fall trawls was compared with the density estimates of age-0 Red Snapper on patch-reefs in October. The CPUE of age-1 Red Snapper from summer trawls was compared with the density estimates of age-1 Red Snapper on patch-reefs in June. For the comparison of trawl CPUE to diver visual data, the densities of juvenile Red Snapper estimated at the Off-Aug2010 and In-Aug2010 reef sets were combined to obtain an estimate of the density of juvenile Red Snapper on patch-reefs for 2010.

Statistical analysis

Annual densities ascribed to various independent (i.e., treatment) variables were compared with generalized linear models with negative binomial distributions and logarithm-link functions (Huelsenbeck and Crandall 1997; Seavy et al.. 2005; Bolker et al. 2009). If significant differences were detected among density according to years, specific differences were identified with a Tukey multiple comparison test (Zar 2010). The relation between age-0 Red Snapper density and age-1 Red Snapper density appeared to be nonlinear, therefore, the natural log (ln) density of age-0 Red Snapper + 1 from diver visual data from patch-reefs, according to month observed, were compared with linear regression, with the ln-density of age-0 Red Snapper as the dependent variable and density of age-1 Red Snapper as the independent variable.

A Pearson's product-moment correlation coefficient was calculated to determine the association between the CPUE from trawls and densities observed on patch-reefs from diver visual data. Differences were considered significant at $P < 0.05$. All statistical analyses were conducted separately, as opposed to repeated measures, for each month for which there were adequate survey data, because not all reef sets were surveyed in all four months analyzed.

Results

Annual variation of juvenile Red Snapper density on patch-reefs

The density of age-0 Red Snapper observed on small artificial patch-reefs in the fall varied widely among years, subsequently the density of age-1 fish the next summer varied less (Figure 1-3). The density of age-0 Red Snapper was significantly different among years in August ($F_{7,81}$ = 19.5, P < 0.001; Figure 1-4), September ($F_{6,63}$ = 23.7, P < 0.001; Figure 1-5) and October ($F_{6,70}$ = 25.8, P < 0.001; Figure 1-6). Similarly, the density of age-1 Red Snapper was significantly different among years in August ($F_{7,81}$ = 6.4, P < 0.001; Figure 1-4), September ($F_{6,63}$ = 4.8, P < 0.001; Figure 1-5), October ($F_{6,70}$ = 3.0, P = 0.01; Figure 1-6) and in June ($F_{6,84}$ = 5.9, P < 0.001; Figure 1-7).

Age-0 and age-1 Red Snapper

Density of age-1 Red Snapper was considered the independent variable that affected ln-density of age-0 Red Snapper (Mudrak and Szedlmayer 2012). There was a significant inverse relation between age-0 ln-density and age-1 density in August (r^2 = 0.26, P < 0.001, N = 89 patch-reefs), in September (r^2 = 0.07, P = 0.02, N = 70 patch-reefs) and in October (r^2 = 0.09, P = 0.007, N = 77 patch-reefs).

Visual density estimates compared to CPUE from trawls

The SEAMAP trawl surveys off coastal Alabama were conducted annually during summer and fall (Gulf States Marine Fisheries Commission 2018). The number of trawl tows ranged from 4 to 12 per season each year, and trawl times ranged from 10 to 96 min (Table 1-3). All catch from trawl surveys was standardized to CPUE = catch/H. There was no significant correlation between the density of age-0 fish observed on patch-reefs in October compared to the CPUE of age-0 fish from fall trawls (r = 0.42, P = 0.41). There was a marginally significant correlation between the density of age-1 fish observed on patch-reefs in June and the CPUE of age-1 fish from summer trawls (r = 0.80, P = 0.055). Also, SEAMAP trawling in June 2015 failed to catch any age-1 Red Snapper, but age-1 fish were observed during patch-reef surveys. This result of no captures of age-1 Red Snapper is likely an outlier, perhaps due to small sample size, surveying in areas of poor Red Snapper habitat (i.e., lack of structure) or reduced effectiveness by trawling over structured (i.e., rugose) habitats. After removal of the data from June 2015, there was a significant correlation between densities of age-1 Red Snapper observed on patch-reefs in June and CPUE from trawl surveys in the summer (r = 0.99, P = 0.001; Figure 1-8).

Discussion

Interannual comparisons

The main objective of the present study was to compare density variation in juvenile Red Snapper among years based on visual estimates from patch-reefs, and to evaluate the effect of the 2010 Deepwater Horizon Oil spill on juvenile Red Snapper density. In the present study, density of juvenile Red Snapper on patch-reefs was considered an index of settlement and movement to reef habitat (Szedlmayer 2011). The timing of the Deepwater Horizon oil spill in 2010 coincided with Red Snapper spawning, and previous studies have suggested that larval condition and juvenile density were reduced in 2010 (SEDAR 2013; Hernandez et al. 2016). In contrast, the densities of age-0 Red Snapper on patch-reefs in October of 2010 and 2011 were similar to densities in years prior to the oil spill (Szedlmayer and Mudrak 2014). Additionally, there were high densities of age-1 Red Snapper on patch-reefs in June 2011 that were from the 2010 year class (Szedlmayer and Mudrak 2014).

In the present study, the lowest density of age-0 Red Snapper among all surveys was observed on the patch-reefs deployed at the offshore location in 2010; however, the density of age-1 Red Snapper the following June was similar to that in other years. Low densities of age-0 Red Snapper were also observed in some surveys of patch-reefs deployed in 2014 and 2015, but again in the following June densities of age-1 Red Snapper were similar to those in other years. The densities of age-0 Red Snapper on the inshore patch-reefs in 2010 were in the middle of the range of densities compared with other years, and again, the densities of age-1 Red Snapper observed the following June were similar to those in other years. Thus, an oil-spill effect on juvenile Red Snapper density either did not occur or was not detected by this survey method beyond the normal, expected variation of density among juvenile Red Snapper. Szedlmayer and Mudrak (2014) also indicated that a year class failure was not detected in 2010, because age-1 Red Snapper were abundant the following year. This earlier conclusion was supported in the present study based on six years of density determinations of age-1 Red Snapper on patch-reefs in June that indicated statistically similar densities for 2010 compared with both before the oil spill (2007) and after the oil spill (2011, 2013, 2014, and 2015; Figure 1-7).

The highest density of age-0 Red Snapper in October was for patch-reefs deployed in 2013 and this strong year class persisted as the highest density of age-1 Red Snapper observed the following June. This indicates that successful Red Snapper settlement and movement to patch-reefs was exceptionally high in 2013 compared with colonization in other years considered here. Age-0 Red Snapper densities were also high in August and October 2011. However, by the following June, the 2011-year class was similar to other years. Also, the September 2009 survey indicated the presence of an exceptionally high density of age-0 Red Snapper. Unfortunately, all patch-reefs deployed in 2009 were destroyed by storms, and it was not possible to conduct surveys for juvenile Red Snapper the following summer.

It was difficult to identify the factors influencing the differences in relative densities of juvenile Red Snapper among years, as the present study was unable to control the environmental, biological or anthropogenic factors associated with these differences. However, two of the three years when high densities were observed corresponded to changes in management of the fishery. The high density of age-0 Red Snapper in 2009 followed severe reductions in the commercial quota and a reduced recreational season (only 65 days) in 2008 (SEDAR 2013, 2018). Similarly, the high density of age-0 Red Snapper observed in 2011 also followed severe reductions in fishing effort, as large areas of the Gulf of Mexico were closed to fishing during the 2010 Deepwater Horizon oil spill (NOAA 2010). This tendency suggested that higher densities of age-0 Red Snapper occurred after the spawning stock biomass had likely increased due to reduced harvest (assuming little adult mortality induced by the oil spill). However, it was difficult to associate the higher density of age-0 Red Snapper in 2013 with any directed management actions. Also, if the increased density of age-0 Red Snapper resulted from increased spawning stock through harvest reductions, for the most part this did not lead to a continuation of high densities of age-0 fish in subsequent years. This lack of continued association between management and the density of age-0 Red Snapper, may have been due to density dependent mechanisms; that is, as density of age-0 fish increased, competition for food or habitat reduced the survival of age-0 fish (Gazey et al. 2008). It is also possible that increases in the spawning biomass of Red Snapper had less effect on juvenile fish density when fishing resumed and catch quotas were subsequently increased. These higher densities of age-0 Red Snapper in particular years may also have been influenced by other environmental or biological factors which were only incidentally related to management actions.

The present study occurred while the Gulf of Mexico Red Snapper stock was being managed under a rebuilding plan, which resulted in an increased spawning biomass (SEDAR 2013, 2018; Szedlmayer et al. 2020). Nevertheless, the densities of age-1 Red Snapper appeared relatively stable over the present study from 2007 to 2015. If spawning biomass was the limiting factor for density of age-1 Red Snapper, density would have increased over the present study period as the stock increased (SEDAR 2018). The lack of an associated increase suggested that factors other than spawning biomass were limiting the density of age-1 fish, and that available spawning biomass was sufficient to saturate available habitat with juvenile Red Snapper. The high densities of juvenile Red Snapper observed on patch-reefs in the present study suggested that later recruitment to the fishery in this portion of the northern Gulf of Mexico may not expand beyond current levels, even if spawning stock biomass continues to increase.

Density dependent mechanisms may cause higher mortality in years with high densities and higher survival in years with low densities (Gazey et al. 2008). In the present study, the density of age-0 Red Snapper varied widely among years, especially early in the settlement season with peak mean density 59 times higher than the lowest observed mean density in August. The variability in density among years was reduced to a 17 fold difference in September, a six fold difference in October, and by June the following year there was only a two-fold difference between the minimum and maximum mean densities of age-1 Red Snapper on patch-reefs. While density dependence may have reduced the differences in density among years, the effect of higher density of age-0 Red Snapper in October was still apparent the following June, at least for the 2013 reef set (Figure 1-3). These differences among years that were observed in October, and again in June, indicated that the later surveys in October may be a better predictor of later recruitment to the fishery than the August or September surveys.

Age-0 and age-1 Red Snapper relations

The present long-term comparison confirmed earlier reports of the inverse relation between the density of age-0 and age-1 Red Snapper (Mudrak and Szedlmayer 2012; Szedlmayer and Mudrak 2014). Workman et al. (2002) also reported that age-0 Red Snapper did not settle on small artificial reefs with age-1 conspecifics, and in a laboratory study, age-1 fish excluded age-0 Red Snapper from structured habitat (Bailey et al. 2001). In September and October, the inverse relation was weaker (7 to 9%) between age-0 and age-1 Red Snapper. This reduced relation in September and October was likely because age-0 fish were larger and logically more able to compete with older conspecifics. Thus, the results supported previous studies, and suppression of age-0 settlement by age-1 fish is likely an important mechanism of density dependence in Red Snapper (Mudrak and Szedlmayer 2012; Szedlmayer and Mudrak 2014).

The patch-reefs used in the present study represented an experimental habitat, not simply because of the artificial materials of which they were composed, but also because they were deployed immediately prior to the peak of Red Snapper settlement (Szedlmayer and Conti 1999). This timing of reef deployments provided an unoccupied habitat for age-0 fish that was free of potential predators and competitors. Under natural conditions, such empty habitat would only be available as a result of environmental disturbances; for example, hypoxic events leading to uninhabitable areas or hurricanes that can deplete resident fishes or uncover buried natural rock habitat. Also, if a patch-reef was available for any length of time, it would become colonized by age-1 Red Snapper. The inverse relation between densities of age-0 and age-1 Red Snapper indicates that these age-1 fish would likely competitively exclude age-0 Red Snapper until the age-1 Red Snapper begin to seek larger structures (Mudrak and Szedlmayer 2012).

Although not used in the interannual comparisons of the present study, such a pattern was observed on the In-Jul2011 reef set, which was surveyed in August and October 2012 (Figure 1-3). In August 2012, the mean density of age-0 Red Snapper ($1.0/m^3$) was much lower on the In-Jul2011 reef set than on the In-Jul2012 reef set ($21.2/m^3$). In October 2012, after age-1 Red Snapper had mostly emigrated from the In-Jul2011 reef set (Figure 1-3), these patch-reefs had similar densities of age-0 Red Snapper ($32.0/m^3$) compared to other years (Figure 1-6). Thus, the timing of patch-reef deployment is important if the study objective is to compare settlement and movement to reef structure of age-0 Red Snapper among years. If patch-reefs were deployed too early, age-1 Red Snapper would colonize and suppress age-0 Red Snapper densities. If patch-reefs were deployed too late, age-0 Red Snapper would already have colonized other structures. Thus, future studies that use patch-reefs to determine age-0 Red Snapper densities need to carefully consider the timing of deployment and potential competitive exclusion by age-1 and older Red Snapper.

Comparison densities on patch-reefs to trawl CPUE

Stock assessments have used trawl surveys for estimating densities of age-0 and age-1 Red Snapper (Pollack et al 2012; SEDAR 2013, 2018). However, the use of trawl surveys to estimate density of juvenile Red Snapper has been questioned. Age-0 Red Snapper move to structured habitat as they grow and most had already moved to such habitat before the SEAMAP fall trawl surveys were conducted in October and November (Szedlmayer and Conti 1999; Szedlmayer and Lee 2004; Szedlmayer 2011). For example, substantially higher densities of juvenile Red Snapper were observed in diver visual data from patch-reefs than were caught in SEAMAP trawl surveys on the continental shelf off coastal Alabama. If the densities on patch-reefs and the CPUE from trawl surveys of open habitat were converted to number of Red Snapper/m^2, diver visual data resulted in density estimates that were 141,373 to 17,395,000 times higher than density estimates from trawl surveys collected at the same time. To clarify, the present study is not reporting that densities of Red Snapper were 100,000 times higher than indicated by CPUE trawl estimates. The implication here is only that trawls surveyed extensive areas that were marginal habitat for juvenile Red Snapper; that is, flat open sand and mud substrates. The premise here is that Red Snapper were only incidentally captured when the trawl passed in close proximity to structured habitat where juvenile Red Snapper resided, or when individuals were transiting over open habitat in search of structure. Thus, visual surveys targeting structured habitats preferred by juvenile Red

Snapper were possibly more effective at determining juvenile Red Snapper density than trawl surveys of large areas of nonpreferred (i.e., open sand and mud) habitat.

There was a significant correlation between densities of age-1 Red Snapper observed via visual surveys and densities derived from trawl surveys in June, but only after the removal of the 2015 outlier (i.e., no age-1 fish were caught in trawls). This result was unexpected, because age-1 Red Snapper have mostly already moved to reef habitat and consequently their capture by trawls should have a lower capture efficiency (Szedlmayer and Conti 1999; Szedlmayer and Lee 2004; Gallaway et al. 2009); for example, the failure of trawl surveys to capture age-1 Red Snapper in 2015, when age-1 Red Snapper were clearly present based on diver visual data from of patch-reefs (Figure 1-7). However, these comparisons between trawl CPUE and diver visual data should be interpreted with caution, because there were only six years of comparisons. In addition, further comparisons are needed from larger areas and longer time series to determine whether densities of juvenile Red Snapper on patch-reefs continue their correlation with trawl CPUE in June.

Supporters of trawl surveys have suggested that offering high quality, preferred patch-reef habitats only estimates the carrying capacity of the reef rather than the variability in densities among years. In contrast, the present study detected significant differences in densities among years with identical patch-reefs in similar areas. Thus, differences in densities were detected rather than just maximum carrying capacity. Probably the greatest advantage of estimating juvenile Red Snapper density from diver visual data from patch-reef was that visual data provided quantitative estimates (number of fish/m^3 of reef structure, as reported here); that is, all Red Snapper were counted on each patch-reef. With trawl samples, quantitative estimates are difficult as the number of fish that escape versus those that are caught cannot be estimated without camera recordings. There are also difficulties with patch-reef surveys that should be considered before applying such methods. Patch-reef surveys rely on visual censuses, which are affected by water clarity. Additionally, patch-reefs generally will not remain intact or in place in areas undergoing intense shrimp trawling or frequently hit by tropical storms. However, despite these difficulties, patch-reef surveys provide more robust quantitative estimates (i.e., more information) of the density of age-0 and age-1 Red Snapper than CPUE estimates from trawl surveys, and their application for assessing juvenile reef fish densities should be continued in future studies.

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Table 1-1. Environmental conditions associated with visual surveys for juvenile Red Snapper: Temperature = Temp, salinity = Sal and dissolved oxygen = DO measured within 1 m of the seafloor during each survey. If more than one measurement was recorded, the mean value is displayed.

	August			September			October			June		
Reef Set	Temp °C	Sal ‰	DO mg/L	Temp °C	Sal ‰	DO mg/L	Temp °C	Sal ‰	DO mg/L	Temp °C	Sal ‰	DO mg/L
Off-Aug2007	–	–	–	–	–	–	–	–	–	22.9	34.3	4.5
Off-Jul2008	–	–	–	–	–	–	–	–	–	–	–	–
Off-Jul2009	23.6	29.0	5.7	28.2	29.3	6.8	–	–	–	–	–	–
Off-Jul2010	23.7	32.2	2.4	26.4	33.1	3.8	–	–	–	–	–	–
Off-Aug2010	–	–	–	26.3	33.0	2.4	24.8	33.7	6.5	–	–	–
In-Aug2010	–	–	–	28.2	30.6	2.0	24.0	36.2	5.8	–	–	–
In-Jul2011	25.3	35.5	2.4	–	–	–	24.2	33.3	5.5	–	–	–
In-Jul2012	–	–	–	–	–	–	–	–	–	–	–	–
In-Jul2013	–	–	–	–	–	–	27.9	31.6	–	–	–	–
In-Jul2014	–	–	–	30.0	32.3	–	–	–	–	27.1	33.6	–
In-Jul2015	28.9	34.3	5.6	–	–	–	25.6	32.5	4.5	23.9	34.8	–

Table 1-2. Location and deployment date for patch-reef sets surveyed off Alabama, in the northern Gulf of Mexico. Reef sets located inshore (12–16 km) are prefixed with “In”, and reef sets located offshore (19–23 km) are prefixed with “Off”. Reef *N* = the number of reefs deployed in each reef set (Reef set name). Survey *N* = number of reefs surveyed for each month (not all reefs deployed were surveyed each month). Dates of surveys are listed within each month.

Reef	Reef		Surveys							
Set name	*N*	Deployed	August	*N*	September	*N*	October	*N*	June	*N*
Off-Aug2007	30	1–9Aug07	–	–	27Sep07	10	26Oct07	10	10–19Jun08	24
Off-Jul2008	10	24–28Jul08	6–15Aug08	10	–	–	–	–	–	–
Off-Jul2009	10	9–10Jul09	4–6Aug09	10	9–10Sep09	10	–	–	–	–
Off-Jul2010	10	14–15Jul10	2–3Aug10	10	9–20Sep10	10	–	–	–	–
Off-Aug2010	10	25Aug10	–	–	9Sep10	10	21Oct10	10	30Jun11	10
In-Aug2010	10	24Aug10	–	–	8Sep10	10	18Oct10	10	9Jun11	10
In-Jul2011	10	19–20Jul11	29–30Aug11	10	–	–	26Oct11	9	14Jun12	9
In-Jul2012	10	19Jul12	8Aug12	10	25Sep12	6	–	–	–	–
In-Jul2013	10	18Jul–1Aug13	27–29Aug13	10	–	–	30Sep–16Oct13	9	5–17Jun14	10
In-Jul2014	14	22–24Jul14	21–22Aug14	14	8–10Sep14	14	30Sep–2Oct14	14	2–4Jun15	14
In-Jul2015	15	28Jul15	21–28Aug15	15	–	–	30Sep–7Oct15	15	13–22Jun16	14

Table 1-3. Mean CPUE ± SE (catch/H) of age-0 and age-1 Red Snapper and the total number of trawl tows conducted by SEAMAP trawl surveys by year. Only years with corresponding visual estimates of juvenile Red Snapper on patch-reefs were compared.

Year	Season	Age	Mean CPUE	Trawl *N*
2007	Fall	0	12.1 ± 4.7	10
2010	Fall	0	1.0 ± 0.8	7
2011	Fall	0	1.1 ± 1.0	6
2013	Fall	0	13.7 ± 13.4	4
2014	Fall	0	7.8 ± 4.9	5
2015	Fall	0	4.8 ± 3.9	5
2008	Summer	1	0.1 ± 0.1	12
2011	Summer	1	0.3 ± 0.3	6
2012	Summer	1	1.9 ± 0.8	8
2014	Summer	1	2.7 ±2.3	5
2015	Summer	1	0 ± 0	5
2016	Summer	1	0.5 ± 0.5	4

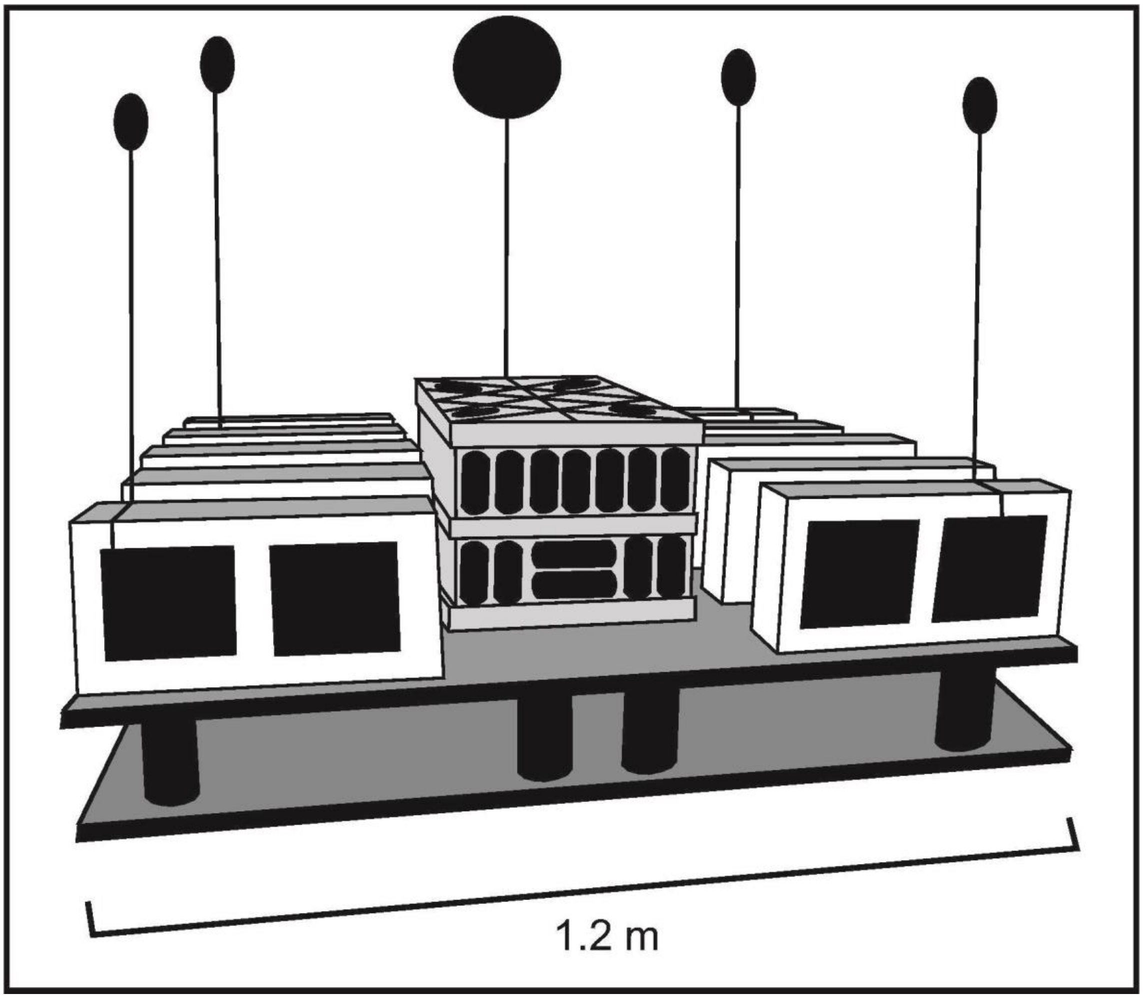

Figure 1-1. Small patch-reef deployed in the present study, off coastal Alabama, United States, in the northern Gulf of Mexico.

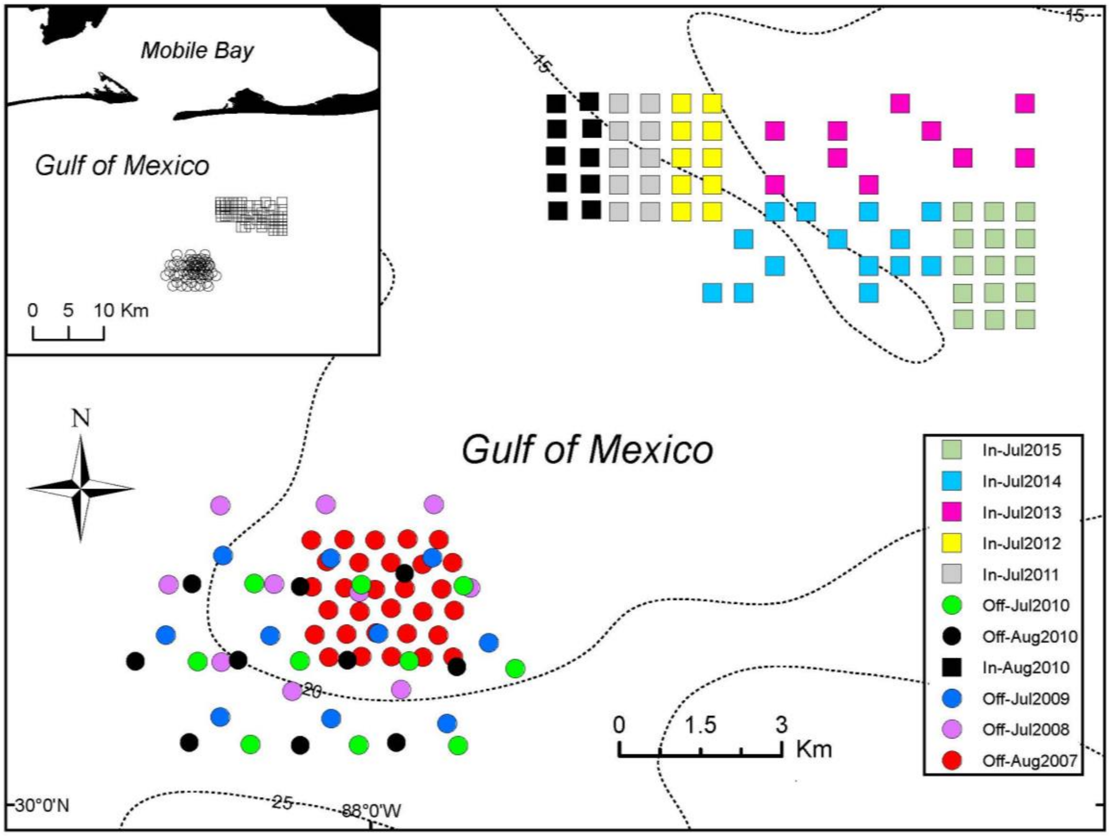

Figure 1-2. Locations of artificial patch-reefs deployed and visually surveyed on the Alabama continental shelf in the northern Gulf of Mexico from 2007 to 2015. Circles = offshore patch-reefs and squares = inshore patch-reefs. All symbols represent individual patch-reefs, and each reef set has the same color. Reef set captions indicate location and month-year of deployment, for example, Off-Aug2007 (red circles) were patch-reefs (N = 30) deployed at the offshore location in August 2007.

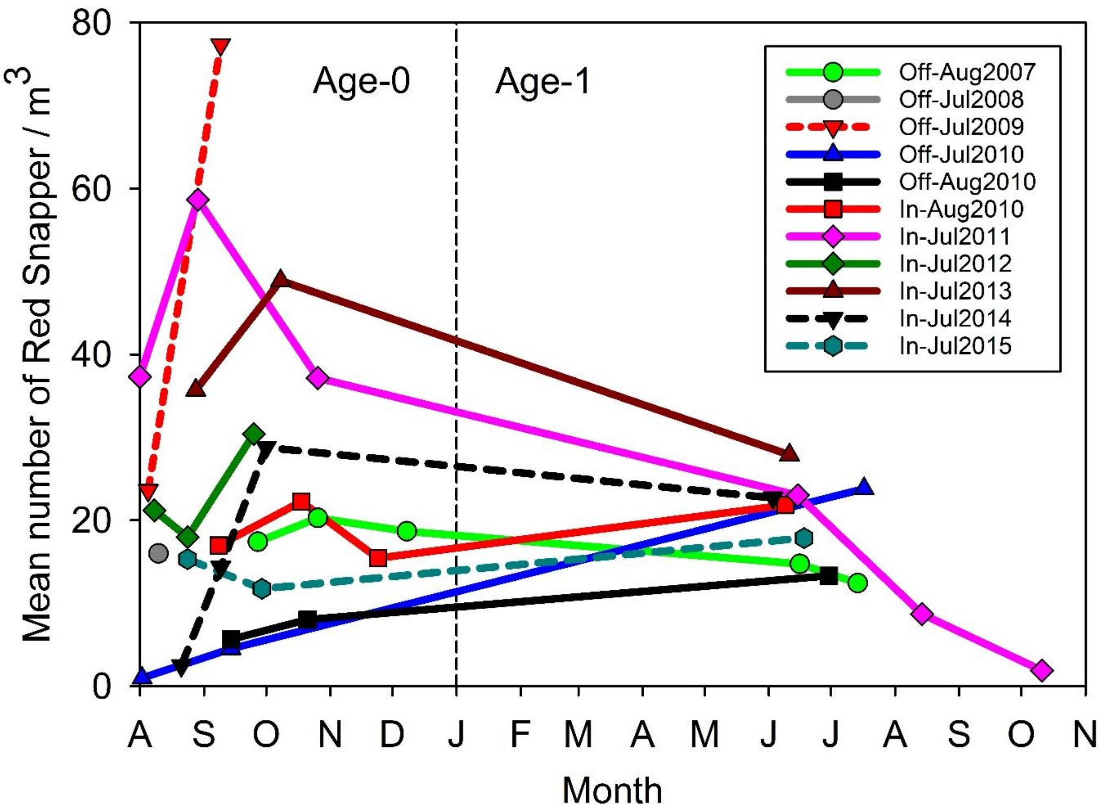

Figure 1-3. Mean density (number/m^3) of Red Snapper on patch-reefs deployed each year. Densities observed prior to 1 January represent age-0 Red Snapper, while densities observed after January 1 represent age-1 Red Snapper.

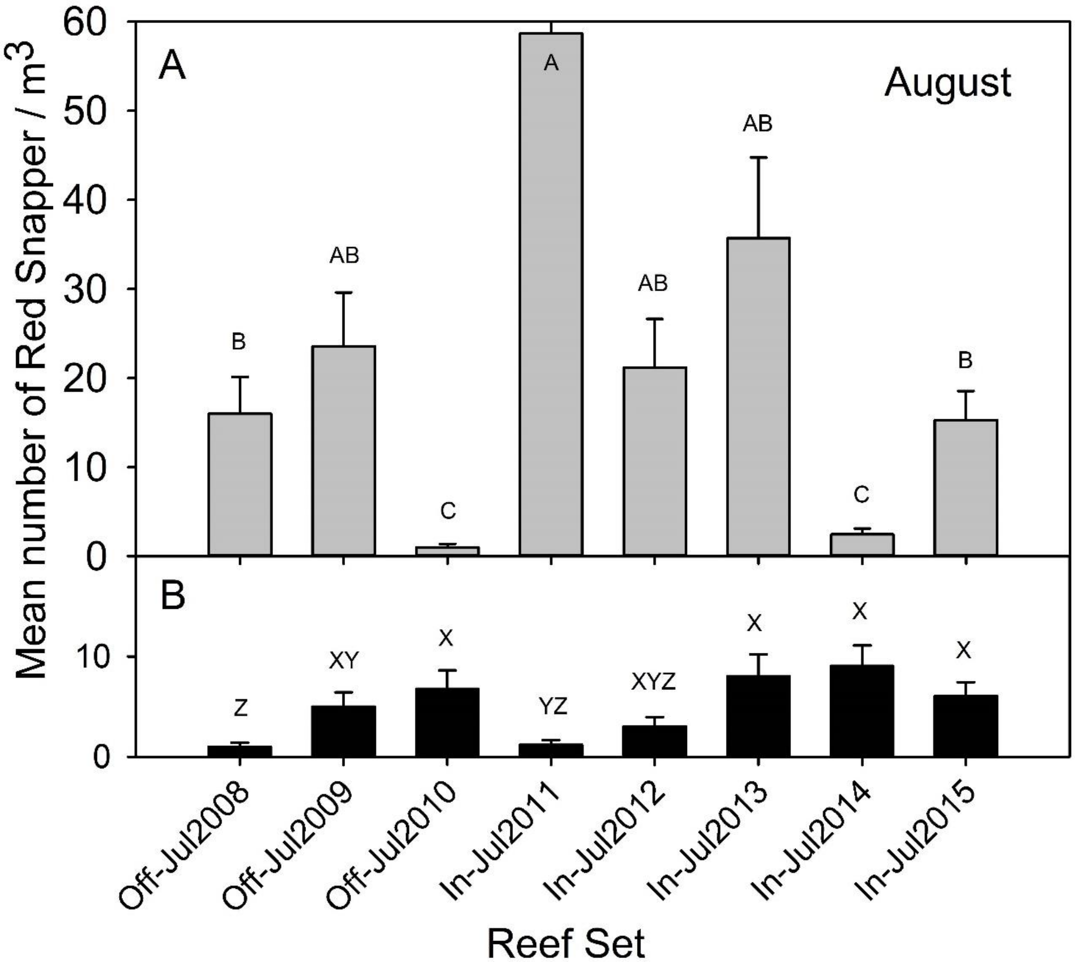

Figure 1-4. Mean densities (number/m^3) of (A) age-0 and (B) age-1 Red Snapper on patch-reefs observed via visual survey in August by year. Different letters indicate significant differences ($P \leq 0.05$), and age-0 and age-1 densities were analyzed separately. Error bars represent standard error (SE).

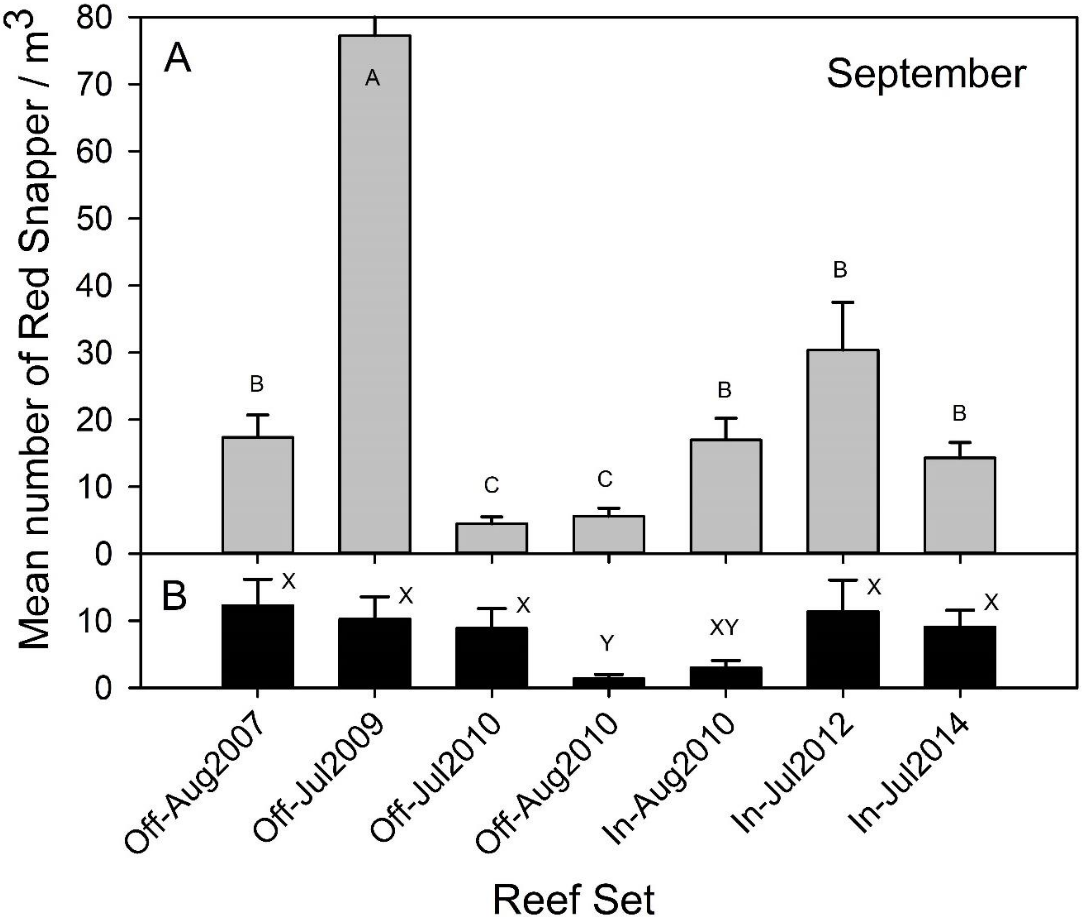

Figure 1-5. Mean densities (number/m^3) of (A) age-0 and (B) age-1 Red Snapper on patch-reefs in September by year. Different letters indicate significant differences ($P \leq 0.05$), and age-0 and age-1 densities were analyzed separately. Error bars represent SE.

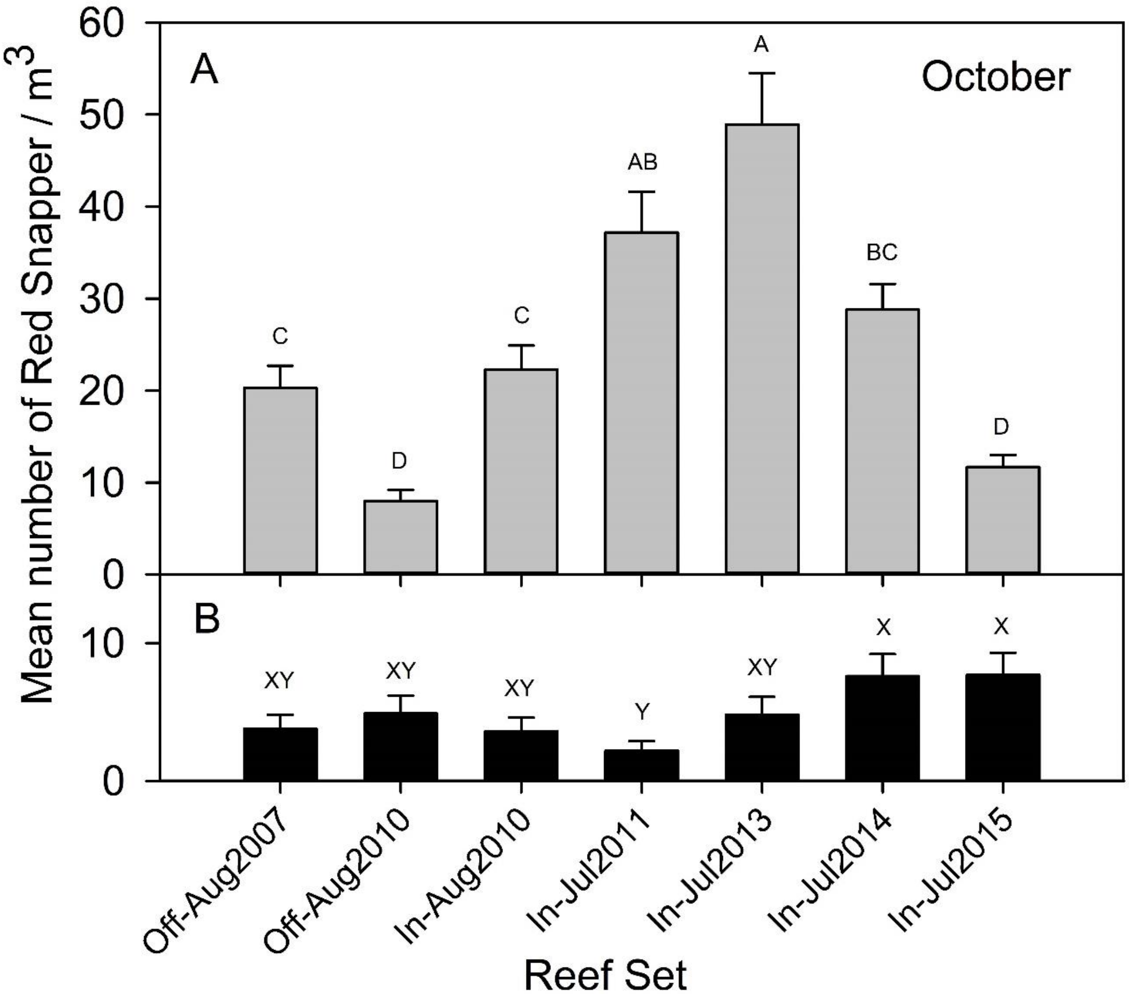

Figure 1-6. Mean densities (number/m^3) of (A) age-0 and (B) age-1 Red Snapper on patch-reefs observed in October by year. Different letters indicate significant differences ($P \leq 0.05$), and age-0 and age-1 densities were analyzed separately. Error bars represent SE.

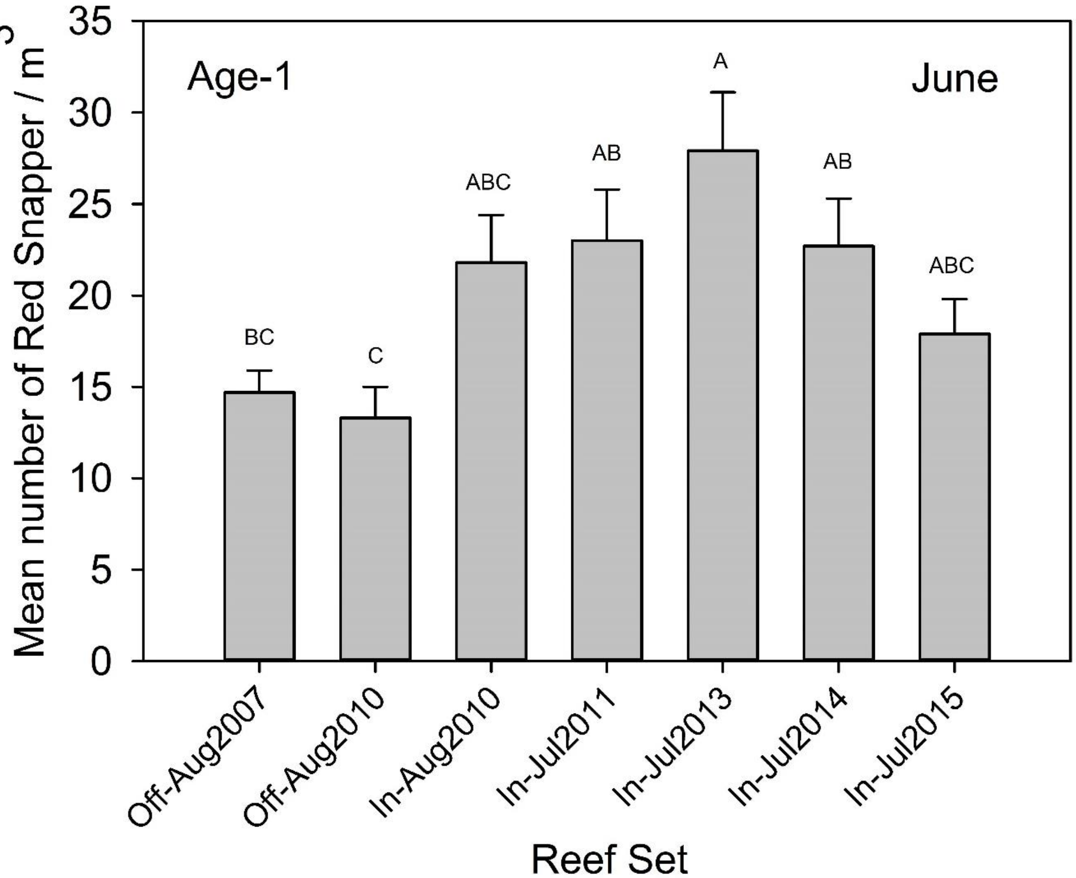

Figure 1-7. Mean densities (number/m^3) of age-1 Red Snapper on patch-reefs observed in June the year after the patch-reefs were deployed. Different letters indicate significant differences ($P \leq 0.05$). Error bars represent SE.

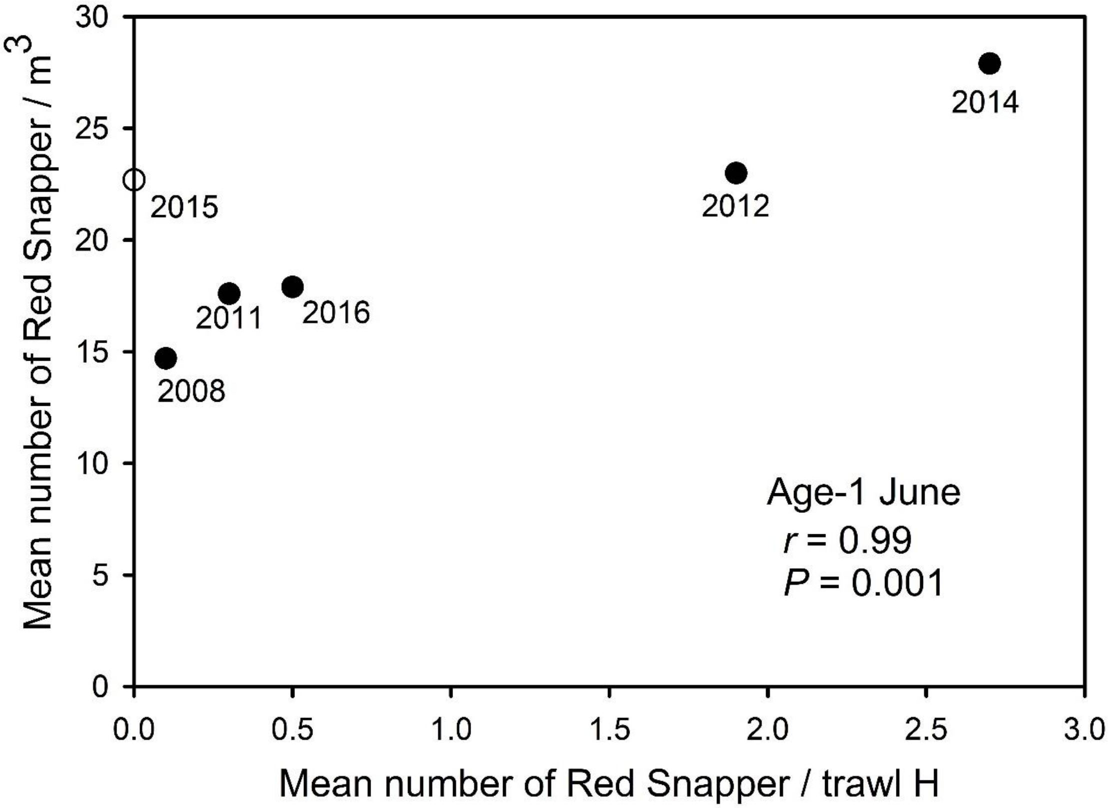

Figure 1-8. Comparison of mean density (number/m^3) of age-1 Red Snapper on patch-reefs in June to mean CPUE (catch/H) of Red Snapper obtained from SEAMAP summer trawl surveys on the Alabama continental shelf in the northern Gulf of Mexico each year. The *r* value was calculated after removal of the 2015 outlier.

Chapter 2:

Fishing mortality estimates for Red Snapper *Lutjanus campechanus*, based on acoustic telemetry and conventional mark-recapture.

Abstract

The management of Red Snapper *Lutjanus campechanus*, in the northern Gulf of Mexico has caused disagreement between fishers, who expect fewer restrictions as stock improves, and managers, who need to keep restrictions in place for continued stock improvement. Therefore, accurate estimates of mortality rates are critical for proper management of the species. The present study estimated tagging mortality, natural mortality, and fisher nonreporting from acoustic telemetry of Red Snapper to calibrate a conventional mark-recapture study on the Alabama continental shelf in the northern Gulf of Mexico. Fishing mortality (F) estimates were higher based on acoustic telemetry in 2015 (F = 1.17), 2016 (F = 0.46), and 2017 (F = 0.37) compared with conventionally tagged fish in 2015 (F = 0.45), 2016 (F = 0.37) and 2017 (F = 0.30). Recreational fishers on private vessels captured the highest number of conventionally tagged fish. Recreational fishers on for-hire vessels and commercial fishers captured similar numbers of conventionally tagged fish. Tag return rates were significantly higher for fish released on large reefs (> 25 m^2) than for fish released on small reefs (< 25 m^2), and higher on reefs with published locations than on reefs with unpublished locations. Capture rates were also higher on reefs closer to shore (< 33 km) than on reefs more distant from shore (33 to 65 km). The calibrated tag return rates for fish captured from large and small reefs were combined with a fishery-independent abundance estimate. This enabled an

adjustment to *F* values according to reef type and an estimate of annual harvest off coastal Alabama in the northern Gulf of Mexico. Mean *F* for Red Snapper greater than 406 mm standard length was $F = 0.22$ in 2015 and 2016, with an estimated annual harvest of 212,237 fish per year. In conclusion, high-quality telemetry data allowed the calculation of calibration rates for a high-reward, conventional-tagging study. Without these calibrations, the results of the conventional tagging study would have been inaccurate. Similarly, without the higher sample sizes provided by the conventional-tagging study, the results of the telemetry study alone may have been biased due to small sample sizes.

Introduction

The management of Red Snapper *Lutjanus campechanus*, in the northern Gulf of Mexico has been controversial. A rebuilding plan was implemented in 2007 that increased Red Snapper stocks (SEDAR 2013, 2018). As the Red Snapper stock improved, catch rates increased and larger fish were landed, but quotas were attained more quickly and resulted in shorter recreational seasons and lower bag limits. This increased stock, coupled with increasing restrictions, resulted in a derby-style recreational fishery; that is, where recreational fishers increased their effort to catch as many fish as possible in the shortest amount of time before the quota was attained and the fishery closed. This led to conflicts between fishers, who were experiencing more abundant Red Snapper and expecting reduced restrictions, and management, which was attempting to limit the harvest to specific quotas that were being attained in shorter time periods

(Simmons et al. 2020). Thus, there was a critical need for accurate estimates of Red Snapper abundance and fishing mortality rates.

Conventional tagging (i.e., mark-recapture) has long been used to estimate fishing mortality (Ricker 1975). However, some variables are difficult to determine in conventional tagging studies, such as tagging mortality, tag loss (e.g., shedding), fisher nonreporting, natural mortality, and emigration of tagged individuals outside the study area (Pollock et al. 2001; Miranda et al. 2002; Vandergoot et al. 2012). Telemetry can directly estimate fishing, natural and tagging mortalities, and emigration (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Topping and Szedlmayer 2013). Also, telemetry can determine fishing mortalities independently of tags returned by fishers. Consequently, telemetry offers a unique ability directly estimate fisher nonreporting.

While telemetry studies can determine mortality rates, they are more costly compared with other tagging methods. There are also limits to the number of transmitters that can be within range of a receiver before signal collisions prevent the detection of tagged fish (Topping and Szedlmayer 2011b). Therefore, telemetry studies have usually had low sample sizes. Thus, questions remain concerning the accuracy of mortality estimates from telemetry studies with small sample sizes. To increase sample sizes, conventional tagging can be used simultaneously with telemetry (Pollock et al. 2004; Bacheler et al. 2009; Kerns et al. 2016). The present study objective was to obtain estimates of tagging mortality, natural mortality, and fisher nonreporting (due to fishers not reporting their catch and tag loss) from transmitter-tagged Red Snapper. These estimates were then applied to fisher tag return rates obtained with conventional tagging of Red Snapper with a larger sample size to increase the accuracy of the mortality estimates.

Methods

Transmitter-tagged Red Snapper

In 2015, transmitter-tagged Red Snapper (*N* = 28) still present within receiver detection areas (Vemco positioning system [VPS], Vemco Ltd, Nova Scotia) from previous studies were incorporated into the present study (Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016a, b, 2017). Also, 46 additional Red Snapper were implanted with transmitters and released.

Each VPS site (*N* = 5) had a receiver (VR2W, Vemco, Nova Scotia) positioned 20 m north of the reef site and four additional receivers placed 300 m north, south, east and west of the reef site (Piraino and Szedlmayer 2014). Each VPS receiver also had a synchronization tag (sync tag, Vemco V16-6x transmission delay 540–720 s) placed 1 m above the receiver to allow for synchronization of the receiver clocks. In addition, a single VR2W receiver was deployed at each of 21 surrounding reefs (1.6 km apart; Williams-Grove and Szedlmayer 2016 a; Figure 2-1). All receivers were moored 4.5 m above the seafloor. A control transmitter was placed on a mooring buoy within each VPS site. The control transmitter estimated the accuracy of VPS-determined positions and determined times when the VPS site failed to detect transmitters due to environmental conditions, high background noise, or receiver malfunction. All VPS sites were located at 18 to 35 m depths. The VPS receivers were retrieved by SCUBA divers and the data were downloaded every 76 to 210 days. Data from the surrounding receivers were downloaded every 200 to 400 days.

Red Snapper were captured with hook-and-line, consisting of an 8/0 barbless circle hook (Eagle Claw, United States) baited with Gulf Menhaden, *Brevoortia patronus*, attached to a 1 m 45 kg leader and a 27 kg mainline. All tagged Red Snapper were larger than the minimum size limits in place during the 2015–2017 fishing seasons for commercial (330 mm total length [TL]) and recreational (406 mm TL) fishers. No internally hooked Red Snapper were tagged with transmitters.

After capture, Red Snapper were anesthetized in 150 mg tricaine methanesulfonate (MS-222)/L seawater for 90 seconds in a 70 L tank. Fish were weighed (to nearest 0.1 kg) and measured (mm standard length [SL], fork length [FL] and TL). Subsequently, a unique transmitter (Vemco V16-6x-R64k, transmission delay = 20–69 s) was surgically implanted into the peritoneal cavity through a vertical incision above the ventral midline. The incision site was sealed with absorbable, plain gut sutures (Ethicon 2-0, metric 3), and an intramuscular injection of 0.4 ml/kg of 250 mg/ml oxytetracycline solution was administered as a prophylactic antibiotic treatment and to serve as a marker on the otolith for other studies (Szedlmayer and Beyer 2011; Szedlmayer et al. 2020a). An externally visible tag (Floy FM-95W internal anchor tag) was inserted into the peritoneal cavity for recognition as a transmitter-tagged fish by fishers. The tag provided information regarding a reward for the tag and carcass. A local telephone number was also provided. After tagging was completed, Red Snapper were placed in a 185 L seawater tank for recovery. Tagged fish were released after they displayed active movements and recovery from the anesthesia (Topping and Szedlmayer

2011a, b, 2013; Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016a, b, 2017).

All tagged Red Snapper were released on the seafloor with a cage (Piraino and Szedlmayer 2014; Williams et al. 2015). This plastic-coated wire mesh cage (62 × 62 × 84 cm) protected fish from predators as the fish was lowered to the seafloor. After the cage reached the seafloor, a door automatically opened. Fish were provided an opportunity to exit the cage for at least 15 min on their own initiative before the cage was retrieved. A tagged Red Snapper that had not exited the cage after cage retrieval was not released. No fish were released if dissolved oxygen was < 2.5 ppm at the seafloor.

To calculate a fish position, the transmitter must be simultaneously detected by at least three receivers. The receivers were placed 300 m apart in the present VPS sites, which allowed high detection efficiency, as 100% of transmitter signals were detected at 400 m (Piraino and Szedlmayer 2014). Fish positions were calculated with Vemco post-processing (Vemco Ltd, Nova Scotia) based the time differential of the transmitter's signal arrival among receivers. To reduce signal collisions, the maximum number of transmitters within a VPS site at one time was limited to 10 (Topping and Szedlmayer 2011b). This included control and stationary transmitters, and transmitter-tagged Gray Triggerfish, *Balistes capriscus*, within the VPS sites in addition to tagged Red Snapper (Herbig and Szedlmayer 2016; McKinzie et al. 2016).

Calculated fish positions and transmitter detection patterns were used to determine the fate of transmitter-tagged Red Snapper (Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016b). If a Red Snapper was caught by a fisher, the tracking patterns had continuous detections of the fish around the reef with an abrupt disappearance near the reef and a lack of detections on surrounding receivers. A US$150 reward was paid for the return of a tagged Red Snapper by a fisher. Fisher returns were used to validate telemetry-identified fishing mortalities. If a Red Snapper emigrated from a VPS site, the tracking data indicated continuous detections around the reef, followed by a series of positions sequentially moving away from the reef, with the final detections of the transmitter recorded on either the north, east, south or west receiver. Emigration patterns could also be subsequently confirmed by detections on surrounding receivers. If a transmitter-tagged fish became stationary within the first six days after tagging, it was considered a tagging mortality, and if the fish became stationary after six days, it was considered a natural mortality. False detections were removed from the data following previously developed detection criteria (Pincock 2012; Williams-Grove and Szedlmayer 2016a, b).

Mortality rates for any Red Snapper still alive within the VPS sites after a six-day tagging recovery period were estimated with a known fate model applied with the MARK program (Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016b). Annual estimates were based on weekly time intervals for each year. The MARK program calculated survival estimates based on the maximum likelihood binomial (MLE; Edwards 1992), expressed as:

$$\mathcal{L}(\theta|n_i, y_i) = \prod_{i=1}^{t} S_i^{yi}(1 - S_i)^{(n_i - y_i)}$$

This equation describes the survival model for the weekly time interval (θ), the number of individuals active during each interval (n_i), the number surviving each interval (y_i), and the MLE of survival during each interval (S_i). In this model, survival was estimated from conditional probabilities of surviving specified events (i.e., fishing or natural mortality). For example, the probability of surviving a mortality event (i) was determined by calculating the number of individuals at risk of dying (n_i) and the number of individuals that survived (y_i) for that time interval (t). Fish that emigrated, or suffered a mortality not under consideration, were removed (i.e., the data were "right censored"). For example, when fishing mortality (F) was estimated, all emigrations and natural (M) mortalities were removed.

On July 9, 2015, the VPS site at R3 was removed because of excessive harvest of tagged fish by fishers. On August 10, 2015, a new VPS site was established at R6. On April 25, 2017 the VPS site at R2 was relocated to R3, because several stationary transmitters at R2 limited the number of fish that could be tracked. Receivers were temporarily removed from R3, R4 and R5 on September 5, 2017 in preparation for the possible arrival of Hurricane Irma. The receivers were replaced at R5 on September 15, 2017, and at R3 and R4 on September 19, 2017 (Figure 2-1).

Conventionally tagged Red Snapper

Conventionally tagged Red Snapper were captured and treated in nearly the same way as the transmitter-tagged fish, but without a transmitter implant. However, the retention time for conventionally tagged Red Snapper was less than the retention time for transmitter-tagged fish because of the reduced handling time. All captured Red Snapper greater than 406 mm TL were tagged. Conventionally tagged Red Snapper were released with the same cage-release procedure as the transmitter-tagged fish. However, up to three conventionally tagged fish were released from the same cage. Also, in contrast to transmitter-tagged fish, which were not released if they did not exit the cage within 15 min, conventionally tagged fish were released at the surface if they did not exit the cage. If a Red Snapper was internally hooked during capture, the line was cut close to the fish's mouth, and the fish was marked with a conventional tag and released. Any internally hooked Red Snapper that did not exit the cage (N = 9) within 15 min were removed from further analyses.

Fishers were provided with a US$150 reward for the return of a conventionally tagged Red Snapper. Posters advertising the reward were displayed at local bait shops, boat ramps, and marinas. Ten Red Snapper were conventionally tagged and released at each reef. To reduce the likelihood of fishers targeting reefs with high-reward tagged Red Snapper, reefs at which conventional tagging occurred were not repeated among years. All conventional tagging reefs were at depths of 18 to 41 m (Figure 2-2). If a reef did not appear to have a Red Snapper density large enough to tag 10 individuals, a new reef was selected. If Red Snapper were abundant at a reef, up to three additional fish were tagged to replace individuals that had been internally hooked or surface released. During each year, all Red Snapper were tagged between January 1 and May 25, allowing at least six days to recover before the June 1 opening date of the federal recreational Red Snapper season.

Immigration and emigration were important variables used to add and remove transmitter-tagged fish available for capture and estimate mortalities at VPS sites, but migration did not affect mortality estimations for conventionally tagged fish. If a conventionally tagged Red Snapper emigrated from its tagging reef, it was still available for capture. In support of this assumption, all fisher-reported capture locations were within the Alabama continental shelf study area. Likewise, immigration was assumed to be equal to emigration of Red Snapper on the Alabama continental shelf and did not affect conventional tagging mortality estimates.

Tagging mortality rates were determined for transmitter-tagged Red Snapper and applied to the conventionally tagged fish. These tagging mortality rates were determined from transmitter-tagged fish that became stationary within six days of release. Any transmitter-tagged fish that emigrated from the VPS sites in less than six days after release were removed from mortality estimates.

The telemetry method used in the present study detected a fish when it was caught by a fisher but not reported. Some recaptured fish were not reported due to intentional fisher behavior, while some unreported fish were due to external tag loss; therefore, the nonreporting rate that was estimated for transmitter-tagged fish also included tag loss. Any transmitter-tagged fish returned by fishers without the external tag were used to estimate tag loss and nonreporting for conventionally tagged fish. For example, some returns were due to fishers finding the transmitter in fish that had lost the external portion of the tag and would not have been reported in the conventional-tagging study. Thus, the final nonreporting rate was based on Red Snapper that were returned without an external tag and fish that were identified as caught by the VPS telemetry and unreported. The probability of nonreporting increased with time at liberty, as some of the nonreporting was attributable to tag loss. Therefore, all harvested transmitter-tagged Red Snapper were binned by days at liberty, and the percentage reported was used to adjust conventional tag returns based on time at liberty.

Fishing mortality for tagged Red Snapper was calculated for each year of the study. In the known fate model used for transmitter-tagged Red Snapper, mortalities were estimated based on the number of fish available during weekly intervals over the year. In contrast, for conventionally tagged fish, only mark-and-recaptures were known, and the timing of tagged fish losses due to fisher nonreporting and natural mortality were unknown. Therefore, F for conventional tagged fish was calculated on an annual basis: $F = -\ln(S)$, where S is the probability of surviving fishing mortality over the year. The number of fish available for capture was the number of fish tagged minus the tagging mortality rate observed in the transmitter-tagged fish. The number of Red Snapper caught each year was the number reported by fishers adjusted by the nonreporting rate from transmitter-tagged fish with the same amount of time at liberty. If a tagged fish was reported as caught and released with the tag in place, it remained in the analysis. If a tagged fish was reported as released with the tag removed, it was removed from the number of tagged fish available. The number of fish remaining after subtracting captured individuals, was reduced by the annual natural mortality rate, and carried over as available for capture in the next year's estimate. Fishing mortality for conventionally tagged fish was calculated with new fish tagged each year included in the number available for capture (i.e., a single F for all fish released over the course of the study) and with fish released each year treated in separate annual analyses (i.e., for fish released in 2015, 2016, and 2017).

Differences in tag return rates among reef types were examined for the first calendar year when a conventionally tagged fish was at liberty with a chi-square test. Three reef type comparisons were examined: 1) availability to public (i.e., published versus unpublished locations), 2) reef size (small [<25 m^2] or large [>25 m^2]), and 3) proximity to shore (near, 13 – 33 km; far, 33 – 65 km). A reef with a published location was defined as any reef with coordinates available from the Alabama Department of Conservation and Natural Resources (ADCNR 2016a) or oil-gas platforms that were visible above the water.

Red Snapper harvest estimate within the study area

The present study distributed tagged Red Snapper nearly equally among different reef types (i.e., equal numbers of fish tagged on large versus small reefs). However, Red Snapper were not evenly distributed among these reef types. To estimate *F* for Red Snapper in the present study area, the capture rates for conventionally tagged fish released on large (> 25 m^2) and small (< 25 m^2) reefs were combined with a stock size estimate for Red Snapper by reef type (Szedlmayer et al. 2020b). This stock size estimate included fish greater than 406 mm TL, at depths of 18 to 55 m, and was also used to calculate the total number of Red Snapper harvested from the study area each year (Szedlmayer et al. 2020b). To calculate *F* based on reef size, conventionally tagged fish were only considered available for recapture in the year they were released. This increased the probability that Red Snapper were still resident on their tagging reef. The tagging mortality and fisher nonreporting rates observed for transmitter-tagged fish were applied to the number of fish available and recaptured from each reef type. To increase sample size, fish tagged in 2015 and 2016 were pooled to estimate a single *F* for each reef type. Conventionally tagged fish released in 2017 were not included in this estimate of *F* due to small sample size and changes in fishing regulations for the private vessel sector of the recreational fishery. To estimate *F* for the Red Snapper stock over the present study area, the different *F* values for large and small reefs were applied to the different density estimates by reef type: that is, 6% of the Red Snapper reside on large reefs and 94% on small reefs (Szedlmayer et al. 2020b). The resulting *F* was applied to the estimated stock size of 1,074,720 Red Snapper greater than 406 mm off coastal Alabama to obtain a mean annual harvest of Red Snapper in 2015 and 2016. The harvest estimate was then partitioned into sectors of the fishery by the percentage of conventional tags returned by each fishing sector over the duration of this study.

Results

Transmitter-tagged Red Snapper

On January 1, 2015, there were 26 active transmitter-tagged Red Snapper on the VPS sites. In 2015, two previously transmitter-tagged Red Snapper entered the study when the VPS site was installed on R6, and 24 new Red Snapper were tagged with transmitters. Five of the newly-tagged Red Snapper emigrated from the VPS sites within the six-day tagging recovery period for a total 47 transmitter-tagged fish in 2015. Among these transmitter-tagged fish, 14 were returned by fishers, six were caught by fishers and not reported, three emigrated, three active fish were removed when the VPS site at R3 was removed, and 21 fish remained active at the end of the year. In 2016, an additional

15 Red Snapper were tagged with transmitters, of which one emigrated within the six-day tagging recovery period and one suffered a tagging mortality for a total of 34 transmitter-tagged fish in 2016. Among these transmitter-tagged fish, 10 were caught and returned by fishers, one was caught and not reported, 13 emigrated and 10 remained active at the end of the year.

In 2017, seven new Red Snapper were tagged with transmitters, of which one suffered a tagging mortality and two emigrated within the six-day tagging recovery period. One transmitter-tagged Red Snapper, tagged at a reef site that was not a VPS site, immigrated onto a VPS site. An additional three transmitter-tagged Red Snapper re-entered the study when the R2 VPS site was moved to R3, and three fish that had emigrated in 2016 returned to the VPS sites in 2017, for a total of 21 transmitter-tagged Red Snapper on VPS sites in 2017. Among these Red Snapper, three were caught and reported by fishers, one was caught and not reported, one was removed when the VPS site was removed from R2, nine emigrated, and seven remained active at the end of the study. No natural mortalities were detected during the three years of the present study; that is, no transmitters became stationary at the VPS sites after the six-day recovery period. At the time of writing, 15 of the 22 Red Snapper defined as emigrating from the VPS sites were later returned by fishers, confirming that these individuals were alive when they emigrated from the VPS site, as opposed to having been consumed by a predator.

The F estimates for transmitter-tagged Red Snapper were: F = 1.17 in 2015, F = 0.46 in 2016, and F = 0.37 in 2017 (Figure 2-3). Among the 46 transmitter-tagged Red Snapper released from 2015 to 2017, a 5.3% tagging mortality rate was observed within six days of tagging, with two mortalities and eight emigrants (fate unknown) and 36 transmitter-tagged fish surviving and remaining on VPS sites longer than six days. Among the 65 transmitter-tagged Red Snapper tracked (i.e., included fish released prior to 2015), no natural mortalities were observed on the VPS sites (instantaneous natural mortality [M] = 0). As M in a population cannot be zero, a natural mortality rate of M = 0.1 was used for conventionally tagged fish. This value was chosen based on the natural mortality rates of M = 0.04 observed by Williams-Grove and Szedlmayer (2016b), M = 0.1 reported by Topping and Szedlmayer (2013) and M = 0.1 used in Red Snapper stock assessments (SEDAR 2013, 2018).

Fisher nonreporting

Conventionally tagged Red Snapper were at liberty for 0 to 346 days in the first year, 221 to 712 days in their second year and 593 to 1,077 days in their third year. In the present study, 35 transmitter-tagged Red Snapper were caught, while present on a VPS site. Of these, four Red Snapper were at liberty longer than the conventionally tagged fish (1,169 to 1,496 days) and were not used for fisher nonreporting estimates. Among the remaining 31 captured Red Snapper; 21 were reported with their external tag intact, three were reported without an external tag (reported due to implanted transmitter), and seven were unreported. Thus, these recaptured, transmitter-tagged fish indicated that the nonreporting rates were 16.7% during the fish's first season at liberty (three not reported out of 18 fish caught at liberty for less than 346 days), 33.3% in the fish's second season at liberty (five not reported out of 15 caught at liberty for 221 to 712 days), and 42.9% in the fish's third season at liberty (three not reported out of seven caught at liberty for 593 to 1,077 days). Therefore, the number of conventionally tagged fish reported by fishers each year was increased in fishing mortality estimates to account for nonreporting and tag loss. The number of conventionally tagged fish reported the same year they were released was multiplied by 1.2, the number of fish reported that were released the previous year was multiplied by 1.5, and the number of fish reported that were released two years previous was multiplied by 1.75 to obtain the total number of conventionally tagged Red Snapper harvested each year.

Conventionally tagged Red Snapper

A total of 774 conventionally tagged Red Snapper were released on 83 reefs (Table 2-1; Figure 2-2). There were 280 conventionally tagged fish harvested and reported by fishers (Table 2-2), three were reported caught and released with the tag in place (one of these fish was subsequently caught again by the same fisher who had released it), and three were reported released with the tag removed. Recreational fishers on private vessels returned the highest number of conventionally tagged fish, while commercial and recreational fishers on for-hire vessels caught fewer conventionally tagged fish at similar levels (Table 2-2).

Fishing mortality estimates determined for the conventionally tagged Red Snapper were lower when surface-released and internally hooked fish were included in the calculation (Table 2-3). This indicated that surface-released and internally hooked fish experienced higher mortalities due to tagging. Therefore, surface-released and internally hooked Red Snapper were not included in further analyses. The fishing mortality observed among conventionally tagged fish was highest in 2015, intermediate in 2016 and lowest in 2017 (Table 2-3). When the conventionally tagged fish released each year were analyzed separately, fish tagged in 2015 had higher F values compared with fish released in 2016 and 2017, and fish released in 2017 had the lowest F values (Table 2-3). The probability that a conventionally tagged Red Snapper would be returned in the same calendar year it was released was significantly higher for fish tagged at large reefs compared with small reefs ($\chi^2 = 38.93$, df = 1, $P < 0.001$; Table 2-4), higher on reefs with published locations than on reefs with unpublished locations ($\chi^2 = 19.32$, df = 1, $P < 0.001$; Table 2-4), and higher on reefs that were closer to shore compared with reefs that were further from shore ($\chi^2 = 7.85$, df = 1, $P = 0.005$; Table 2-4).

Fishing mortality and harvest estimates

In 2015 and 2016, 115 out of 328 fish released at the seafloor (excluding surface-released and internally hooked fish) on large reefs were returned by fishers in the same year as they were released, and 46 out of 317 fish released at the seafloor on small reefs were returned in the same year as they were released. After application of the telemetry-based estimates of tagging mortality and fisher nonreporting rates, the fishing mortality estimates were $F = 0.59$ for large reefs and $F = 0.20$ for small reefs. When applied to the Red Snapper distribution estimate that 6% reside on large reefs and 94% reside on small reefs (Szedlmayer et al. 2020b), the total $F = 0.22$ in the present study area. The absolute density estimate was 1,074,720 Red Snapper greater than 406 mm in the present study area (5,973 km^2; Szedlmayer et al. 2020b), which indicated a mean annual harvest of 212,237 Red Snapper greater than 406 mm for 2015 and 2016. In the present study, commercial fishers returned 18.6 % and recreational fishers returned 81.4 % of all recaptured conventionally tagged Red Snapper. Thus, commercial fishers harvested 39,476 Red Snapper, and recreational fishers harvested 172,761 Red Snapper each year in the present study area.

Discussion

Recreational fishers on privately owned vessels accounted for 64% (179/280) of the conventionally tagged Red Snapper returned despite being assigned only 28% of the total Red Snapper quota in the Gulf of Mexico and the shortest federal fishing seasons (NOAA 2015). However, in the present study, we may have underestimated *F* for the commercial Red Snapper fishery, because all tagging took place in the spring, before the federal recreational seasons began in June. In contrast, commercial fishers were subject to an individual transferable quota (ITQ) with a year-round fishing season, and most (63%, 33/52) of the conventionally tagged fish returned by commercial fishers were caught in the spring before the start of the recreational fishing season. Thus, commercial fishing was occurring when not all the conventionally tagged fish were available for capture. However, transmitter-tagged Red Snapper were available for capture all year, and only one recapture of a transmitter-tagged Red Snapper was reported by a commercial fisher. Also, most (75%, 6/8) of the transmitter-tagged fish that were caught and not reported were caught while the federal recreational fishing seasons were open. Thus, it was unlikely that commercial fishers harvested substantially greater numbers of Red Snapper within the study area compared with the observed rate of 18.6%. This difference between recreational and commercial tag returns indicated that while the Gulf of Mexico Red Snapper quota was divided relatively evenly between commercial (51%) and recreational (49%) fishers, off coastal Alabama in the northern Gulf of Mexico, Red Snapper were primarily harvested by recreational fishers.

The fishing mortality rates observed in both the conventionally tagged and transmitter-tagged Red Snapper declined in each year of the study. In transmitter-tagged fish, one possible cause for the reduction in F from 2015 to 2016 was the relocation of the VPS site at R3 to another site, because R3 was subjected to heavy fishing mortality. The reduction in fishing mortality observed in the conventionally tagged Red Snapper was possibly caused by a violation of the assumption that the tagged individuals intermix evenly with the population (Ricker 1975). This was apparently not the case for Red Snapper. The present study and several other telemetry-tagging studies (Topping and Szedlmayer 2011b; Williams-Grove and Szedlmayer 2016a), have observed high residency for Red Snapper on reefs, with some individuals still present at the original tagging reef up to 1,096 days after release (Williams-Grove and Szedlmayer 2016a). Thus, an important variable affecting the probability that a Red Snapper will be recaptured is the particular reef site where released. If the reef is heavily fished, the tagged fish on that reef will undergo heavy fishing mortality. If a selected reef is subjected to low fishing effort, fishing mortality for those fish will be low. The present study indicated that Red Snapper were more likely to be caught on reefs that were large, had published locations, and were closer to shore. In relation to the decrease in F from 2015 to 2016, in 2016 a higher proportion of the conventionally tagged Red Snapper were released on reefs that were small (61%), unpublished (67%) and further offshore (66%; i.e., reefs that received lower fishing pressure), compared with 2015 tagging reefs

(38% small, 58% unpublished, 44% offshore). This result was similar to the observation that fish tagged in 2015, but still available for recapture in 2016, had the same high *F* as in 2015, while fish tagged in 2016 had lower *F* in 2016. This supports the contention that the reefs selected for tagging in 2015 simply received higher fishing effort than reefs selected in 2016.

In 2017 sample sizes for both the conventionally tagged and transmitter-tagged fish were reduced, with only 25 conventionally tagged fish and 21 transmitter-tagged fish released. The federal private vessel recreational season, which accounted for most of the tag returns, was 10 days in 2015 and 11 days in 2016 (NOAA 2015, 2016). The 2017, federal private vessel recreational season was three days (NOAA 2017a), but the season was reopened for an additional 39 days later in the year (NOAA 2017b). This longer season may have alleviated some of the effects of the derby-style fishery and actually reduced harvest, or the confusion caused by reopening the season may have reduced fishing effort. Some fishers may have been unaware of the additional fishing opportunities or unable to fish because they had not planned their trips in advance. However, the present study's low sample size in 2017 makes it difficult to determine whether the lower *F* values observed in 2017 were due to reduced fishing effort or whether there were not enough tagged fish available for fishers to catch.

Red Snapper may spend multiple years on the same reef where they were tagged and released (Topping and Szedlmayer 2011b; Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016a). This lack of movement or lack of mixing represents a challenge, as tagged individuals will be slow to disperse. It means that the number, location, and type of reefs where Red Snapper were tagged, and not just the number of tagged fish, are important variables in a Red Snapper tagging study. The present study tagged Red Snapper with relatively equal numbers of fish on each reef type, as opposed to tagging Red Snapper on different reef types in the proportions observed in the study area. However, the present tagging results were combined with reef type density estimates (Szedlmayer et al. 2020b) to calculate *F* for the Red Snapper stock in the study area. The result was an estimate of $F = 0.22$ that was lower than observed *F* estimates from either the telemetry study or the conventional tagging.

The differences in tag return rate by reef type observed in the present study are of interest to organizations and natural resource managers who deploy artificial reefs. Red Snapper were more likely to be harvested on reefs that were large, had published locations, or were closer to shore. If the goal of an artificial reef program is to increase fishing or harvest opportunities for fishers, it would be more beneficial to build large reefs, which seem to be popular among fishers. If the goal of an artificial reef project is to increase biomass, or to provide refuge from harvest, it would be more effective to build small reefs, place them further from shore, and not publish their locations.

The telemetry methods used in the present study were able to directly determine tagging mortality. This was a major advantage over conventional tagging techniques, in which the survival of a tagged fish can only be confirmed by its recapture. However, the greatest difficulty with telemetry were high costs and relatively low sample sizes. Another possible difficulty was increased stress caused by implanting a transmitter compared with less invasive conventional tagging. If the tagging mortality rate for conventionally tagged fish was substantially lower than for transmitter-tagged fish, fishing mortality would be overestimated. However, the tagging mortality rate observed in transmitter-tagged fish was low (5.3%) as a result of the cage-release method (Piraino and Szedlmayer 2014), and all conventionally tagged fish were also cage released, indicating that tagging mortality effects had little effect on F estimates. It is notable that without cage release methods, tagging mortality rates can be very high (39%) as previously reported by Piraino and Szedlmayer (2014).

No natural mortalities were detected in transmitter-tagged Red Snapper for the duration of the present study. One explanation was that fishing mortality was high in the transmitter-tagged fish, and the fish were caught before they had a chance to die of natural causes. Another possibility was that a sample size of 65 transmitter-tagged fish was too small for natural mortalities to be detected. A third possibility was that natural mortalities were being misidentified as emigrations when the transmitter of a deceased fish exits the VPS site in the stomach of a predator or in a drifting carcass. However, predators such Sandbar Shark *Carcharhinus plumbeus*, Bull Shark *C. leucas*, and Nurse Shark *Ginglymostoma cirratum*, have been tagged and released with transmitters in the same study area and have very different tracking patterns compared with Red Snapper (Altobelli and Szedlmayer in press). Also, over the three years of the present study, 22 fish were classified as emigrations from the VPS data. Among these fish that emigrated, 15 were later caught and returned by fishers and confirmed that these fish were alive when they left the VPS site. This left seven transmitter-tagged Red Snapper that emigrated with unknown fates, and even if all of these individuals were natural mortalities and not emigrations, the conclusion of low natural mortality (M = 0.1) was still valid.

A high reward (US$150) was paid for the return of all tagged fish in the present study. This contributed to the high reporting rates observed for both transmitter-tagged and conventionally tagged Red Snapper. The telemetry techniques used in the present study proved effective at directly measuring fisher nonreporting. However, the study design did not allow separation of intentional nonreporting behavior of fishers and non-reporting caused by tag loss. Although the reporting rate was high, 83% in the first year at liberty, it should be noted that it was not 100%. It was unlikely that all nonreporting observed in the present study were due to tag loss, and studies that assumes 100% reporting because of a high reward will underestimate exploitation rates (Pollock et al. 2001; Sackett and Catalano 2017).

The Alabama Department of Conservation and Natural Resources implemented regulations that required recreational fishers to report all Red Snapper harvested and landed in Alabama starting in 2014. The resulting estimates of recreational Red Snapper harvest in Alabama were 129,810 Red Snapper in 2015 (ADCNR 2015) and 178,894 Red Snapper in 2016 (ADCNR 2016b). The present study estimated a very similar mean annual recreational harvest of 172,761 Red Snapper, only 3 % (6,133 fish) different from the 2016 ADCNR estimate. The fact that these two independent estimates of harvest were essentially the same indicated that an accurate estimate of Red Snapper harvest by recreational fishers in Alabama was achieved.

In conclusion, the present study used high-quality telemetry data to calculate calibration rates for a high-reward, conventional tagging study. Without these calibrations, the results of the conventional tagging study would have been less certain. Similarly, without the higher sample sizes provided by the conventional tagging study, the results of the telemetry study alone may have been biased due to small sample sizes. However, both the conventional tagging and telemetry methods may have overestimated exploitation rates, because tagged Red Snapper were not distributed among different reef types in proportion to their abundance in the population. To address this difficulty, an accurate estimate of Red Snapper distribution within the present study area was applied from a fishery-independent survey (Szedlmayer et al. 2020b) to calibrate the results of this tagging study. Similarly, the Red Snapper distributions could be applied to select reef types prior to starting a new Red Snapper tagging study.

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Table 2-1. The number of reefs (*N*) and the number of Red Snapper released by different methods for each year. Internal = number of fish tagged that were internally hooked, but left the release cage. Surface = number of fish that failed to leave the release cage and were released at the sea surface. Bottom = number of fish that left the release cage on the seafloor. Internally hooked fish that failed to leave the release cage were not included in the analysis and are not shown.

Year	*N*	Internal	Surface	Bottom	Total
2015	38	3	29	328	360
2016	42	12	51	317	380
2017	3	1	8	25	34
Total	83	16	88	670	774

Table 2-2. The number of conventionally tagged Red Snapper harvested and reported by fishers in each fishing sector each year.

	Year			
Fishing Sector	2015	2016	2017	Total
Commercial	17	13	22	52
Charter for Hire	15	25	9	49
Private Recreational	70	81	28	179
Total	102	119	59	280

Table 2-3. Instantaneous fishing mortality (*F*) for conventionally tagged Red Snapper by year. Fishing mortalities were estimated for fish that were not internally hooked or surface released (Bottom Release), all fish released (All Fish), only fish that were internally hooked or surface released (Problem Release) and bottom released fish tagged each year (2015, 2016, 2017). All *F* rates were calculated with an instantaneous natural mortality rate (*M*) = 0.1.

	F by Year Caught		
Released	2015	2016	2017
Bottom Release	0.45	0.37	0.30
All Fish	0.45	0.33	0.26
Problem Release	0.41	0.15	0.10
2015	0.45	0.45	0.32
2016	–	0.32	0.31
2017	–	–	0.16

Table 2-4. Number of conventionally tagged Red Snapper that were harvested and reported in the same year they were released by reef size (large > 25 m^2 ; small < 25 m^2), availability (reefs with published versus unpublished locations), and distance from shore (inshore reefs were less than 33 km from land; offshore reefs were 33 to 65 km from land).

Reef Type	Tagged	Returned	%
Large	328	115	35
Small	342	49	14
Published	243	83	34
Unpublished	427	81	19
Inshore	349	101	29
Offshore	321	63	20
Total	670	164	24

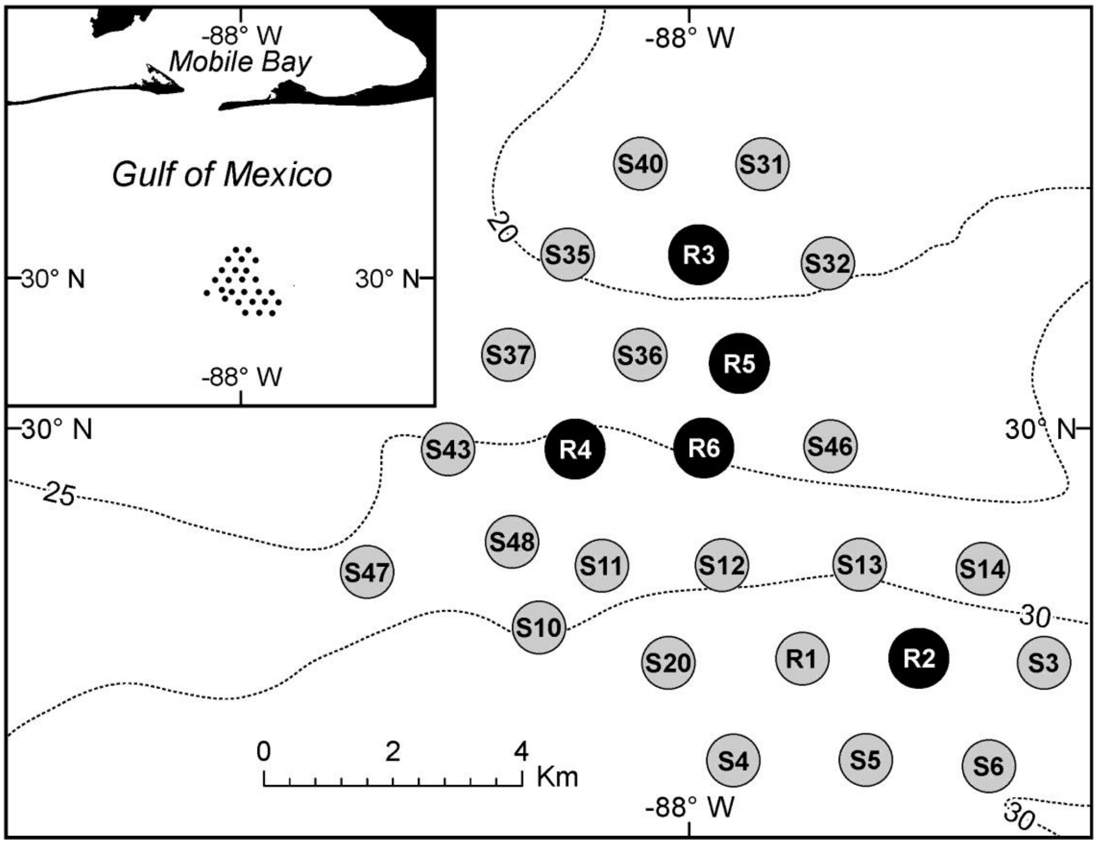

Figure 2-1. Location of the telemetry receiver array, 23 to 35 km south of Dauphin Island Alabama, United States, in the northern Gulf of Mexico. Sites with single receivers are shown with gray circles, and VPS sites consisting of five receivers are shown with black circles.

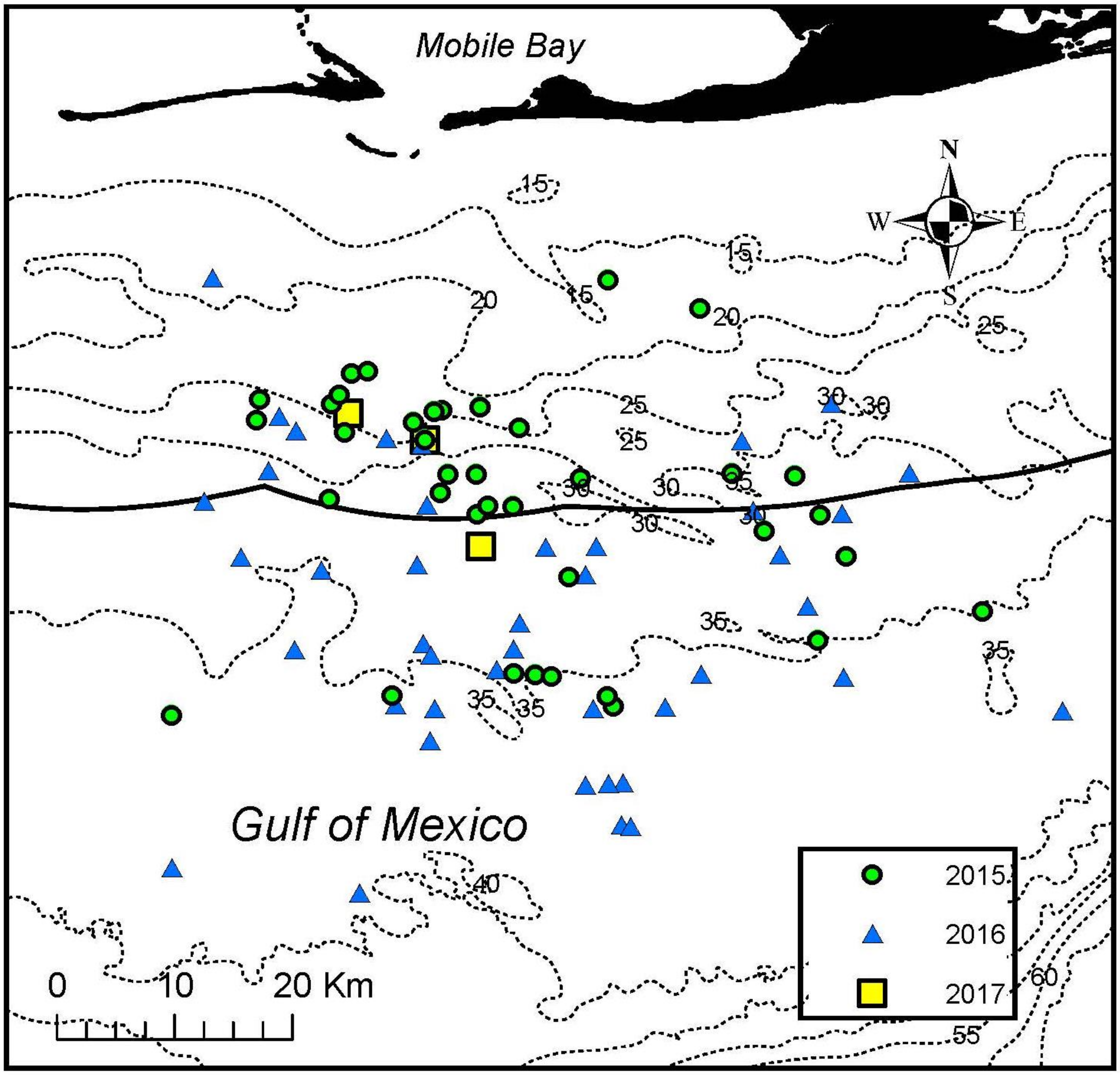

Figure 2-2. Locations of reefs where conventionally tagged Red Snapper were released in 2015 (circles), 2016 (triangles) and 2017 (squares). The solid line represents the division between reefs that was considered close (< 33 km) and far (33 – 65 km) from shore.

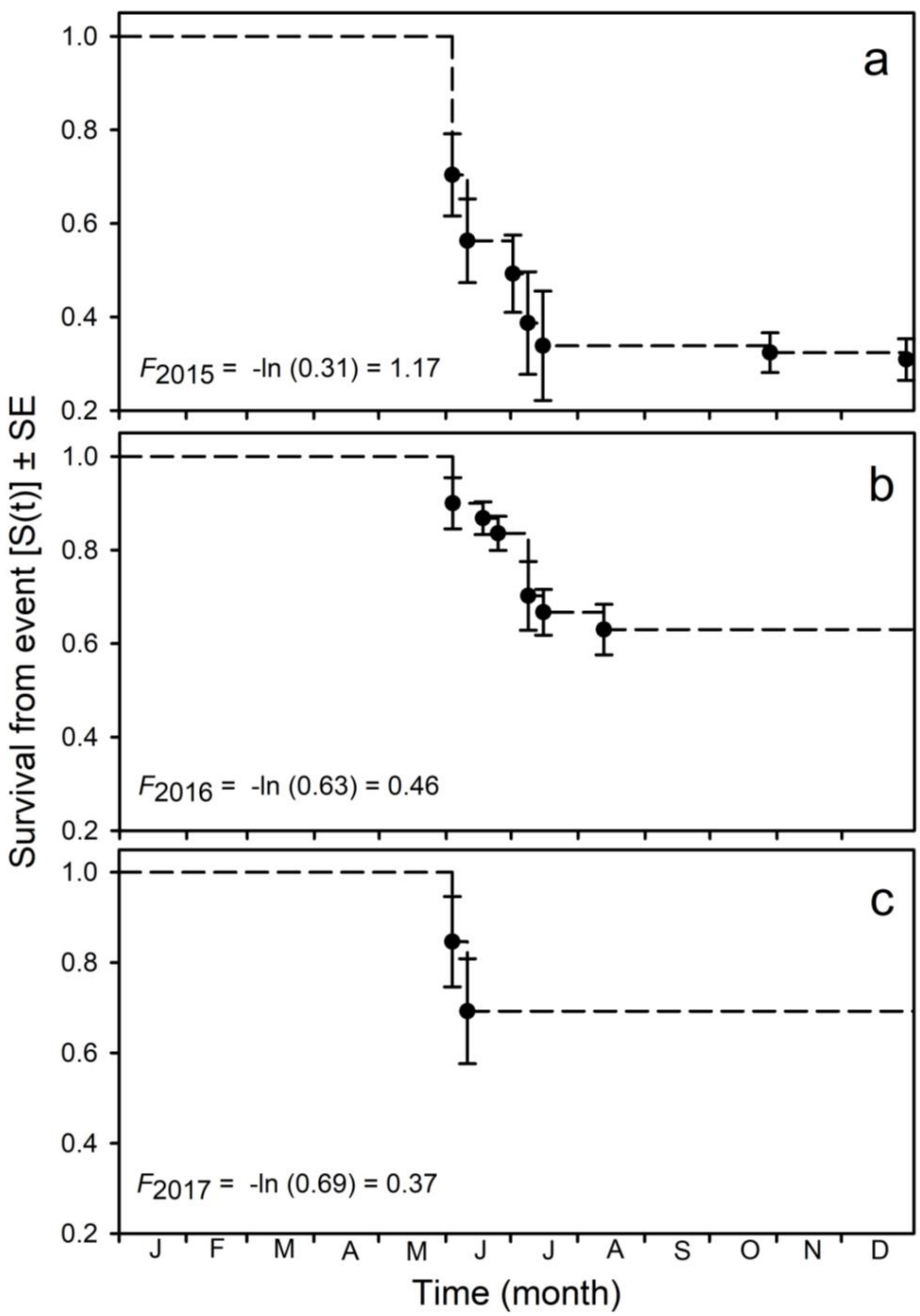

Figure 2-3. Survival (*S*) of transmitter-tagged Red Snapper from fishing mortality by year: (a) 2015, (b) 2016 and (c) 2017. Dashed line shows proportion of fish surviving fishing mortality after each weekly interval. Instantaneous fishing mortality rates (*F*) were calculated from *S* at 52 weeks. Points and error bars (SE) were conditional estimates of *S* for time intervals with a mortality event.

Chapter 3:

A comparison of home range, site fidelity and mortality of Red Snapper, *Lutjanus campechanus*, on artificial and natural reefs in the northern Gulf of Mexico.

Abstract

For the main purpose of improving fishing opportunities, artificial reefs have been widely deployed in the northern Gulf of Mexico. Red Snapper, *Lutjanus campechanus*, is a dominant component on these artificial reefs and highly targeted by both recreational and commercial fishers. However, questions remain about the function of artificial reefs and how they compare to natural reef structure. In the present study acoustic telemetry was used to compare movement patterns, site fidelity and mortality rates of Red Snapper between fish residing on natural and artificial reefs. Red Snapper had similar mortality rates, site fidelity and movement patterns on natural and artificial reefs. These measures also had similar relations to changing seasons and temperature on these two reef types. Diel patterns in home range differed among individual reefs. There was a significant interaction effect when home range was compared between diel periods and depth, with the largest home rages observed on shallow (< 20 m) reefs at night, and the smallest home ranges observed at deep (> 20 m) reefs at night. Red Snapper residing on larger reefs had larger home ranges and fish on natural reefs had larger home ranges than fish on artificial reefs. The present study observed similar Red Snapper behaviors on artificial and natural reefs and indicated that these two reef types have similar ecological functions for Red Snapper. Importantly, fishing mortality rates were nearly identical on both reef

types and provided little evidence that artificial reefs disproportionally concentrate Red Snapper and increase exploitation compared to natural reefs.

Introduction

Artificial reefs have been deployed around the world. However, questions remain about the functional ecology of artificial reefs and marine fish populations. For example, do artificial reefs increase fishery production, or simply aggregate existing fishery resources making them easier to exploit (Bohnsack 1989; Grossman et al. 1997; Bortone 1998). In the northern Gulf of Mexico, Red Snapper are often one of the most abundant species on artificial reefs (Strelcheck et al. 2005; Gallaway et al. 2009; Jaxion-Harm and Szedlmayer 2015; Jaxion-Harm et al. 2018). Many artificial reefs have been constructed in the northern Gulf of Mexico both intentionally, and as the result of offshore energy production, creating Red Snapper fisheries in areas where they would otherwise not exist (Minton and Heath 1998; Shipp and Bortone 2009; Streich et al. 2017). For example, Szedlmayer et al. (2020b) estimated that 1.78 million individual Red Snapper > 330 mm Total Length [TL] were resident in an area off the Alabama coast with extensive artificial reefs but few natural reefs. Gallaway et al. (2020) estimated 1.94 million age-2+ Red Snapper resided on oil and gas platforms in the northern Gulf of Mexico in 2017. Considering these high abundances of Red Snapper on artificial reefs, it is important to determine if artificial reefs have similar ecological functions compared to natural reefs, or are they causing faster depletion by concentrating the species and increasing fishing mortality.

Acoustic telemetry is an advantageous method that can provide detailed descriptions of habitat use, residency, and site fidelity in marine fishes (Reubens et al. 2013; Piraino and Szedlmayer 2014; Wolfe and Lowe 2015). Telemetry can also be used to measure mortality, as the fate of tracked individuals can often be determined (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Pollock et al. 2004; Mudrak and Szedlmayer 2020b). Several studies have used telemetry to study Red Snapper movements (Williams-Grove and Szedlmayer 2020), but most of these studies examined movements around artificial reefs. Exceptions were a few studies that tracked Red Snapper on both artificial and natural reef sites (Topping and Szedlmayer 2011b, 2013; Froehlich et al. 2019; Getz and Kline 2019). However, the natural reef studied by Topping and Szedlmayer (2011b; 2013) differed from most natural reefs in the northern Gulf of Mexico in that the structures were old tree trunks surrounding a drowned riverbed, rather than natural rock outcrops. Also, the earlier telemetry methods used by Topping and Szedlmayer (2011b; 2013) did not allow for fine scale positioning. Froehlich et al. (2019) primarily tracked fish on a large artificial reef, with a few natural rock reef patches on the perimeter. However, the transmitter-tagged Red Snapper spent little time on the natural reefs or were not detected on natural reefs due to the location of the natural reefs on the periphery of the receiver array. The third study that used telemetry to compare Red Snapper behaviors between natural and artificial reefs was not capable of measuring fine scale movements (Getz and Kline 2019).

Thus, there is little information available on comparing the habitat use patterns of Red Snapper between artificial and natural reefs. The purpose of the present study was to compare home range sizes, site fidelity, diel behaviors, and mortality rates of Red

Snapper between natural and artificial reefs. All reefs were examined over similar areas and time periods, 15 to 52 km south of coastal Alabama, United States, on the continental shelf in the northern Gulf of Mexico. The present study provides a comparison of the functional ecology of artificial and natural reefs for Red Snapper that will help in the evaluation of the utility of artificial reef deployments.

Methods

Study area and receiver array design

Red Snapper were tracked on small artificial reefs, gas platforms, and natural reefs. The small artificial reefs examined in the present study were the same reefs and receiver array described in previous telemetry studies (Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016a, 2016b, 2017; Herbig and Szedlmayer 2016; Mudrak and Szedlmayer 2020b). The small artificial reef sites (n = 26) consisted of steel cage artificial reefs (2.5 x 1.3 x 2.4 m) that were deployed from 2006 to 2010 at unpublished locations (Figure 3-1). Distances between steel cages ranged from 1.4–1.6 km and water depth ranged from 18 to 35 m. Three of these small artificial reefs had Vemco positioning systems (VPS, Vemco Ltd, Nova Scotia) consisting of five receivers (VR2W, Vemco, Nova Scotia), and were included in the present study starting on January 1, 2018. The remaining 23 steel cage reefs had single receivers. At VPS site R3, two additional steel cage reefs were located 150 m northeast and 270 m to the northwest of the central steel cage reef for a total reef area of 18 m^2. The VPS site at R4 also encompassed an additional concrete pyramid reef 160 m to the northwest of the central steel cage reef yielding a total reef area of 10.5 m^2. The VPS site at R6 contained no other reef structures, for a total reef area of 6 m^2. To compare Red Snapper movement behaviors on different reef types, an additional five VPS receiver arrays were deployed on two gas platforms and three natural reefs (Figure 3-1).

The first gas platform site (P1) was included in the present study starting May 4, 2018 following a previous study (Everett et al. 2020). This platform was a large complex comprised of three connected platforms each separated by 40 m. The total area encompassed by P1 was 1,454 m^2. The second VPS site at a platform (P2) was started on May 23, 2018 and contained a single platform with four legs and a 337 m^2 area. These platforms are visible above the water's surface and are well-known by local fishers. The first VPS site (N1) at a natural reef was started on June 6, 2018 and is a locally well-known fishing location (Southeast Banks) that consists of many low vertical relief natural rock outcrops (0.5 m) that are distributed over an area of approximately 237,700 m^2. The second VPS site (N2) at a natural reef was started on August 6, 2018 at another well-known fishing location (Southwest Rock) and consisted of two rock outcrops with areas of 111 and 34 m^2, 8 m apart, with 1 m of vertical relief. An additional two rock outcrops with 5 and 13 m^2 areas were located 80 m southeast of the larger outcrops at N2, for a total area of 163 m^2 of reef within the VPS site. The third VPS site (N3) at a natural reef was started on June 12, 2019 at an unpublished reef location and consisted of a rock outcrop with an area of 152 m^2 and 1 m vertical relief. Site N3 also had an additional rock outcrop with an area of 29 m^2 that was located 65 m to the south of the larger outcrop, for a total reef area of 181 m^2 for this VPS site (Table 3-1).

Each small artificial reef VPS site (N = 3) had a center receiver (VR2W, Vemco, Nova Scotia) positioned 20 m north of the reef and four additional receivers placed 300 m north, south, east, and west of the center receiver (Piraino and Szedlmayer 2014). Each VR2W VPS receiver also had a synchronization tag (Vemco V16-6x, transmission delay 540-720 s) placed 1-m above the receiver to allow for synchronization of the receiver clocks. All VPS sites on natural reefs (N = 3) and platforms (N = 2) had VRTx receivers with built in synchronization tags (Vemco, Nova Scotia). Receiver arrays on natural reefs were identical to the arrays on small artificial reef VPS sites. The VPS receiver arrays on the platforms included six receivers: with a center receiver placed 20 m north of each platform, and additional receivers placed 300 m to the northeast, northwest, southeast, and southwest of the center receiver and one receiver placed 415 m south of the center receiver (Everett et al. 2020).

All receivers were moored 4.5 m above the seafloor. Temperature loggers (U22-001, Onset Incorporated) were placed both adjacent to the receiver, and 0.25 m from the seafloor. The temperature loggers sampled at 1-hour intervals, with data retrieved and loggers replaced at the same time as the receivers at each VPS site. When possible, temperature, salinity and dissolved oxygen were also measured from a surface vessel operated YSI meter (Model 6920 or Exo2, YSI Incorporated) at each VPS site during field site visits. A control transmitter was also placed on a mooring buoy within each VPS site. The control transmitter estimated the accuracy of VPS calculated positions and determined time periods when the receivers failed to detect transmitters due to environmental conditions, high background noise or receiver malfunction. The VPS receivers were retrieved by SCUBA divers and detection data were downloaded every 66 to 208 days. Data from the surrounding single receivers were downloaded every 348 to 392 days.

Tagging and release procedures

Red Snapper were captured with hook-and-line, with an 8/0 barbless circle hook (L2004F, Eagle Claw), baited with Gulf Menhaden *Brevoortia patronus*, attached to a 1 m 45 kg leader and a 27 kg mainline. All tagged Red Snapper were larger than the minimum size limits in place during the 2018 – 2020 fishing seasons for commercial (330 mm TL) and recreational (406 mm TL) fisheries.

After capture, Red Snapper were anesthetized in 150 mg Tricaine Methanesulfonate (MS-222)/L seawater for 90 seconds in a 70 L tank. Fish were weighed (to nearest 0.1 kg) and measured (mm standard length [SL], fork length [FL] and TL). Subsequently, a unique transmitter (Vemco V16-6x-R64k, transmission delay = 20–69 s) was surgically implanted into the peritoneal cavity through a vertical incision above the ventral midline. The incision site was sealed with absorbable, plain gut sutures (Ethicon 2-0, metric 3), and an intramuscular injection of 0.4 ml/kg of 250 mg/ml oxytetracycline solution was administered as a prophylactic antibiotic treatment and to serve as a time mark for otolith annual increment validation studies (Szedlmayer and Beyer 2011; Szedlmayer et al. 2020a). An externally visible tag (Floy FM-95W internal anchor tag) was inserted into the peritoneal cavity, for recognition as a transmitter-tagged fish by fishers. After tagging was completed, Red Snapper were placed in a 185 L seawater tank for recovery. Tagged fish were released after they displayed active movements and recovery from the anesthesia (Topping and Szedlmayer 2011a, b, 2013;

Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016a, b, 2017; Mudrak and Szedlmayer 2020b). Fishers were provided a US$150 reward for the return of a tagged Red Snapper. Posters advertising the reward were displayed at local bait shops, boat ramps and marinas.

All tagged Red Snapper were released on the seafloor with a cage (Piraino and Szedlmayer 2014; Williams et al. 2015). This plastic-coated wire mesh cage (62 x 62 x 84 cm) protected fish from predators as the fish was lowered to the seafloor. After the cage reached the seafloor, a door automatically opened. Fish were provided an opportunity to exit the cage for at least 15 min on their own initiative before the cage was retrieved. A tagged Red Snapper that had not exited the cage after cage retrieval was not released. No fish were tagged if dissolved oxygen was < 2.5 ppm at the seafloor.

Fish positions

To calculate a fish position, the transmitter must be simultaneously detected by at least three receivers. The receivers were placed at distances of 300 m from the center reef site in the present VPS sites, which provided a high detection efficiency as 100 % of transmitter signals were detected at 400 m (Piraino and Szedlmayer 2014). Fish positions were based on the time differential of the transmitter's signal arrival among receivers and prior to May 2019 were calculated by Vemco post-processing (Vemco Ltd, Nova Scotia). Starting in May 2019 all subsequent fish positions were calculated with Fathom software (Innovasea, Nova Scotia). To reduce signal collisions, the maximum number of active transmitters within a VPS site at one time was limited to 10 (Topping and Szedlmayer 2011b). This limitation included transmitter-tagged Red Snapper, control transmitters, stationary transmitters, and transmitter-tagged Gray Triggerfish, *Balistes capriscus*, within each VPS site (Herbig and Szedlmayer 2016; McKinzie et al. 2016).

Mortality and residency estimates

Calculated fish positions and transmitter detection patterns were used to determine the fate of transmitter-tagged Red Snapper (Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016b). If a Red Snapper was caught by a fisher, the tracking patterns had continuous detections of the fish around a reef that was followed by an abrupt disappearance near the reef and a lack of detections on surrounding receivers. Fisher returns were used to validate telemetry-identified fishing mortalities. If a Red Snapper emigrated from a VPS site, the tracking data indicated continuous detections around the reef, followed by a series of positions sequentially moving away from the reef, with the final detections of the transmitter recorded on either the north, east, south, or west receiver. Emigration patterns could also be subsequently confirmed by detections on surrounding receivers. A fish was classified as emigrated if it was absent from the VPS site for more than three days. If a transmitter-tagged fish became stationary within the first six days after tagging it was considered a tagging mortality, while fish that became stationary after six days were considered natural mortalities. Any emigration within six days of tagging was considered tagging stress, and these fish were not included in residency or mortality estimates. False detections were removed from the analysis following previously developed detection criteria (Pincock 2012; Williams-Grove and Szedlmayer 2016a, b).

Mortality and residency rates for any Red Snapper still alive within the VPS sites after a six-day tagging recovery period were estimated with a known fate model applied with the program MARK (White and Burnham 1999; Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016b; Mudrak and Szedlmayer 2020b). Annual estimates were based on weekly time intervals for each year. The MARK program calculated survival estimates based on the maximum likelihood binomial (MLE; Edwards 1992). In this model, survival was estimated from conditional probabilities of surviving specified events (*i.e.*, fishing, natural mortality, or emigration). For example, the probability of surviving a mortality event was determined by calculating the number of individuals at risk of dying and the number of individuals that survived for each time interval. Fish that underwent an event not under consideration were removed (*i.e*., "right censored"). For example, when fishing mortality (F) was estimated, all emigrations and natural mortalities (M) were removed.

Fishing and natural mortality rates were calculated with a staggered entry model, while residency estimates were based on a common start date (Topping and Szedlmayer 2011b, 2013; Williams-Grove and Szedlmayer 2016a, b). Survival curves were tested for significant differences between reef types with a log rank test (Pollock et al. 1989). Differences in fish return rates to artificial and natural reef sites after emigrating were compared with a chi square test. Mortality rates were not calculated for 2020 due to limited data for that year; but tracking data from 2020 were used in site fidelity and residency estimations. Median residence time was defined as the period when 50% of the tagged Red Snapper were still present, while site fidelity was the percentage of tagged fish remaining at their VPS site one year after release (Schroepfer and Szedlmayer 2006;

Topping and Szedlmayer 2011b; Herbig and Szedlmayer 2016; Williams-Grove and Szedlmayer 2016a).

Home range area

Fish positions were analyzed with the R program (R Core Team 2020) to calculate 95% kernel density estimate (KDE) areas by monthly time intervals for each fish, and by total night and day diel periods for each month for each fish (Venables and Ripley 2002; Calenge 2006; Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016a). Home range areas were compared among VPS sites, between natural and artificial reef types, and over diel and seasonal time periods. Home range areas were also compared to mean monthly bottom temperatures measured at each VPS site. All statistical analyses were computed in Statistical Analysis Software (SAS 9.4, North Carolina, United States), with generalized linear mixed models (proc GLIMMIX) with fish as a random factor (i.e., a fish was repeatedly measured over time) and assumed negative binomial distributions (Venables and Dichmont 2004; Seavy et al. 2005; Bolker et al. 2009). After significant differences were detected with the mixed models, a Tukey Kramer test was used to show specific differences. Seasons were divided into summer (June through August), fall (September through November), winter (December through February) and spring (March through May). Diel periods were compared as day and night based on astronomical twilight times throughout the year obtained from the NOAA Solar Calculator website (https://www.esrl.noaa.gov/gmd/grad/socalc/). Diel periods were also compared by two depth zones, i.e., shallow VPS sites that were less than 20 m and deep VPS sites greater than 20 m. Mean monthly KDEs for all fish on each VPS site were compared to total reef area within each VPS site with linear regression.

Results

Fish tagging and tracking

The present study started on January 1, 2018 and 16 transmitter-tagged Red Snapper from previous studies were still active and included here (Williams-Grove and Szedlmayer 2016a, b, 2017; Mudrak and Szedlmayer 2020b; Everett et al. 2020). The present study tagged an additional 181 Red Snapper with transmitters. Among these newly transmitter-tagged Red Snapper, 24 (13.2%) were not released due to surgical complications or because the fish failed to leave the release cage. Thus, there were 157 transmitter-tagged Red Snapper released. Among released Red Snapper, eight fish (5%) suffered tagging mortalities within six days of release and 10 fish (6.4%) emigrated within the six-day tagging recovery period and were not used in analysis. Thus, the present study tracked 155 transmitter-tagged Red Snapper (139 present study + 16 from a previous study) for more than six days and obtained 7,270,329 accurate locations. Among tracked Red Snapper, 59 were caught and reported by fishers, 11 were caught and not reported, five suffered natural mortalities, 51 emigrated, one fish was reported caught and released which caused the fish to emigrate, and 28 fish were still active at end of the study.

Fishing mortality, natural mortality and residency

In 2018, 12 Red Snapper were caught and returned by fishers, and one (7.7%) was caught and not reported. In 2018, overall F = 0.68 (95% CI = 0.25 to 1.47) among the 56 Red Snapper that were tracked and available for recapture. Fishing mortality in 2018 was not significantly different between reef types with F = 0.67 (95% CI = 0.23 to 1.48) among 38 Red Snapper tracked on artificial reefs, and F = 0.65 (95% CI = 0.32 to 1.13) among 18 Red Snapper tracked on natural reefs (df = 1, χ^2 = 0.46, P = 0.496).

In 2019, 43 Red Snapper were caught and returned by fishers, and nine (17.3%) were caught and not reported. In 2019, overall F = 2.07 (95% CI = 1.50 to 2.69) among 123 Red Snapper tracked. Fishing mortality in 2019 was not significantly different between reef types with F = 2.18 (95% CI = 1.44 to 3.00) among 87 Red Snapper tracked on artificial reefs, and F = 2.00 (95% CI = 1.11 to 3.05) among 36 Red Snapper tracked on natural reefs (df = 1, χ^2 = 0.01, P = 0.907).

In 2018, no transmitters became stationary after the six-day recovery period, resulting in M = 0 for all reefs that year. In 2019, three transmitters became stationary after 8,245, and 654 days from their tagging date. One of these Red Snapper died on a natural reef, and two died on artificial reefs. These mortalities indicated a total natural mortality in 2019 of M = 0.11 (95% CI = 0.03 to 0.32). Natural mortality in 2019 was not significantly different between reef types with M = 0.07 (95% CI = 0.01 to 0.43) on natural reefs and M = 0.11 (95% CI = 0.02 to 0.40) on artificial reefs (df = 1, χ^2 = 0.04, P = 0.833). At the time of analyses, 19 of the 51 (37.2%) Red Snapper that were defined as emigrants from the telemetry data were returned by fishers, which confirmed that these individuals were alive when they emigrated as opposed to suffering a predation event.

The single fish that emigrated after being caught and released was right censored from residency estimates, because the stress of being captured likely caused the fish to emigrate. Overall, Red Snapper median residency time was 21 weeks, and site fidelity was 0.43 ± 0.05 (95% CI = 0.34 – 0.54; N = 155 fish). Site fidelity and residency survival curves were not significantly different between reef types (df = 1, χ^2 = 0.98, P = 0.323). On artificial reefs median residency time was 26 weeks and site fidelity was 0.48 ± 0.06 (95% CI = 0.36 – 0.60; N = 108 fish), and on natural reefs median residency time was 18 weeks and site fidelity was 0.33 ± 0.09 (95% CI = 0.17 – 0.53; N = 47 fish). Fish that emigrated from natural reefs were significantly more likely to return than fish that emigrated from artificial reefs (df = 1, χ^2 = 6.03, P = 0.014). On natural reefs, 21 fish emigrated and nine (43%) later returned to the natural reef site after absences of 5 to 154 days. On artificial reefs, 41 fish emigrated and six (15%) of these later returned to the artificial reef site after absences of between 5 and 173 days.

Several observations were made of group emigrations, where multiple fish emigrated from the same reef site on the same day. On June 2, 2018, four fish left P1 with the last detection of each fish ranging between 01:03 and 02:23 CDT. Two of these fish were last detected within one minute of each other. Among the four fish that emigrated, two returned three to five days after emigrating, while the other two did not return. A second group emigration was observed at P1 on May 16, 2019 when two fish emigrated between 02:04 and 03:00 CDT. Both fish were later caught and reported by fishers 16 and 51 days after they emigrated. At P2, 62% (8 of 13) of transmitter-tagged Red Snapper present emigrated between May 12, 2019 and May 24, 2019. Two fish emigrated on May 12, 2019 at 02:01 and 02:11 CDT, and both were caught and reported by fishers outside of the VPS site, 20 and 76 days after emigrating. An additional three fish emigrated at 06:21, 07:33 and 07:34 CDT on 16 May 2019. Among these three emigrants, one moved to P1 after 174 days, one was caught and reported by a fisher 30 days after emigrating, and one did not return. Lastly, three fish emigrated between 23:42 and 23:59 CDT on May 24, 2019. Among these three emigrants, one returned 14 days after emigrating, one was caught and reported eight days after emigrating, and one did not return. On R4, three fish emigrated between 13:08 and 13:11 on February 13, 2019. Among these three emigrants, two were caught and reported by fishers 108 and 299 days after emigrating and one returned 173 days after emigrating. On N2, two fish emigrated at 00:35 and 05:55 on March 10, 2020, and had not returned or been reported caught at the end of the study. None of these emigrations corresponded to major storm events, i.e., wave heights > 2 m.

Home range

Monthly KDE areas significantly differed among individual reefs ($F_{7, 771}$ = 58.61, P < 0.0001; Figure 3-2; Figure 3-3), and were significantly larger on natural reefs (least square mean ± standard error; 17,098.00 ± 1,648.26) compared to artificial reefs (3,999.33 ± 256.66; $F_{1, 766}$ = 157.39, P < 0.0001). There was a significant positive linear relation between reef area and mean monthly KDE area ($F_{1, 7}$ = 62.57, P = 0.0002, r^2 = 0.9125). Diel home range varied among individual reefs (Table 3-2). There was a significant interaction between diel period and depth, with the largest home ranges observed on shallow (< 20 m) sites at night, and the smallest home ranges at deep (> 20 m) sites at night ($F_{3, 1660}$ = 66.56, P < 0.0001; Figure 3-4).

Mean monthly bottom temperatures ranged from 16.7 to 28.6 °C. Observed dissolved oxygen concentrations within 1 m of the seafloor during site visits ranged from 0.44 to 7.50 ppm, and salinity ranged from 30.16 to 36.12 ppt. Monthly KDE areas were significantly larger in the warmer fall and summer seasons compared to the cooler spring and winter seasons on artificial reefs ($F_{3, 542}$ = 13.13, $P < 0.0001$), natural reefs ($F_{3, 224}$ = 18.45, $P < 0.0001$), and on all reefs combined ($F_{3, 769}$ = 31.55, $P < 0.0001$; Figure 3-5). Similarly, there was a significant positive relation between monthly KDE area and mean monthly bottom temperature on artificial reefs ($F_{1, 544}$ = 38.66, $P < 0.0001$), natural reefs ($F_{1, 226}$ = 107.63, $P < 0.0001$), and on all reefs combined ($F_{1, 765}$ = 116.94, $P < 0.0001$).

Discussion

Mortality

Fishing mortality was high (*F* ranged from 0.65 to 2.18) for the duration of the present study. However, fishing mortality was similar between the natural and artificial reef sites. These similar fishing mortalities between reef types are surprising because three of the five artificial reef sites were small with unpublished locations. These small unpublished reefs would be expected to have lower fishing mortality, presumably because fewer fishers know their locations (Mudrak and Szedlmayer 2020b). However, they also support smaller numbers of Red Snapper compared to the larger reefs (Szedlmayer et al. 2020b). Therefore, it appears that even if only a small number of fishers are able to locate a small artificial reef, they are still able to exert high fishing mortalities on the fish residing on that particular reef.

Natural mortality was low and similar to the natural mortality of $M = 0.1$ used in fishery management (SEDAR 2018). The natural mortality of $M = 0.11$ measured in 2019 may even be an overestimate, because one of the fish that died did so only eight days after tagging and may have been a delayed tagging mortality. Also, the fish that died after 654 days did so on a Saturday when recreational Red Snapper season was open. This suggests that the fish may have suffered a release mortality and that the fisher did not report the catch, possibly because the fish's external tag had been shed. The telemetry methods used here were unable to separate natural and release mortalities if the catch was not reported by the fisher (Hightower et al. 2001). If transmitter-tagged fish died due to release mortality, fishing mortality would be underestimated, while natural mortality would be overestimated. Fortunately, there were few transmitters that became stationary and the possible error in fishing and natural mortality estimates is low.

If a transmitter-tagged Red Snapper was preyed upon and the transmitter leaves the VPS site inside of a predator, the event may be misinterpreted as an emigration resulting in an underestimate of natural mortality. However, tracking patterns of potential Red Snapper predators, e.g., Bull Sharks, *Carcharhinus leucas*, and Sandbar Sharks, *Carcharhinus plumbeus*, show very different movement patterns compared to Red Snapper and these differences can be used to separate predation events from emigrations events (Altobelli and Szedlmayer in press). One of the fish lost from the VPS sites less than six days after tagging subsequently showed tracking patterns similar to those reported for sharks and indicated a shark predation event. Also, the release cages used here failed to protect at least two transmitter-tagged Red Snapper from predation by bottlenose dolphin, *Tursiops truncates*, as observed in video recordings from inside the cages. One of the preyed upon Red Snapper subsequently showed a tracking pattern similar to shark movement patterns, while the transmitter of the other fish remained stationary within the array. These preyed upon fish did not affect mortality estimates because they suffered mortality less than six days after tagging. However, they do indicate that it is possible to identify predation events if the predator stays within the tracking array long enough for detection of movement patterns. In the present study, 37% of the Red Snapper that were classified as emigrations were later returned by fishers, confirming that they were alive when they left the VPS site. These fisher returns reduced the number of fish that could have been preyed upon and misidentified as emigrations.

Residency and site fidelity

Site fidelity was not significantly different between natural and artificial reefs. However, fish that emigrated from natural reefs were more likely to later return to the reef than fish that emigrated from artificial reefs. The site fidelities observed in the present study were lower than previously reported estimates (Topping and Szedlmayer 2011b; Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016a). A substantial difference here from two of these previous studies was that several reef types were examined here compared to only small steel cage reefs in previous studies (Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016a). For example, Everett et al. (2020) observed similar lower site fidelity on oil and gas platforms, which was one of the reef types in the present study. Another possible cause of the lower residency and site fidelity was the higher fishing mortality observed over the present study period compared to these previous studies. The large number of transmitter-tagged Red Snapper prematurely removed by fishers (removed before they would have emigrated on their own initiative) may make the residency and site fidelity estimates lower than would occur without fishing mortality. For example, in 2019 the probability that a fish residing on the VPS sites would be harvested by a fisher was 87.4 % per year, this left few transmitter-tagged fish available for long term site fidelity estimates. Residency and site fidelity could have been higher if these fish were not removed by fishers and may have more closely matched previous estimates that were observed under lower fishing mortality rates (Topping and Szedlmayer 2011b; Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016a).

Group emigrations

Previous movement studies of Red Snapper have observed multiple emigrations on the same day. These multiple emigrations were attributed to tropical storms (Topping and Szedlmayer 2011b), and low temperatures in the winter (Topping and Szedlmayer 2011b; Williams-Grove and Szedlmayer 2016a). The present study observed multiple group emigrations by Red Snapper, but they did not occur during storm events. Most of the emigrations occurred in May and June rather than with minimum bottom temperatures observed in the winter. Therefore, it is unclear what caused these fish to emigrate.

Low dissolved oxygen is an event that might cause Red Snapper to emigrate, but low dissolved oxygen concentrations (< 2.5 ppm) were only observed on site visits in August and September 2019 and did not correspond to the group emigrations. Also, fish were still present on sites P1, P2, N1 and R6 when dissolved oxygen concentrations were below < 1 ppm at the bottom. This indicated that Red Snapper remaining on the reefs and likely survived low dissolved oxygen concentrations by moving higher up in the water column rather than emigrating.

A notable group emigration was observed on the platforms in May 2019, when multiple fish emigrated from both P1 and P2 on the same day. This indicated that Red Snapper were responding to the same environmental or biological factors on separate reefs in the same geographic area. However, it is unknown what factor caused the fish to emigrate. In the present study, several of the group emigrations were detected within minutes of each other, suggesting that the Red Snapper may have emigrated together as a school. This is important because there is a lack of information on schooling behavior in Red Snapper despite the well-known aggregations around reef structure. Unfortunately, the time intervals between fish positions were too long (most > 10 min) to confirm that the fish were traveling together, and once the fish left the VPS site further associations were undetermined. Telemetry methods that provide more positions over shorter time periods (e.g., < 1 minute) would be required to measure how Red Snapper interact with each other on the same reef. Also, larger VPS arrays would be needed to determine how long fish remain together after moving to other reefs.

Diel patterns in home range

Previous studies have indicated different Red Snapper diel movement patterns, with studies observing larger home ranges at night (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a, b), larger areas during the day (Piraino and Szedlmayer

2014) and both patterns depending on the particular reefs (Williams-Grove and Szedlmayer 2016a; Everett et al. 2020). In the present study both patterns were observed with larger home ranges at night at four reef sites, larger home ranges in the day at two reef sites, and no difference between day and night at two reef sites. Also, patterns of larger area use during night or day were not consistent between reefs of the same type. For example, among natural reefs, one reef had larger home ranges at night and two reefs had larger home ranges in the day. Among artificial reefs three reefs had larger home ranges at night, while no significant differences were detected at two reefs. Thus, it is difficult to attribute diel patterns to reef type. In addition, there was a significant interaction between reef depth zone and diel periods with the largest home ranges observed at night at the shallower reef sites, and the smallest home ranges observed during the night at the deeper reef sites. As previously suggested, there may be increased visibility due to less light attenuation at the shallower reefs at night making nocturnal foraging more advantageous, or there may be differences in prey availability at the different reef sites due to differences in substrate (Williams-Grove and Szedlmayer 2016a). However, the depth range examined in the present study is relatively small compared to the range of depths occupied by Red Snapper and future studies should examine Red Snapper movements over greater ranges in depth.

Home range area by season, reef, and reef type

As in previous studies, Red Snapper had larger home ranges in months with warmer water temperatures (Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016a; Froehlich et al. 2019; Getz and Kline 2019; Everett et al. 2020).

Unlike diel behaviors that differ among studies, and even individual reefs, increased home range with increasing temperatures appears to be a consistent pattern in Red Snapper behavior. Importantly, home range areas increased with temperature on both natural and artificial reefs. This is another similarity in Red Snapper movement behavior between the two reef types, and further evidence that natural and artificial reefs perform similar functions for this species.

Monthly KDE areas were significantly greater on natural reefs than on artificial reefs. Part of this difference is related to reef size, rather than ecological differences between artificial and natural reefs, as the natural reefs were larger than most of the artificial reefs. However, fish on the natural reefs N2 and N3 had larger home ranges than fish on the artificial reefs P1 and P2, even though P1 and P2 had more reef area. One possible explanation for this pattern is that there is additional reef habitat that was not included in reef area estimations on the N2 and N3 reef sites. These natural reef sites appear in areas where rock formations lie close to the surface of the substrate and there were many low relief rocks scattered around some of the larger rock outcrops. This was observed to the northwest of the N2 site and within the N1 site. These scattered low relief rock outcrops were not included in the estimates of reef area within each VPS site due to the difficulty in detecting and mapping such small structures. Therefore, the rock reef area within the natural reef sites may have been underestimated in reef to home range area comparisons. These low relief structures may provide prey resources in the form of reef fish and invertebrate species consumed by Red Snapper, thus causing Red Snapper in the natural reef sites to travel further to take advantage of these resources. These low relief reef structures may also act as reef bridges that allow the fish to access more area without having to stray away from reef structure. In contrast, artificial reefs typically do not have additional reef structure past the discrete boundaries of the individual reef. Without additional reef structures, Red Snapper on artificial reefs typically have access to less reef area and less open habitat surrounding the reef without leaving the predation refuge provided by reef structure resulting in smaller home ranges.

Froehlich et al. (2019) tracked Red Snapper on a large artificial reef complex composed of a sunken vessel and 4,800 concrete culverts. This study reported larger KDE area estimates than any previous Red Snapper study. After accounting for differences in methods, some of the KDE areas for individual fish on the N1 and N2 sites fell within the lower range of KDE areas observed by Froehlich et al. (2019). However, Froehlich et al. (2019) did not use VPS positioning, and based home range areas on center of activity methods and this less precise method may at least in part account for some of the differences. However, based on the larger KDE areas on the larger reefs in present study, and the larger KDE areas observed by Froehlich et al. (2019), it appears that increasing the amount of available reef structure within a given area will increase the home range of Red Snapper. In turn, Froehlich et al. (2019) did report two non-overlapping areas of use for transmitter-tagged Red Snapper within their artificial reef complex. If the spacing among reefs or other physical barriers did not cause these non-overlapping home range areas, then these areas reported by Froehlich et al. (2019) may be approaching the upper limit for Red Snapper.

Differences between natural and artificial reefs

Opponents of artificial reefs argue that artificial reefs simply attract fish away from natural reefs, and concentrate fish making them easier to harvest (Bohnsack 1989; Grossman et al. 1997; Bortone 1998). While the smaller home range size of Red Snapper on artificial reefs might support the notion that artificial reefs concentrate fish, the similar fishing mortalities observed on the natural and artificial reef sites indicate that fish were not at higher risk of fishing mortality on artificial reefs. Rather, it appears that if fishers are able to locate a reef (either natural or artificial) the fish on that reef will be subject to high fishing mortality. The natural reefs used in present study were well-known to fishers, and thus afforded little protection from fishing mortality. Similarly, the small artificial reefs used here had been in the same location for over eight years, and while the locations of these reefs were not published, it appears that enough fishers had located these reefs over time to cause high fishing mortality. Thus, both reef types were exposed to high rates of exploitation.

If artificial reefs attract Red Snapper away from natural reefs, then telemetry should detect fish leaving natural reefs and taking up residence on artificial reefs. In the present study, the only fish movement detected between sites was from one platform to another platform. It could not be determined whether the other 61 fish that emigrated (98%) moved to artificial reefs, natural reefs or open habitats. However, 97% of the reefs in the study area are artificial (Szedlmayer et al. 2020b). Therefore, if Red Snapper have no preference for natural or artificial reef habitat, there is a 97% probability that an emigrating fish moved to an artificial reef. This makes it difficult in the present study to determine if Red Snapper emigrating from natural reefs prefer to colonize natural or artificial reefs, because there are few natural reefs available. However, the present study observed similar site fidelities on both reef types indicating little tendency for Red Snapper to leave natural reefs in favor of the abundant artificial reefs.

An increasing number of studies indicate that it is uncommon for adult Red Snapper to make large scale movements or migrations (Szedlmayer and Shipp 1994; Watterson et al. 1998; Williams-Grove and Szedlmayer 2016a). Thus, in the adult stage if artificial reefs did attract Red Snapper away from natural reefs, it would consist of movements of individuals between reefs at relatively small spatial scales. These small-scale movements would likely be inconsequential to the Red Snapper population. If artificial reefs did in fact attract Red Snapper away from natural reefs, it would likely occur when juvenile Red Snapper transition from low relief juvenile habitat to high relief adult habitat at age-1 or age-2 (Szedlmayer and Lee 2004; Gallaway et al. 2009). For example, in the northeast Gulf of Mexico, high quality juvenile habitat exists in areas that are relatively shallow and close to shore (Szedlmayer and Conti 1999; Szedlmayer and Lee 2004; Mudrak and Szedlmayer 2020a), but there are few high relief natural reefs in the surrounding area. If the artificial reefs in these areas were not available, Red Snapper would need to migrate to the edge of the continental shelf to locate the higher relief natural reef needed as adults (Gardner et al. 2001; Szedlmayer et al. 2020b). The construction of the Alabama artificial reef zones provided these young adults with suitable higher relief habitat in areas closer to their juvenile habitat (Minton and Heath 1998). This may intercept fish, and hold them in areas closer to shore, where they can be more easily exploited. If the Red Snapper population were recruitment limited rather than habitat limited, this interception of young adults would cause lower Red Snapper densities on natural reefs located farther offshore.

While the attraction of Red Snapper away from natural reefs may have ecological consequences, there would be little effect on spawning stock biomass because the Red Snapper fishery is managed with a total allowable catch quota (SEDAR 2018). If Red Snapper were intercepted by the Alabama artificial reef zones and held closer to shore, fishery regulations may need to be increased because less time and fuel is required to reach the fishing grounds, which increases access to the fishery, but total harvest would remain the same. So, while it is unclear if artificial reefs increase Red Snapper production, there is little risk of attraction of fish away from natural reefs harming a well-managed fishery.

The objective of the present study was to use telemetry to compare the mortality rates, site fidelity, diel behaviors, and home range area of Red Snapper residing on artificial and natural reefs in the same geographic area. Red Snapper on artificial and natural reefs had similar mortality rates, site fidelity, and behavioral responses to seasonal and environmental changes. Diel behaviors showed different patterns among individual reefs, but these differences were not consistent for artificial or natural reef types. The main difference in Red Snapper behavior identified between natural and artificial reefs was that Red Snapper on natural reefs had larger home ranges than Red Snapper on artificial reefs. Thus, Red Snapper use both natural and artificial habitats in similar ways. Practically, if resource managers desire to make artificial reefs function more like natural reefs, they should consider placing multiple small artificial reefs within close proximity to allow fish to increase their home ranges similar to patterns observed here on natural reefs.

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Table 3-1. Summary of VPS sites showing reef type, depth (m), the number of known reefs within the VPS site, the combined area (m^2) of the reefs within the VPS site, the start and end dates of the VPS site, and the number of Red Snapper tracked within each VPS site over the course of the study. The number of individual reef structures within the N1 VPS site could not be enumerated. The reef area within the N1 VPS site represents the outline of the area known to contain many small rock features.

Site	Type	Published	Depth	Reefs	Reef Area	Start	End	Fish
R3	Artificial	No	18.6	3	18	1Jan18	4Apr20	13
R4	Artificial	No	25.9	2	10.5	1Jan18	3Apr20	26
R6	Artificial	No	25.2	1	6	1Jan18	26Mar20	22
P1	Artificial	Yes	16.2	3	1,454	4May18	5Jun20	19
P2	Artificial	Yes	18.2	1	337	23May18	17May20	28
N1	Natural	Yes	23.8	–	237,700	6Jun18	21Apr20	20
N2	Natural	Yes	19.5	4	163	6Aug18	17Mar20	22
N3	Natural	No	37.2	2	181	12Jun19	14Oct19	5

Table 3-2. A representation of significant differences in least square mean diel KDE area with VPS sites sorted by depth.

Site	Depth (m)	Larger Home Range	Day (m^2)	Night (m^2)	*P*
P1	16.2	Night	5,153 ± 419	6,302 ± 517	0.0001
P2	18.2	Night	3,242 ± 196	6,174 ± 373	0.0001
R3	18.6	Night	4,561 ± 604	3,419 ± 448	0.0067
N2	19.5	Night	7,679 ± 711	11,230 ± 1,037	0.0001
N1	23.8	Day	26,261 ± 2,386	20,976 ± 1,906	0.0001
R6	25.2	No Difference	2,557 ± 294	2,508 ± 289	0.7608
R4	25.9	No Difference	2,308 ± 363	2,204 ± 347	0.5365
N3	37.2	Day	13,600 ± 1,752	8,012 ± 1,032	0.0001

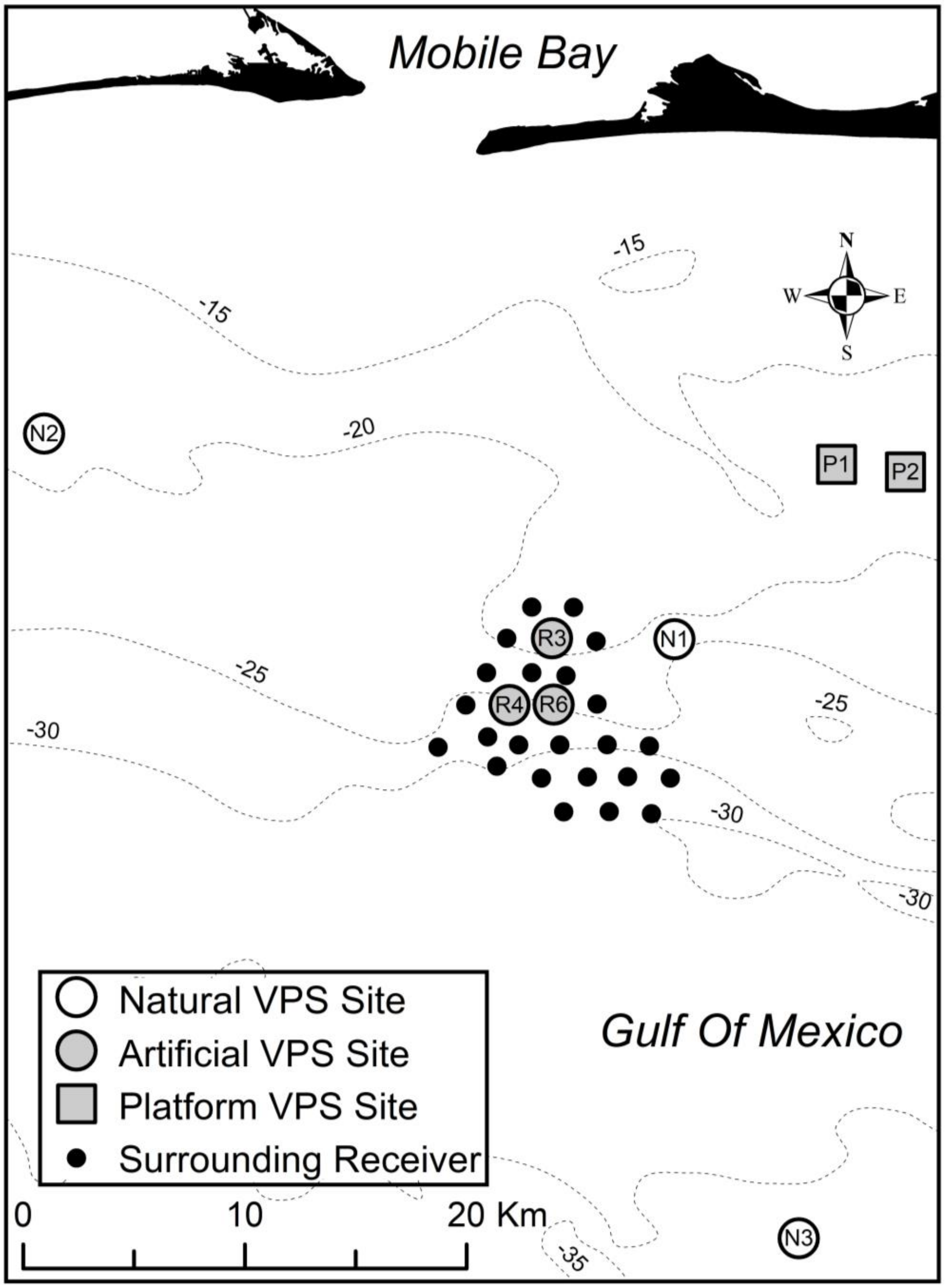

Figure 3-1. Locations of telemetry receivers, 15 to 52 km south of Dauphin Island, Alabama, United States, in the northern Gulf of Mexico. Each artificial reef VPS site (gray circles) and natural reef VPS site (white circles) contained five receivers each, platform VPS sites (gray squares) contained six receivers each, and surrounding receivers (black circles) had only a single receiver at each location.

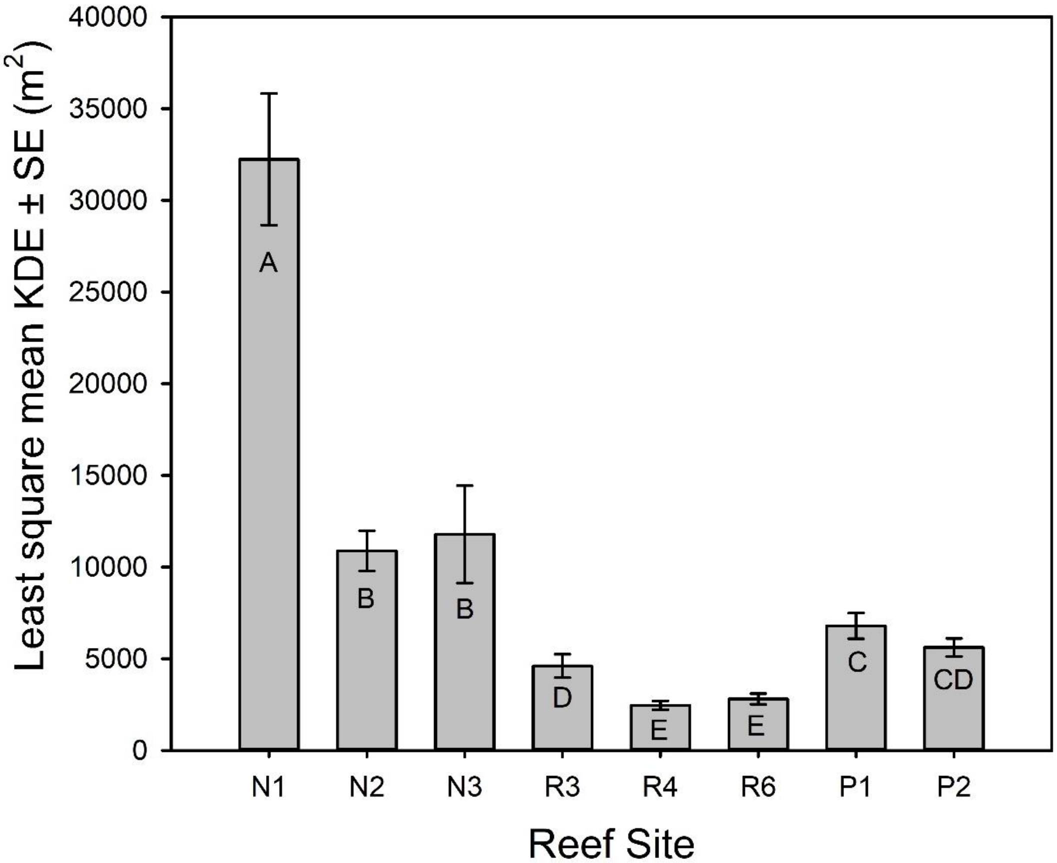

Figure 3-2. Least square mean monthly 95% KDE ± SE (m^2) for fish residing on each VPS site. Different letters indicate significant differences ($P \leq 0.05$).

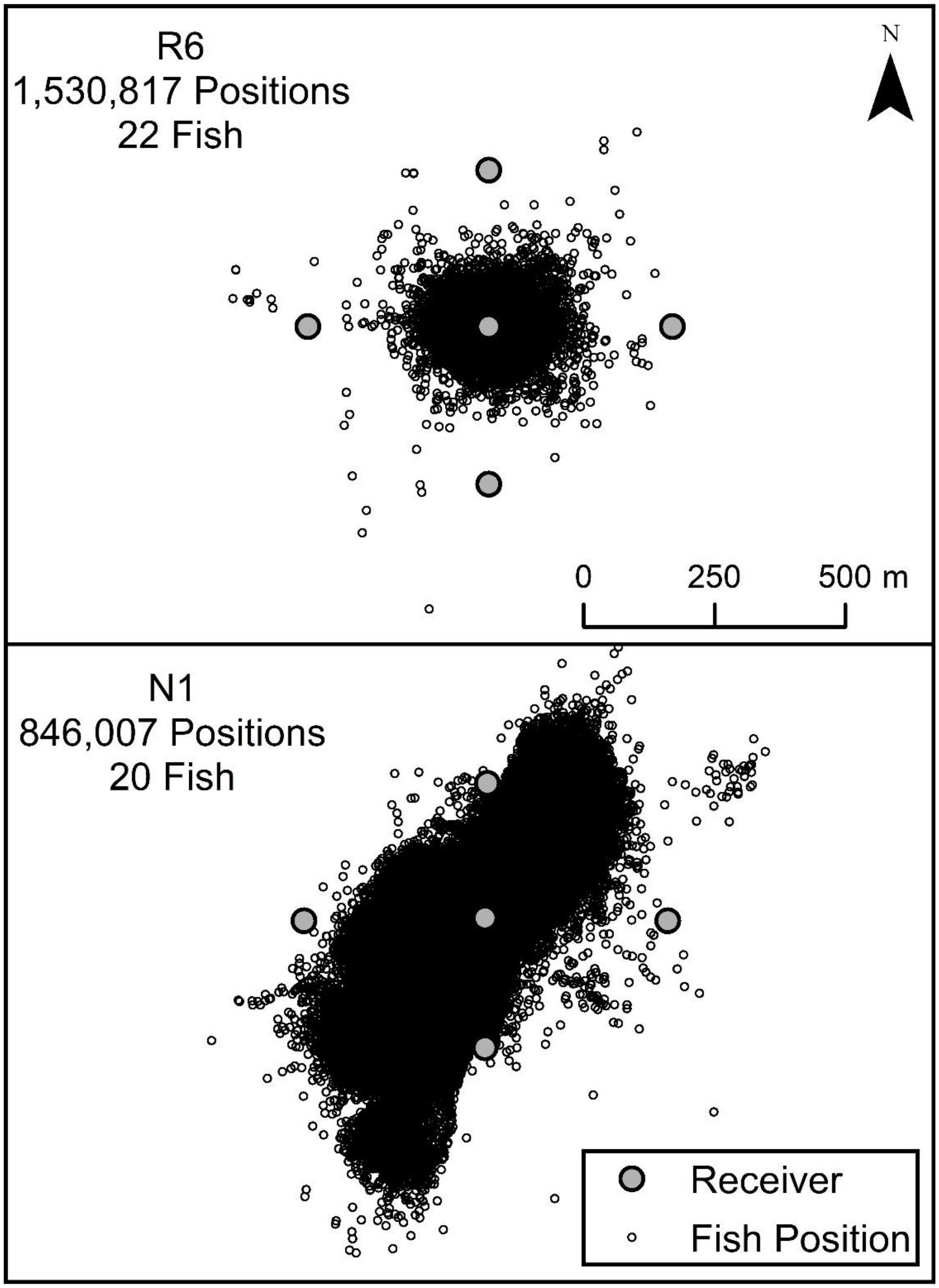

Figure 3-3. All VPS calculated fish positions (hollow circles) on R6, a small artificial reef where Red Snapper had the smallest home ranges observed in this study, and N1 a larger natural reef where the largest home ranges were observed. Gray circles represent the locations of tracking receivers.

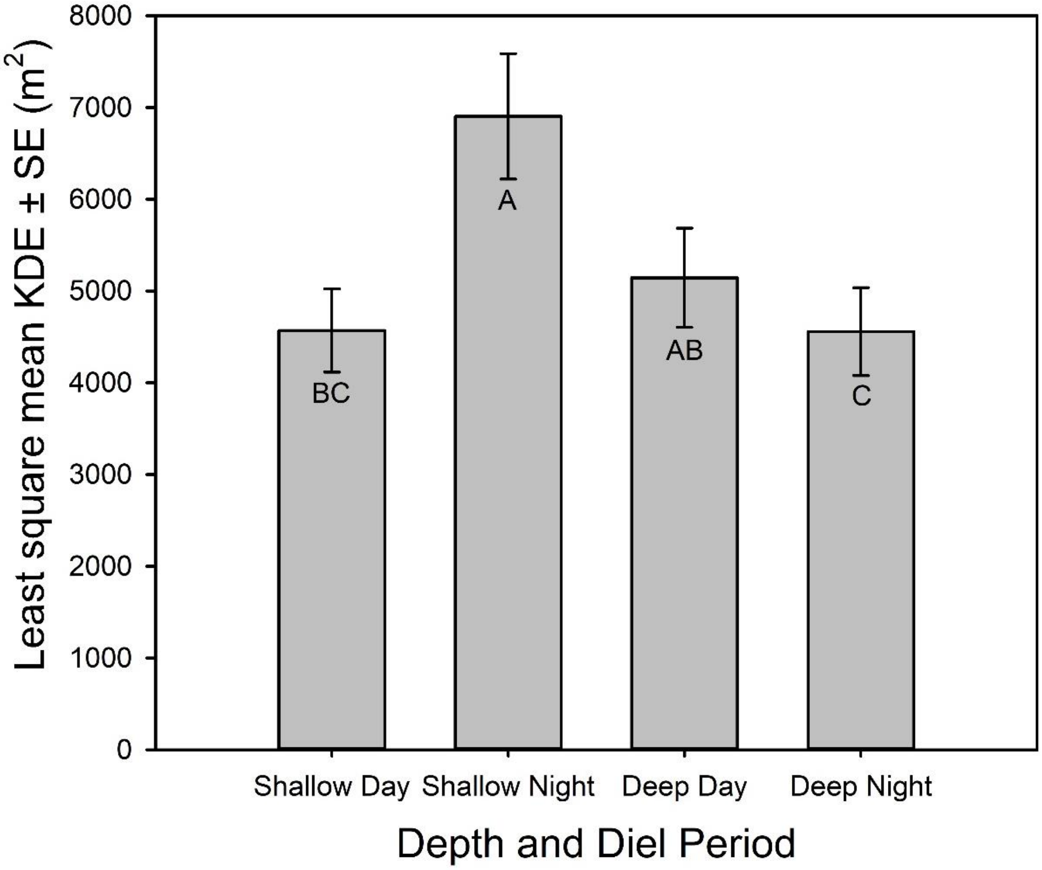

Figure 3-4. Diel period and depth effects on Red Snapper, *Lutjanus campechanus*. Least square mean 95% KDE ± SE (m^2) is displayed by depth (Shallow < 20 m; Deep > 20 m) and diel period. Different letters represent significant differences ($P \leq 0.05$).

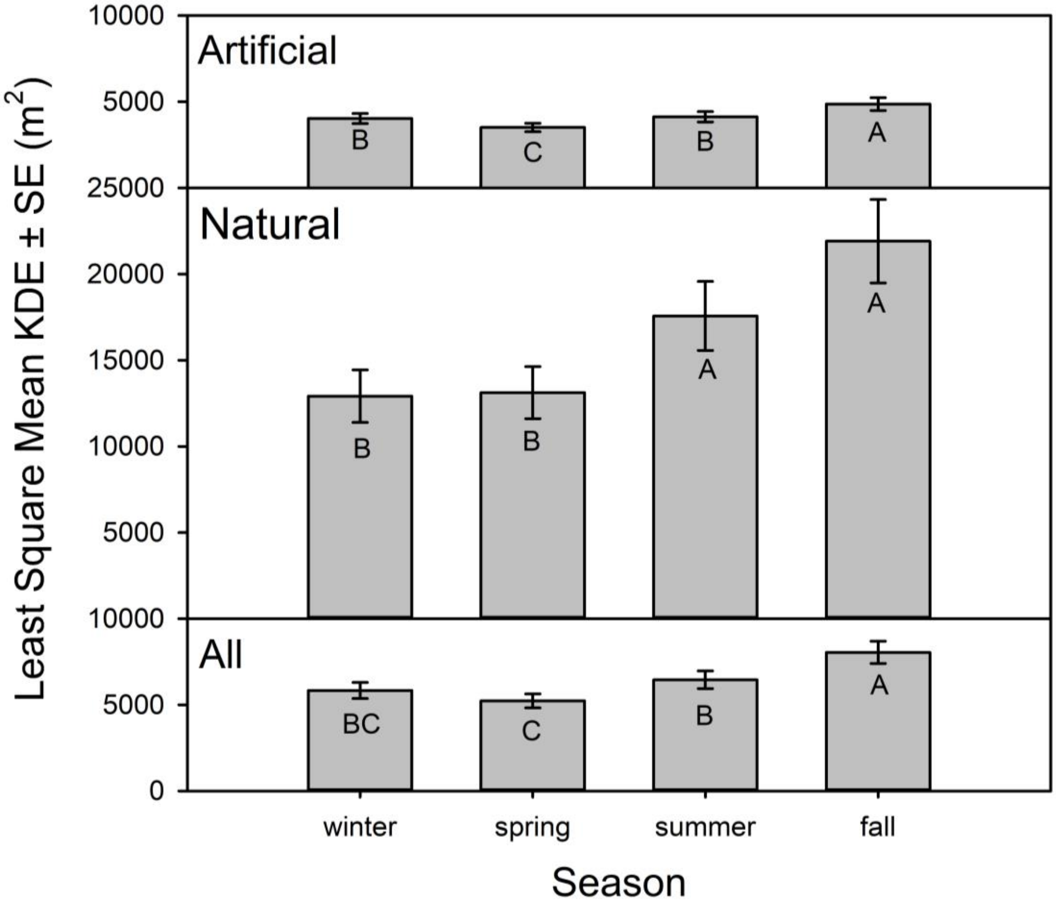

Figure 3-5. Least square mean 95% KDE ± SE (m^2) by season for artificial reefs, natural reefs and all reefs combined. Different letters represent significant differences ($P \leq 0.05$).