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ARTICLE

Development of Survey Methods to Effectively Sample Juvenile Red Snapper along the Atlantic Coast of Florida

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Abstract
Understanding of the early life history of Red Snapper *Lutjanus campechanus* throughout the U.S. Atlantic Ocean (hereafter, “Atlantic”) is limited, in part, due to the paucity of juveniles (<150 mm TL) collected in long-term fishery-independent surveys in the region. This is in sharp contrast to the Gulf of Mexico (hereafter, “Gulf”), where juvenile Red Snapper have been consistently collected in surveys. This apparent regional disparity is poorly understood. Red Snapper nursery habitats may differ between the Atlantic and the Gulf, previous Atlantic surveys may not have included important nursery habitat, or sampling gear used in the Atlantic may not be effective at collecting juveniles. A 2-year fishery-independent study was conducted along the Atlantic coast of Florida to test whether juvenile Red Snapper could be effectively sampled with two types of gear not commonly used there: a semi-balloon trawl like those used in long-term groundfish surveys in the Gulf and small-mesh Z-traps. In total, 194 Red Snapper were collected in the trawl samples and 202 Red Snapper were collected in the Z-trap samples—mostly juveniles (age 0 and age 1) captured in nearshore waters (<30 m deep). Like the Gulf, shallow coastal waters in the Atlantic likely function as nursery habitat for Red Snapper. Primarily small age-0 Red Snapper were collected during trawl sampling, which targeted unconsolidated nonreef habitats, whereas larger age-0 and age-1 and older Red Snapper were collected during trap sampling, which targeted hard-bottom reef habitats. Although this study represents the most successful sampling of juvenile Red Snapper in the Atlantic to date, further research is required to delineate the northern and southern extents of Red Snapper nursery grounds. Nevertheless, our results provide a framework for developing a fishery-independent survey that targets juvenile Red Snapper in the Atlantic to provide valuable data for quantifying recruitment and monitoring the status and recovery of this economically important species.

Time series of relative abundance or biomass are critical to the accurate assessment of managed fish stocks (Hilborn and Walters 1992). Fishery-dependent data on catch and effort can provide information on changes in abundance (NMFS Sustainable Fisheries Branch 2014, 2015; Santos et al. 2017; SEDAR 2017), but increasingly restrictive and

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complex management measures designed to reduce overfishing and rebuild overfished stocks (e.g., reduced bag or trip limits, quotas, and area or seasonal closures) have often altered fishing behavior and eroded the utility of fishery-dependent data for assessing population trends (Bryan and McCarthy 2015; Smith et al. 2015; SEDAR 2018a). A clear example is the Red Snapper *Lutjanus campechanus* stock in the U.S. Atlantic Ocean (hereafter, "Atlantic"), where harvest has largely been prohibited since 2010 due to the stock being estimated as overfished and undergoing overfishing for at least the past decade (SEDAR 2009, 2010, 2017, 2021). Accordingly, most fishery-dependent indices of relative abundance for Atlantic Red Snapper cited in recent assessments terminate in 2009, which limits their ability to support accurate assessments of potential stock recovery (NMFS Sustainable Fisheries Branch 2014; Sauls et al. 2017; SEDAR 2017, 2021).

Due to limitations in available data, significant efforts have been made to improve the availability of fishery-independent data in the Atlantic. Most notably, the long-term (1990–present) Marine Resources Monitoring, Assessment, and Prediction Program (MARMAP) and the South Atlantic (SA)-Southeast Area Monitoring and Assessment Program (SEAMAP) were augmented in 2010 by the initiation of the Southeast Fishery-Independent Survey (Ballenger and Smart 2015a, 2015b). Collectively referred to as the Southeast Reef Fish Survey (SERFS), these efforts have involved an increase in sampling extent and intensity of the long-term chevron trap survey (Collins 1990; MARMAP 2009) as well as the implementation of trap-mounted video cameras (Bacheler et al. 2013a, 2013b, 2013c, 2014; Bacheler and Smart 2016). This expanded survey has yielded valuable insight into the status and trends of Red Snapper stocks in the Atlantic, and using data from this survey, fishery-independent indices of relative abundance were constructed for the most recent Red Snapper stock assessment (SEDAR 2021).

The SERFS trap and video survey has provided valuable fishery-independent data for adult Red Snapper, but juveniles (<150 mm TL; Rindone et al. 2015)—primarily age-0 fish that are well below the size of maturity (males: 223 mm TL; females: 378 mm TL; White and Palmer 2004; Brown-Peterson et al. 2009; Lowerre-Barbieri et al. 2015)—are rarely captured or observed (Ballenger and Smart 2015a, 2015b). In fact, very few juvenile Red Snapper have ever been collected in the Atlantic during more than 30 years of fishery-independent surveys of nearshore and offshore waters using traps and trawls (i.e., SA-SEAMAP trawl survey, MARMAP trawl survey, SERFS chevron trap survey, and Northeast Fisheries Science Center trawl survey; Rindone et al. 2015). A survey capable of providing data on the abundance of early life history stages of fishes, especially postsettlement juveniles, can generate valuable indices of year-class or recruitment strength that could help in forecasting stock productivity (Smith 1993; Koenig and Coleman 1998; Coleman et al. 1999; Switzer et al. 2012) or, in some instances, could provide estimates of spawning stock biomass (Beare et al. 2005).

The paucity of information on juvenile Red Snapper in the Atlantic is perplexing, especially considering the wealth of information on juvenile Red Snapper derived from surveys in the Gulf of Mexico (hereafter, "Gulf"; Gallaway et al. 2009; Rindone et al. 2015; Switzer et al. 2015). To address this lack of information on juvenile Red Snapper in the Atlantic, we conducted a 2-year study to (1) evaluate how effective the benthic otter trawls used in the Gulf of Mexico (GM)-SEAMAP surveys and small-mesh Z-traps would be in capturing juvenile Red Snapper in the Atlantic, (2) identify nursery areas or habitats that are important for juvenile Red Snapper in this region, and (3) based on project results, assess the feasibility of using these methods in a long-term survey to provide data on juvenile Red Snapper recruitment in the Atlantic.

METHODS

Study site.— Sampling was conducted in 2015 and 2016 along the Atlantic coast of Florida between 28°N and 31°N latitude in an area of the shelf that roughly corresponds to National Marine Fisheries Service statistical reporting zones (hereafter, "zones") 722, 728, and 732 (Figure 1). This area was chosen because it represents the historical center of Red Snapper distribution in the Atlantic (SEDAR 2009; Mitchell et al. 2014) and presumably contains Red Snapper nursery habitat as well. Sampling was restricted to 10–70-m depths based on our understanding of the distribution of juvenile Red Snapper from the Gulf (Workman and Foster 1994; Gallaway et al. 1999; Switzer et al. 2015). All sampling was conducted between July and November based on the timing of peak Red Snapper spawning condition in the region (June–September; White and Palmer 2004; Brown-Peterson et al. 2009; Guenther et al. 2013; Brodie and Switzer 2015; Lowerre-Barbieri et al. 2015) and the corresponding timing of peak juvenile abundance in the Gulf (July–November; Holt and Arnold 1982; Szedlmayer and Conti 1999; Rooker et al. 2004; Switzer et al. 2015).

In the Gulf, Red Snapper typically settle on low-relief, sediment- or shell-dominated, soft-bottom habitats (Workman and Foster 1994; Szedlmayer and Howe 1997; Szedlmayer and Conti 1999; Rooker et al. 2004; Patterson et al. 2005; Lingo and Szedlmayer 2006; Piko and Szedlmayer 2007; Gallaway et al. 2009) before moving to hard-bottom reef habitats at around age 1 (Workman et al. 2002; Szedlmayer and Lee 2004; Wells et al. 2008; Gallaway et al. 2009; Cowan et al. 2010); accordingly, we sampled on both reef and nonreef habitats. Our sampling frame was developed by first gridding the entire project area into

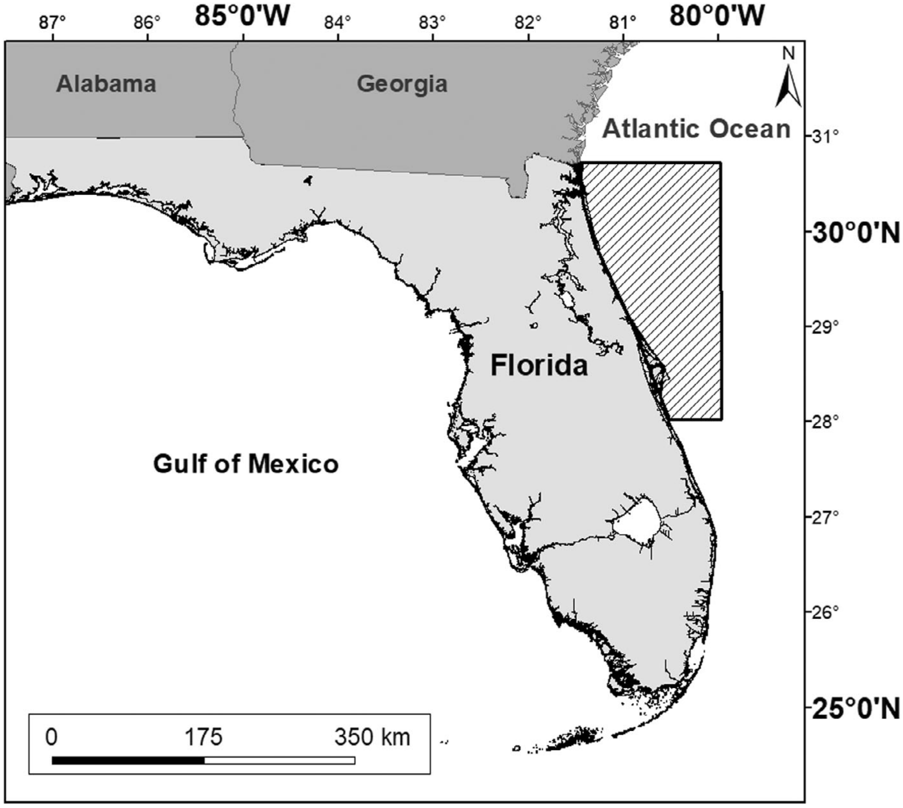

FIGURE 1. Map of the study area (diagonal solid lines) where fishery-independent trawl and trap sampling was conducted along the Atlantic coast of Florida in 2015 and 2016.

0.1852- × 0.5556-km (0.1- × 0.3-nautical mile) sampling units. This sampling frame was then intersected with all known hard-bottom reef locations compiled from databases maintained by SERFS, the State of Florida's artificial reef program, fishery-independent reef fish surveys conducted in the region by the Florida Fish and Wildlife Conservation Commission, and sites suggested by industry partners. All sampling units that intersected at least one reef site were included in the hard-bottom sampling universe; all remaining sampling units were included in the soft-bottom universe. Our intent was to sample 168 soft-bottom (trawl) and 90 hard-bottom (trap) stations during each project year based on what we anticipated could be completed given the project's logistical and funding constraints. Sites were randomly selected, and effort was proportionally allocated based on the total number of available sampling units in each of the three zones (722, 728, and 732) and two depth strata (nearshore [<30 m] and offshore [≥30 m]).

Collection and sample processing.— Standard 12.8-m GM-SEAMAP semi-balloon trawls were used to sample soft-bottom habitats because they have been shown to capture age-0–1 Red Snapper (Adriance and Sweda 2012; Pollack et al. 2012; Switzer et al. 2015) more effectively than any other trawl types that have been used in the Atlantic (Rindone et al. 2015). Each trawl had 41.4-mm cod-end mesh and was held open with two 2.4- × 1.0-m wooden doors. Bosom, wing, and corner webbing were constructed using 50.8-mm mesh (NMFS and GSMFC 2001). Trawls were not equipped with turtle exclusion or bycatch reduction devices. All trawl sampling was conducted during August and September of each year using the R/V *Georgia Bulldog* and following standard GM-SEAMAP sampling protocols, with one notable exception. In the Gulf, 24-h sampling is conducted, but the R/V *Georgia Bulldog* was incapable of 24-h operations. Accordingly, sampling was conducted during daytime hours (1 h after sunrise to 1 h before sunset) in 2015 and during evening hours (1 h after sunset to 1 h before sunrise) in 2016 in case the availability of Red Snapper to the sampling gear differed notably with time of day (though evidence from the Gulf indicates that this likely is not the case; Matheson et al. 2017). To avoid trawling over sensitive reef habitat, the vessel's echo sounder was used at each site to conduct an exploratory pass before we deployed the trawl. Once we had confirmed appropriate habitat, a 30-min trawl was pulled at approximately 4.63 km/h (2.5 knots) into prevailing surface currents. A

Eureka Manta-2 water quality datasonde was deployed after each successful trawl to measure bottom water temperature (°C).

Small-mesh, Antillean-style Z-traps were used to sample hard-bottom reef habitats following Sheaves (1992, 1995) and Flaherty-Walia et al. (2017). Each trap was constructed of 12.8-mm^2 coated-wire mesh and measured $0.6 \times 0.7 \times 1.1$ m, with two opposite-facing conical throat entrances (200 mm long × 55 mm wide). Each trap was equipped with a small bait box at the bottom of the trap and a blowout panel fastened with a magnesium release to minimize the possibility of ghost fishing in the event of trap loss. Each trap was equipped with a single-point bridle constructed of 6.35-mm galvanized-wire rope to aid in deploying and retrieving the traps. Affixed to the inside of each end of the trap was a 45.7-cm section of steel rebar that supported the bridle and served as weight for the trap. Marked surface buoys were attached to each trap via a 9.5-mm polypropylene line. All trap sampling was conducted during daylight hours with the use of chartered fishing vessels. Three to six traps (depending on the amount of hard-bottom habitat available) were deployed at least 100 m apart at each sampling station; the presence of hard-bottom habitat was verified, and its area was estimated using the onboard echosounder during an exploratory predeployment pass. Each trap was baited with three cut Atlantic Mackerel *Scomber scombrus* and was allowed to soak for at least 90 min. Bottom temperature (°C) was recorded using a HOBO U22 temperature logger affixed to the inside of at least one trap at each station.

For each gear type, geographic coordinates, depth (m), and time of day were recorded at each sampling site; for trawls, these parameters were recorded at the start and end of each tow. All Red Snapper collected were identified, counted, and measured (SL, FL, and TL; mm) before being placed on ice for processing of life history samples in the laboratory. Only TL measurements were used in data summaries and analyses.

In the laboratory, sagittal otoliths were extracted from collected Red Snapper and used for aging following Secor et al. (1991). Transverse sections (~0.4 mm) were cut at and adjacent to the core of the otolith with a Buehler Iso-Met low-speed saw equipped with four equally spaced diamond wafering blades. Otolith sections were then mounted on glass slides using a toluene-based permanent mounting medium (Shandon-Mount, Thermo Fisher Scientific) liquid coverslip. Smaller otoliths were embedded whole in two-part epoxy and mounted on card stock before they were sectioned. Otolith annual increments were counted using a stereomicroscope with either reflected or transmitted light under 8–32× magnification. Each otolith was examined at least twice, and disagreements in counts were resolved by a third examination. If a consensus could not be reached after re-examination, the otolith was rejected from age analysis (Campana 2001; Allman et al. 2005). Ages were assigned to year-classes by using a January 1 birthdate, as opposed to an actual spawning date, to clearly separate fish from different recruitment years (Lowerre-Barbieri et al. 2015).

Data analysis.— Length frequencies of Red Snapper collected during this study were summarized by gear type (trawl or trap) and year (2015 or 2016); we also summarized length frequency data for Red Snapper that were collected concurrently during SERFS chevron trap surveys (Christina Schobernd, National Oceanic and Atmospheric Administration [NOAA], Southeast Fishery-Independent Survey, personal communication) to determine the degree to which the size composition of Red Snapper in our collections overlapped with the size composition in that survey. The SERFS length frequency data represent all Red Snapper collected from 2015 (April–September) and 2016 (May–October) from Cape Hatteras, North Carolina, to St. Lucie Inlet, Florida. Length frequencies of Red Snapper collected during the current study were also plotted against estimated ages by sampling gear type (all years combined).

Estimates of CPUE were calculated as the mean (±SE) number of Red Snapper collected per trawl or trap deployed by year (2015 or 2016), zone (722, 728, or 732), and depth stratum (nearshore or offshore) and were standardized. The trawl data were modeled using a Poisson generalized linear model (GLM) with a log link; potential explanatory fixed variables included year, month, zone, depth stratum, bottom temperature (°C), and day of year (given the assumption that age-0 Red Snapper would be recruiting to the gear across the study months). The trap data were modeled using a Poisson generalized linear mixed model (GLMM) with a log link; potential explanatory fixed variables included year, month, zone, depth stratum, habitat type (natural or artificial hard bottom), bottom temperature (°C), and station, which was treated as a random effect (given that 3–6 traps were deployed per station).

Models were developed using the R package “glmmTMB” (Brooks et al. 2017) in the R statistical environment (R Core Team 2017). Explanatory variables were selected using stepwise backward selection from the fully parameterized model based on Akaike’s information criterion, with the objective of estimating year, zone, and depth stratum effects. Residuals were analyzed using probability-integral transform residuals—a simulation-based approach to create scaled residuals for fitted GLMs and GLMMs—created from the DHARMa package (Hartig 2022). This method simulated replicated data sets from the predictive distribution of the data (conditional on estimated fixed and random effects) and calculated probability-integral transform residuals from the observed and simulated values. The residuals were transformed into a uniform distribution between 0 and 1 and were evaluated through visual inspection. Parametric bootstrap resampling methods were used to characterize the uncertainty associated with each data set, where each model was fit to 1,000 bootstrapped data sets to produce estimates of the SE and the coefficient of variation.

To identify potential ontogenetic changes in habitat preference for juvenile Red Snapper in the Atlantic, we compared depth (m) and temperature (°C) among sites from which Red Snapper were absent (zero catches) to sites at which specific age-classes of Red Snapper were collected for all years combined. Median and mean values, interquartile ranges, and the 10th and 90th percentiles were calculated for each category (i.e., zero catches, age 0, age 1, and age 2 and older [age 2+]). Trawl depth is presented as the average depth (m) of each trawl tow and was calculated as (start depth + end depth)/2. Due to small sample sizes, all age-2+ Red Snapper were combined into a single age-class.

RESULTS

Trawl Sampling

In total, 196 trawl samples were completed during August and September of each year of the study: 93 samples in 2015 and 103 samples in 2016 (Figure 2a; Table 1). Red Snapper were encountered in 33 of the 196 trawls deployed during this project (16.8% occurrence). The number of Red Snapper collected ranged from 1 to 43 fish/set. All Red Snapper collected in 2015 trawls ($n = 83$) were collected in the nearshore (<30-m) depth stratum, with the majority ($n = 63$; 76%) collected in zone 728. In total, 111 Red Snapper were collected during trawl sampling in 2016; 102 were collected in the nearshore (<30-m) depth stratum and 9 were collected in the offshore (≥30-m) stratum. The majority ($n = 80$; 72%) of Red Snapper from 2016 trawls were collected in zone 728, and all individuals collected in the offshore stratum were collected in zone 732.

Trap Sampling

We sampled a total of 159 trap stations (86 in 2015, 73 in 2016) during the 2-year study, resulting in 697 individual trap deployments (Figure 2b; Table 1). Red Snapper were encountered in 70 of the 697 traps deployed during this project (10.0% occurrence). The number collected ranged from 1 to 16 fish/trap deployment. In total, 111 Red Snapper were collected in 401 trap deployments from July through October 2015, with the majority ($n = 63$; 57%) collected in zone 732. Of the 111 individuals collected in the 2015 trap sampling, 100 were collected in the nearshore (<30-m) depth stratum and 11 were collected in the offshore (≥30-m) stratum. Ten of the 11 Red Snapper collected during 2015 in the offshore stratum came from zone 732. Overall, 91 Red Snapper were collected in 296 trap deployments from September through November 2016, with the majority ($n = 50$; 55%) collected in zone 732. Of the 91 individuals collected in the 2016 trap sampling, 72 were collected in the nearshore (<30-m) depth stratum: 5 fish from zone 722, 32 fish from zone 728, and 35 fish from zone 732. Fifteen of the 19 Red Snapper collected in the offshore stratum during 2016 came from zone 732.

Catch per Unit Effort

The Poisson GLM and the Poisson GLMM both converged, and the explanatory fixed variables year, zone, and depth stratum were retained based on Akaike's information criterion through stepwise backward selection. Visual inspection of the probability-integral transform residuals indicated reasonable fits for both models as median values were largely centered around 0.5 for each variable. Lastly, fits to the bootstrapped data sets for both models experienced 100% convergence.

For trawls, the standardized CPUE (number of Red Snapper per set) estimates were highest in the nearshore depth stratum for both sampling years and were found to increase in trend between sampling years (Figure 3; Table 2). This was supported by an ANOVA performed on the Poisson GLM, which indicated significant effects of both year and depth stratum (Table 3). It is worth noting, however, that due to the lower sample sizes within each year, zone, and depth stratum of the trawl data, the associated SE and coefficient of variation values were more elevated (Table 2).

For traps, the standardized CPUE estimates were also highest in the nearshore depth stratum during both sampling years (Figure 3; Table 4). The CPUE estimates were low in the offshore stratum of zones 722 and 728, whereas they were notably higher in zone 732. Moreover, the estimated CPUE for the nearshore stratum within zone 732 was also higher compared to the other two zones. An ANOVA performed on the Poisson GLMM further supported these results as the fixed effects of zone and depth stratum were found to be significant (Table 5).

Length and Age

The size composition of Red Snapper differed markedly between trawl and trap samples; smaller fish were collected with trawls (Figure 4). The mean size ± SD of Red Snapper collected in trawls (all years combined; $n = 191$) was 94.7 ± 48.0 mm TL, with a range of 36–406 mm. Red Snapper collected in the traps (all years combined; $n = 202$) were larger than those in trawls and had a mean size of 299.0 ± 62.5 mm TL, with a range of 156–499 mm.

Of the 191 Red Snapper that were collected in trawls and aged, 180 (94.2%) were age 0 (Swanson 2017) and

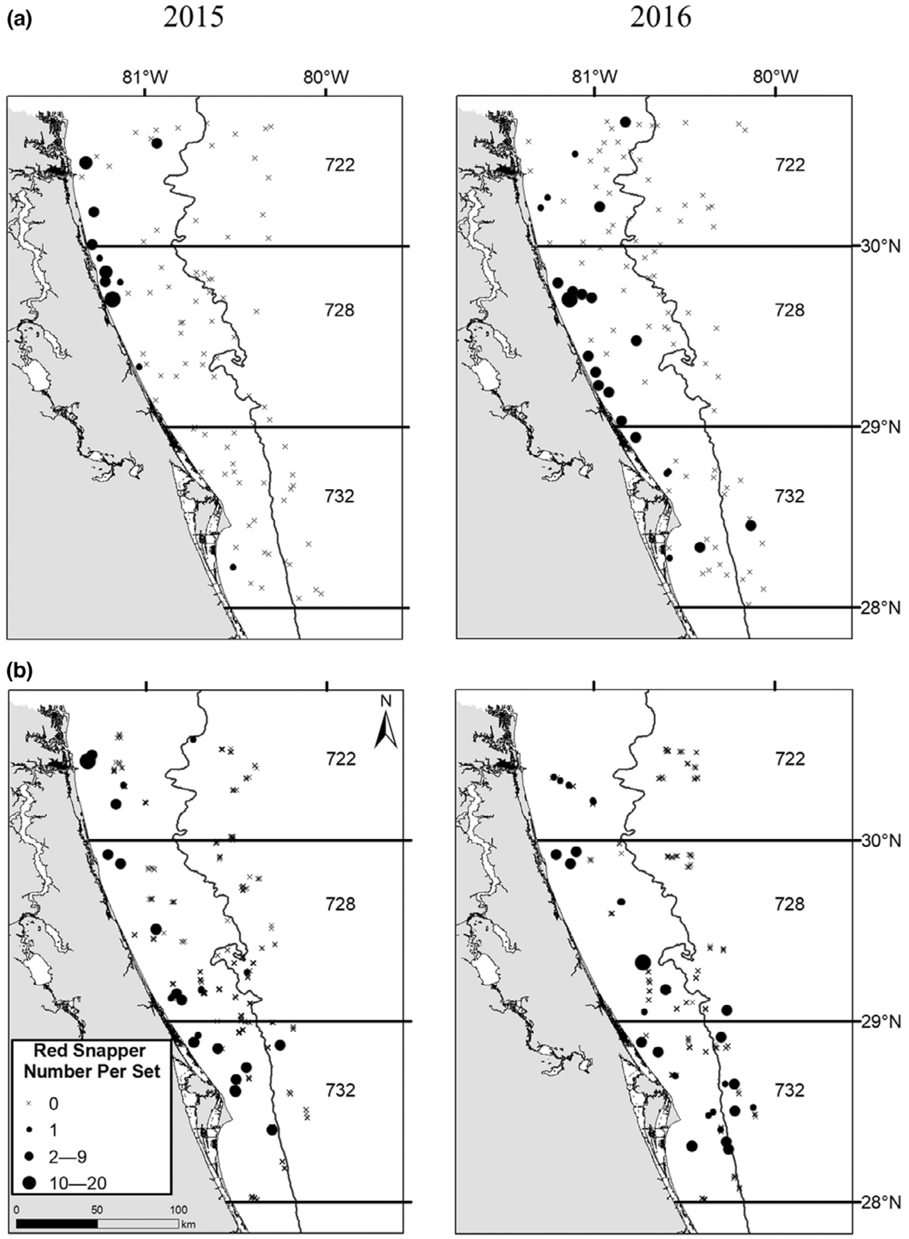

FIGURE 2. Bubble plots showing the locations of Red Snapper collected during **(a)** trawl sampling and **(b)** trap sampling along the Atlantic coast of Florida within National Marine Fisheries Service statistical reporting zones 722, 728, and 732 by year (2015 [left panels] and 2016 [right panels]). The size of each circle corresponds to the number of Red Snapper collected at each site as indicated in the legend (× = sample locations where no Red Snapper were collected). The solid black bathymetry line represents the 30-m isobath.

ranged in size from 36 to 134 mm TL (Figures 5 and 6). Eleven age-1 Red Snapper, all collected in 2016 trawl sampling, ranged in size from 204 to 406 mm TL. Among the 202 Red Snapper that were collected in traps and aged, fish ranged from age 0 to age 4, with the greatest proportion at age 1 in 2015 and 2016 (Figure 5). The median size of Red Snapper collected in traps was variable and increased with age (Figure 6).

Age-0 Red Snapper collected in trawls were smaller than those collected in traps (Figure 6). The median size of age-0 Red Snapper collected in traps ($n = 5$) was 162.0 mm TL, with a range of 156–205 mm. The median size of age-0 Red Snapper collected in trawls ($n = 180$) was 87.0 mm TL, with a range of 36–134 mm.

Habitat Association

Trawl sampling was conducted in water that was 10.1–60.6 m deep and that ranged in temperature from 17.6 to 29.2°C (Figure 7). Age-0 Red Snapper collected in trawls ($n = 180$; 36–134 mm TL) were predominantly found in

TABLE 1. Number of Red Snapper collected in each National Marine Fisheries Service statistical reporting zone (Zone) and depth stratum (nearshore [<30 m] and offshore [≥30 m]) during trawl and trap sampling along the Atlantic coast of Florida by year (2015 and 2016). Numbers in parentheses represent the total number of trawls or traps deployed in each zone for that year and depth stratum.

		Zone 722		Zone 728		Zone 732		
Gear type	Year	Nearshore	Offshore	Nearshore	Offshore	Nearshore	Offshore	Total
Trawl	2015	19 (16)	0 (9)	63 (36)	0 (3)	1 (18)	0 (11)	83 (93)
	2016	8 (26)	0 (16)	80 (26)	0 (8)	14 (17)	9 (10)	111 (103)
	Total	27 (42)	0 (25)	143 (62)	0 (11)	15 (35)	9 (21)	194 (196)
Trap	2015	23 (52)	1 (38)	24 (142)	0 (49)	53 (86)	10 (34)	111 (401)
	2016	5 (21)	0 (39)	32 (81)	4 (34)	35 (87)	15 (34)	91 (296)
	Total	28 (73)	1 (77)	56 (223)	4 (83)	88 (173)	25 (68)	202 (697)

shallow-water habitats (11.8–27.2 m) with generally higher water temperatures (22.1–29.2°C). Age-1 Red Snapper ($n = 11$) were collected during only three trawl sets, with water depth ranging from 18.1 to 48.3 m. Age-0 and age-1 fish were never collected in the same trawl sample.

Trap sampling was conducted in water that was 11.0–56.0 m deep and that ranged in temperature from 17.6°C to 29.2°C. Age-0 Red Snapper collected in traps ($n = 5$; 156–205 mm TL) were collected in water from 19.0 to 27.0 m deep, with water temperatures from 24.3°C to 26.7°C. Age-1 and age-2+ Red Snapper were collected in similar water depths from 14.0 to 51.0 m. Age-1 Red Snapper were collected in water temperatures from 23.8°C to 28.7°C, and age-2+ fish were collected in water temperatures from 19.3°C to 28.8°C. Different age-classes of Red Snapper were often collected in the same trap sample.

DISCUSSION

During this 2-year pilot study, nearly twice as many Red Snapper (<150 mm TL) were captured in the Atlantic than had been captured during the 44 years of combined survey efforts through 2011. Our results demonstrated that both types of gear tested were able to effectively capture juvenile Red Snapper. The trawl used in this project collected primarily small age-0 Red Snapper over unconsolidated nonreef habitats, providing data on a size range that is absent from ongoing surveys conducted by SERFS (Figure 4). In contrast, large age-0 and age-1+ Red Snapper were captured over hard-bottom reef habitats in the small-mesh Z-traps.

Although this study was conducted within the historical center of distribution of Red Snapper in the Atlantic (SEDAR 2009; Mitchell et al. 2014), observed densities of juveniles collected in the trawl samples were well below those typically observed in the Gulf (Adriance and Sweda 2012; Pollack et al. 2012; Switzer et al. 2015), where tens of thousands of juveniles have historically been collected (Rindone et al. 2015; Switzer et al. 2015; SEDAR 2018b). The difference in juvenile densities between the Gulf and the Atlantic is striking and could be at least partly attributable to differences in the overall abundance of Red Snapper populations within the two regions. The most recent abundance estimate for the Gulf (256,277,000 fish; SEDAR 2018b) is over two orders of magnitude greater than the estimate for the Atlantic (2,070,500 fish; SEDAR 2021), so it is reasonable to conclude that recruitment and juvenile abundance would also be greater in the Gulf. Additionally, juvenile Red Snapper may be more widely distributed in the Atlantic or they may occupy subtly different nursery habitats that are less conducive to trawl sampling than those found in the Gulf. In the Gulf commercial shrimp fishery, Red Snapper are a regular component of the trawl bycatch, which is estimated to include millions of juveniles annually, but they have not been documented as bycatch in the Atlantic shrimp fishery (Scott-Denton et al. 2012; Rindone et al. 2015; SEDAR 2018b). Other physiographic differences between the regions, such as the slope and width of the continental shelf, composition of the benthic substrates, freshwater and nutrient inputs, and the strength and stability of prevailing ocean currents, are likely also important, although investigating such processes would require that studies be conducted across much broader temporal and spatial scales than were examined in the present study.

It is not entirely clear why this study was more successful than historical surveys at capturing Red Snapper smaller than 150 mm TL; the greater success may have been due to our use of a more effective type of sampling gear than had been used previously, or our study area may have better encompassed the spatial extent of juvenile Red Snapper habitat in the Atlantic relative to the study areas in earlier work. The present study used a GM-SEAMAP trawl (single 12.8-m semi-balloon trawl) rather than the SA-SEAMAP trawl (paired 22.9-m, mongoose-type Falcon trawls) that had been used in previous Atlantic studies. The Falcon trawl is nearly twice as wide as the semi-balloon trawl used in this study, but the meshes

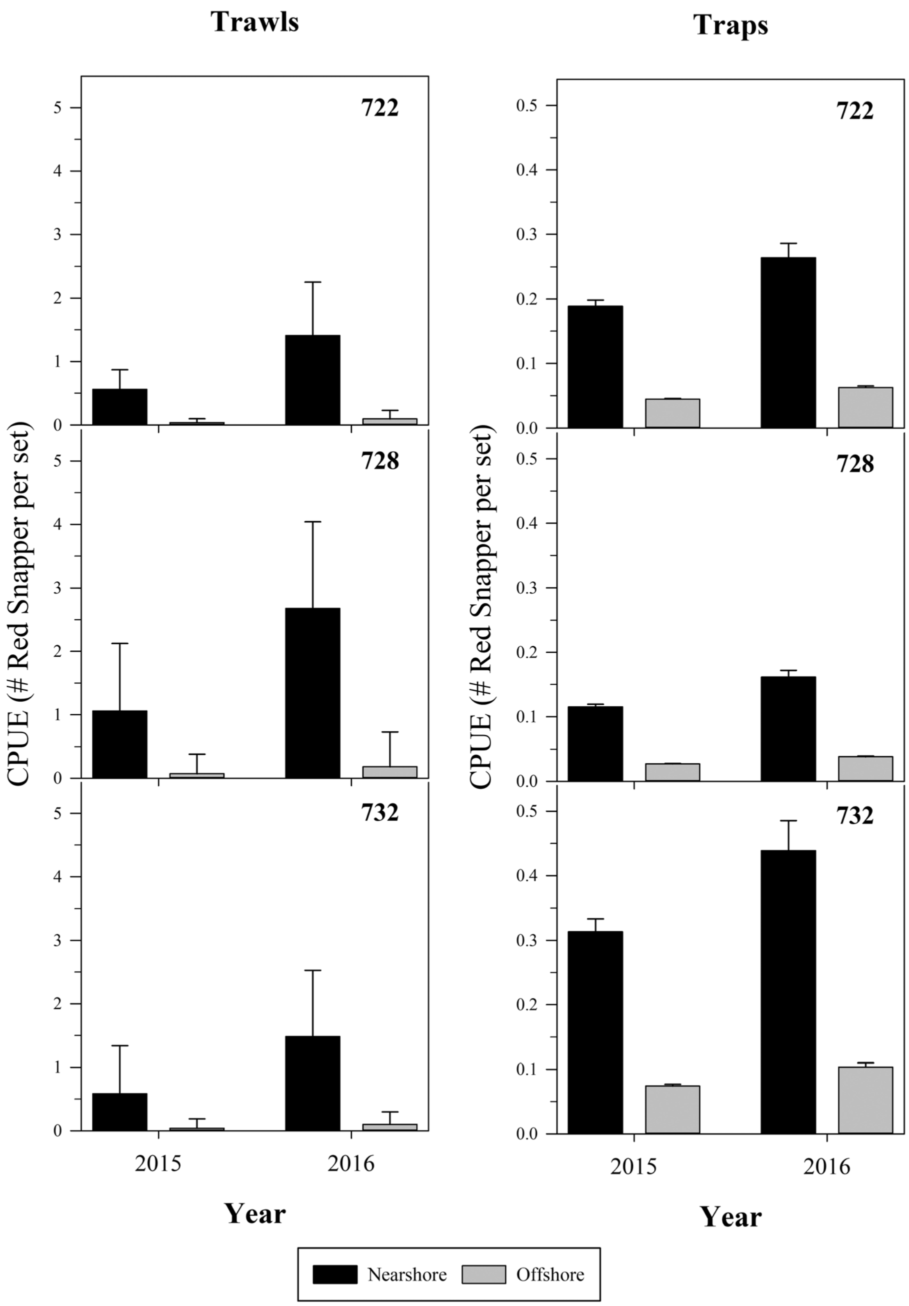

FIGURE 3. Standardized CPUE estimates (±SE) of Red Snapper collected during trawl and trap sampling along the Atlantic coast of Florida by National Marine Fisheries Service statistical reporting zone (722, 728, and 732), depth stratum (nearshore [<30 m] and offshore [≥30 m]), and year.

making up the trawl body (Falcon: 47.6 mm; semi-balloon: 50.8 mm) and the cod end (Falcon: 41.3 mm; semi-balloon: 41.4 mm) are similar in both. Both trawls appear to be well suited to capturing fish less than 150 mm TL, as was documented by Matheson et al. (2017) for the Gulf and by Rindone et al. (2015) for the Atlantic.

Despite apparently similar gear selectivity of the two trawls, SA-SEAMAP collected only five juvenile Red Snapper smaller than 150 mm TL in the 1989–2011 surveys (Rindone et al. 2015) and only three during the years in which the present study was conducted (2015: $n = 1$; 2016: $n = 2$; Jeanne Boylan, South Carolina Department of Natural Resources, personal communication). All of those juveniles were collected during October in the shallow waters off North Carolina and South Carolina, whereas none was collected off the east coast of Florida. Differences in the number of juvenile Red Snapper collected in the present study and the SA-SEAMAP trawl

TABLE 2. Standardized CPUE (number of fish per set) of Red Snapper collected during trawl sampling along the Atlantic coast of Florida by year, National Marine Fisheries Service statistical reporting zone (722, 728, and 732), and depth stratum (nearshore [<30 m] and offshore [≥30 m]). *N* represents the number of trawls deployed.

Year	Zone	Depth stratum	*N*	CPUE	SE	CV
2015	722	Nearshore	16	0.5566	0.3105	0.5578
	722	Offshore	9	0.0379	0.0621	1.6370
	728	Nearshore	36	1.0574	1.0669	1.0090
	728	Offshore	3	0.0720	0.3099	4.3020
	732	Nearshore	18	0.5854	0.7518	1.2842
	732	Offshore	11	0.0399	0.1468	3.6804
2016	722	Nearshore	26	1.4097	0.8400	0.5959
	722	Offshore	16	0.0960	0.1298	1.3514
	728	Nearshore	26	2.6781	1.3601	0.5079
	728	Offshore	8	0.1825	0.5447	2.9851
	732	Nearshore	17	1.4826	1.0436	0.7039
	732	Offshore	10	0.1010	0.1953	1.9332

TABLE 3. Analysis of variance results for the fixed effects within the Poisson generalized linear model for trawls using the Wald chi-square test. *P* is the probability of a greater chi-square value. Asterisks (*) denote significant values ($P < 0.05$).

Variable	Chi-square	df	*P*
Year	6.11	1	0.0134*
Zone	3.1099	2	0.2112
Depth stratum	6.9653	1	0.0083*

TABLE 4. Standardized CPUE (number of fish per set) of Red Snapper collected during trap sampling along the Atlantic coast of Florida by year, National Marine Fisheries Service statistical reporting zone (722, 728, and 732), and depth stratum (nearshore [<30 m] and offshore [≥30 m]). *N* represents the number of traps deployed.

Year	Zone	Depth stratum	*N*	CPUE	SE	CV
2015	722	Nearshore	52	0.1887	0.0097	0.0512
	722	Offshore	38	0.0445	0.0010	0.0232
	728	Nearshore	137	0.1154	0.0040	0.0347
	728	Offshore	49	0.0272	0.0005	0.0183
	732	Nearshore	86	0.3133	0.0200	0.0639
	732	Offshore	28	0.0740	0.0026	0.0351
2016	722	Nearshore	21	0.2642	0.0217	0.0820
	722	Offshore	22	0.0624	0.0025	0.0393
	728	Nearshore	77	0.1616	0.0103	0.0639
	728	Offshore	38	0.0382	0.0013	0.0337
	732	Nearshore	78	0.4388	0.0466	0.1063
	732	Offshore	43	0.1036	0.0061	0.0589

TABLE 5. Analysis of variance results for the fixed effects within the Poisson generalized linear mixed model for traps using the Wald chi-square test. *P* is the probability of a greater chi-square value. Asterisks (*) denote significant values ($P < 0.05$).

Variable	Chi-square	df	*P*
Year	0.8626	1	0.3530
Zone	6.1955	2	0.0452*
Depth stratum	9.6291	1	0.0019*

survey are therefore likely attributable to the depths and seasons of sampling. Trawl sampling during the present study was conducted in August and September of each year in depths from 10 to 70 m, which is beyond the 4.6–9.1-m depths of the historical SA-SEAMAP trawling surveys conducted annually during the spring, summer, and fall (Rindone et al. 2015). The SA-SEAMAP survey has sampled in water as deep as 19 m (1990–1999), but this deeper sampling was limited and done only off the east coast of Florida from early April to mid-May (ASMFC 2000), well before the expected settlement of age-0 Red Snapper inferred from the timing of peak mature Red Snapper spawning condition in the region (June–September; White and Palmer 2004; Brown-Peterson et al. 2009; Lowerre-Barbieri et al. 2015). Furthermore, recent estimates of Atlantic Red Snapper hatching date frequencies support that spawning occurs in May–August, with unimodal peak activity in June (Swanson 2017). Because we did not directly compare the two types of trawls or overlap our sampling depths and sampling period with the depths and period sampled by the SA-SEAMAP surveys, it is unclear whether the lack of juvenile Red Snapper in historical surveys is the result of gear selectivity, low sample size, or spatial and temporal sampling efforts. This should be investigated in future studies.

In the Atlantic, habitat preferences of juvenile Red Snapper appear to change with ontogeny in a manner similar to that documented in the Gulf. Settlement and recruitment of age-0 Red Snapper in the Gulf take place primarily in water between 18 and 55 m deep on nonreef habitats, such as mud, sand, relict shell–ridge habitat, and, to a lesser extent, low-relief microhabitats consisting of sponges, rubble patches, and debris (Workman and Foster 1994; Szedlmayer and Howe 1997; Szedlmayer and Conti 1999; Rooker et al. 2004; Patterson et al. 2005; Lingo and Szedlmayer 2006; Piko and Szedlmayer 2007; Wells et al. 2008; Gallaway et al. 2009). Late age-0 and age-1 individuals transition to high-relief reef habitats (Workman et al. 2002; Szedlmayer and Lee 2004; Wells et al. 2008; Gallaway et al. 2009; Cowan et al. 2010). Results from this study appear to corroborate the Gulf results; small age-0 Red Snapper (<150 mm TL) were collected

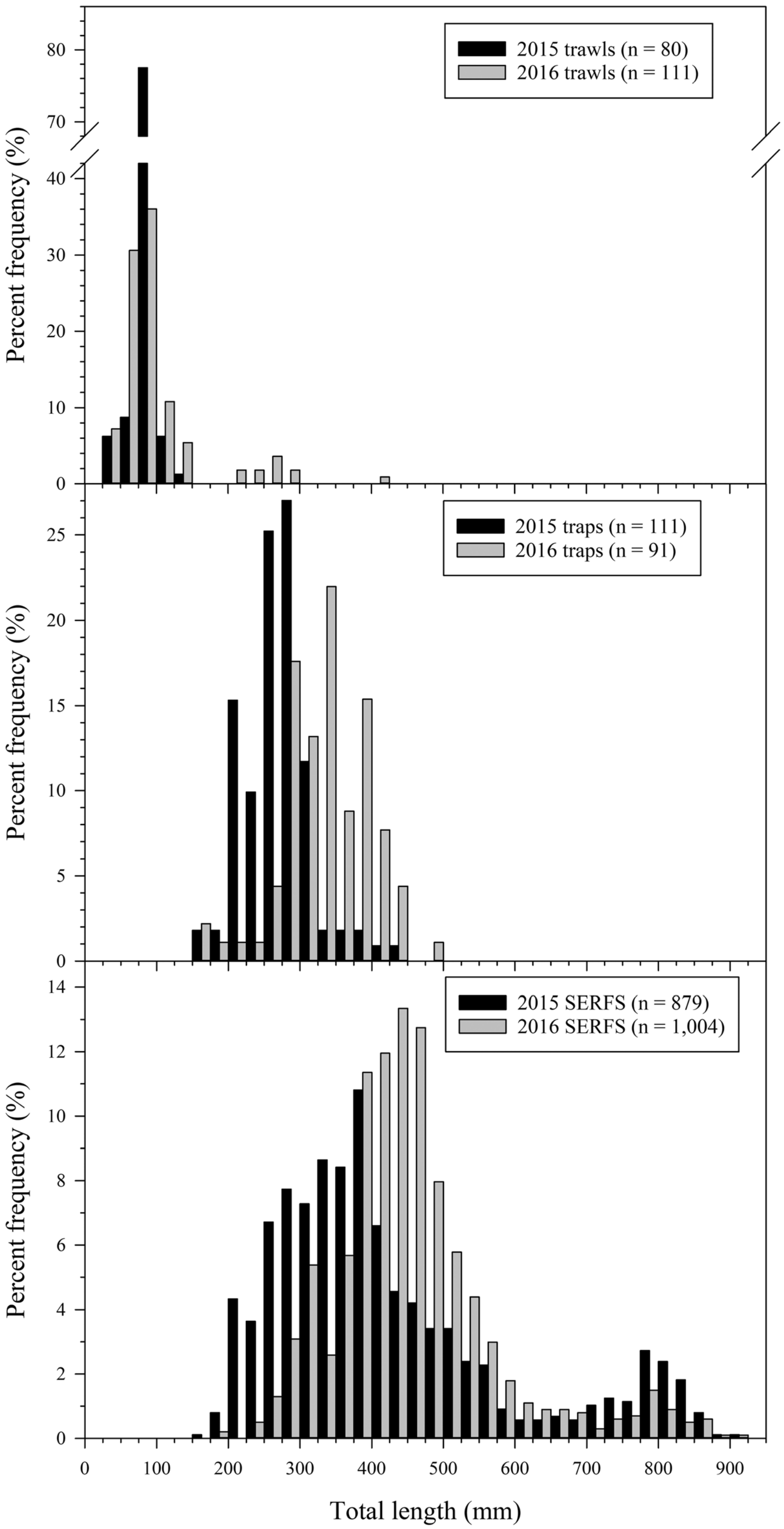

FIGURE 4. Length frequency (TL, mm) of Red Snapper collected during trawl (top panel) and trap (middle panel) sampling along the Atlantic coast of Florida and Southeast Reef Fish Survey (SERFS) chevron trap (Schobernd, personal communication) surveys along the southeastern USA (bottom panel) during 2015 and 2016. Total number (*n*) of Red Snapper collected during each study year is shown in parentheses.

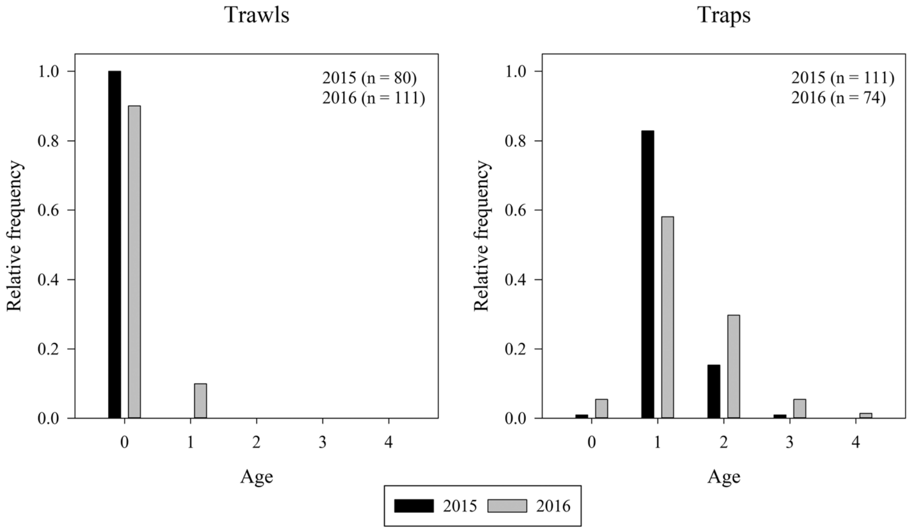

FIGURE 5. Age (years) frequency of Red Snapper collected during trawl and trap sampling along the Atlantic coast of Florida by study year. Total number (*n*) of Red Snapper included from each study year is shown in parentheses.

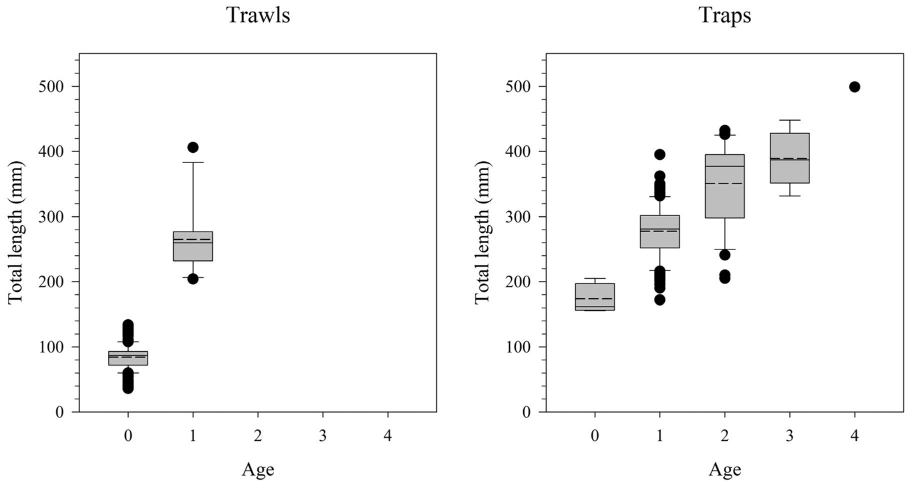

FIGURE 6. Size (TL, mm) at age (years) of Red Snapper collected during trawl and trap sampling along the Atlantic coast of Florida (2015 and 2016 sample years combined). Boxes represent the interquartile range; solid horizontal lines are the median values; dashed horizontal lines are the mean values; and whiskers represent the 10th and 90th percentiles.

primarily during trawl sampling conducted on nonreef habitats, whereas late age-0 and age-1+ Red Snapper were collected primarily during trap sampling on reef habitats. Although there was some indication of size differences between age-0 Red Snapper collected in trawls and those collected in traps (i.e., larger age-0 individuals in traps), it is unclear whether the differences are due to the size selectivity of each sampling gear or a temporal effect of capture date, as trawl sampling and trap sampling were conducted independently of each other within each annual project sampling period (July–November). No Red Snapper less than 150 mm TL were collected in traps during this project, even though the small-mesh Z-traps used have been shown to retain fish much smaller than that size (Flaherty-Walia et al. 2017). Fine-scale habitat characterization was beyond the scope of this study, so it cannot be determined whether the lack of small Red Snapper (<150 mm TL) captured in association with reef habitats was due to subtle differences in habitat selection through ontogeny or to competitive exclusion by larger Red Snapper (Bailey et al. 2001; Syc and Szedlmayer 2012; Jaxion-Harm and Szedlmayer 2015). Thus, future studies should incorporate detailed habitat characterization (e.g., benthic grabs, video habitat analyses, and habitat mapping) to

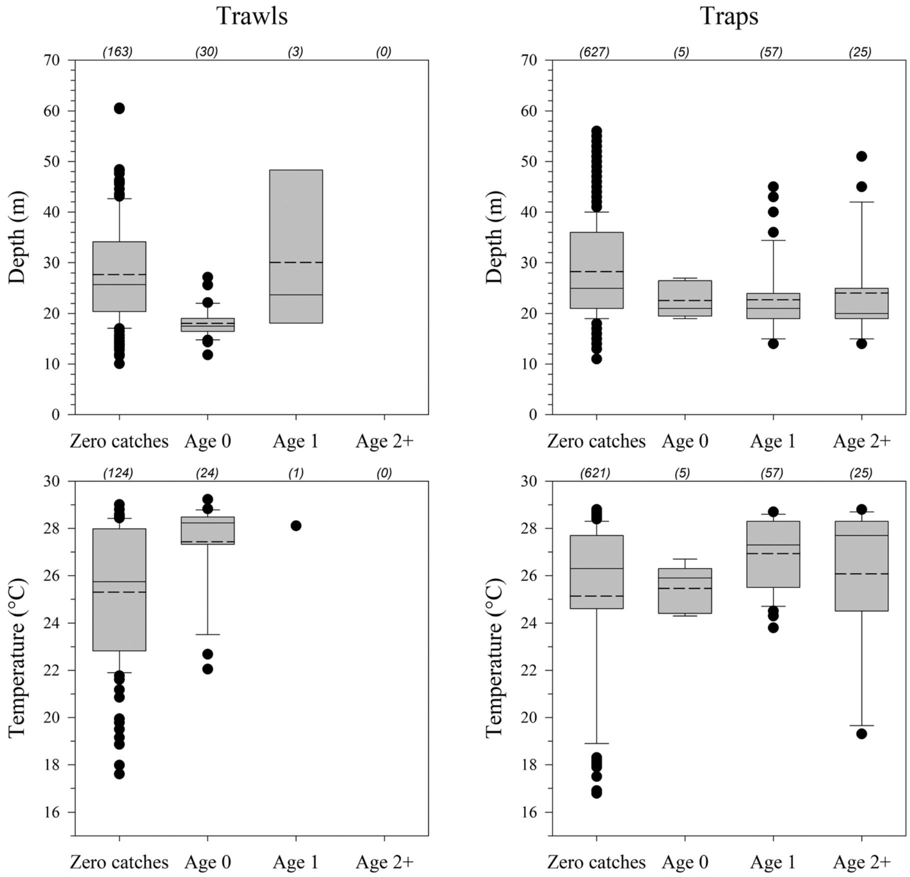

FIGURE 7. Depth (m) and temperature (°C) of sites sampled during trawl and trap sampling along the Atlantic coast of Florida (2015 and 2016 sample years combined) by Red Snapper age-class (age 0, 1, and 2+ [2 and older]). Zero catches represent sites where no Red Snapper were collected. Boxes represent the interquartile range; solid horizontal lines are the median values; dashed horizontal lines are the mean values; and whiskers represent the 10th and 90th percentiles. Italicized numbers in parentheses above each plot represent the number of observations for each category.

better quantify microhabitat selection of juvenile Red Snapper in the Atlantic.

Interestingly, the trawl used during this study captured very few individuals that were age 1 or older. Although age-0 Red Snapper make up the majority of the Red Snapper catch in the fall GM-SEAMAP surveys, age-1+ individuals are routinely collected during the summer GM-SEAMAP surveys (Switzer et al. 2015). Overall, only 11 age-1 Red Snapper were collected in our Atlantic trawl sampling, with all of them captured in three trawls during 2016. The small number of age-1 individuals collected in our trawl sampling may be the result of the project's limited temporal sampling period each year (August–September). As such, expanded trawl sampling over a longer time frame should be conducted to better understand the size and age selectivity of juvenile Red Snapper by this sampling gear over the entire recruitment period. Alternatively, the collection of age-1 fish in our trawl sampling may have been a result of trawls that either encountered or came close to reef habitats. Since trawl sampling in 2016 was conducted at night (as opposed to the daytime sampling conducted in 2015), these individuals may have been less able to detect or avoid the trawl, or they may have been captured during nighttime off-reef foraging (Gallaway et al. 1981; Szedlmayer and Lee 2004; Peabody and Wilson 2006). In the Gulf, aggressive conspecific behavior is thought to influence the timing and degree of ontogenetic habitat transitions (i.e., from low to high relief) of juvenile Red Snapper (Bailey et al. 2001; Workman et al. 2002; Szedlmayer and Lee 2004; Piko and Szedlmayer 2007; Mudrak and Szedlmayer 2012), likely in response to competition for food or habitat resources that would displace smaller, younger fish from their preferred habitat. Ultimately, population recovery may result in higher densities of Red Snapper on reef habitats and concomitant shifts in habitat selection of smaller individuals, although multiyear survey efforts over a longer temporal sampling period, along with fine-scale habitat utilization studies of juvenile Red Snapper, would be required to fully test this hypothesis.

Surveys that accurately estimate interannual variability in juvenile recruitment are especially valuable to the assessment and management of fisheries stocks when they are capable of forecasting future fisheries production. In the Gulf, Red Snapper stock assessment models have generally fit the GM-SEAMAP trawl indices poorly (SEDAR 2018b), indicating that data from surveys of juvenile (age-0 and age-1) Red Snapper provide limited information on subsequent year-class strength. It is possible that in the north-central Gulf, where age-0 and age-1 Red Snapper densities are high (Switzer et al. 2015), density-dependent mortality is sufficient to decouple the relationship between recruitment and subsequent success of a particular age-class (Gazey et al. 2008; Gallaway et al. 2017). However, results from recent survey efforts along the Gulf coast of Florida indicate that strong age-0 and age-1 Red Snapper recruitment, as identified through trawl survey efforts (Pollack and Hanisko 2022), is reflected in fishery-independent surveys of larger individuals associated with reef habitats (Thompson et al. 2022). Given the relatively low densities of Red Snapper observed in the current study, and if that holds true for the entire range of Red Snapper in the Atlantic, it is possible that age-0 and age-1 recruitment may be a much better predictor of Red Snapper year-class strength in the Atlantic than it has been historically in the Gulf, although a lengthy time series (5–10 years) of juvenile recruitment data would be necessary to effectively test this hypothesis.

The small-mesh trap used in this study was effective at capturing a broad size range (156–499 mm TL) and age range (age 0–4) of Red Snapper, but age-1 Red Snapper accounted for the greatest proportion of the trap catch. Natural mortality among age-0 individuals has typically been estimated to be very high in both the Gulf and Atlantic Red Snapper assessments (SEDAR 2017, 2018b); therefore, age-1 fish may represent a better index of subsequent recruitment and may provide a better estimate of the contribution made by different year-classes to the fishery. The Red Snapper captured in the small-mesh trap sampling during this project did overlap in size with those captured in surveys conducted by SERFS during the same years (Figure 4), although the SERFS chevron trap survey also collected larger fish. Accordingly, the Antillean-style Z-traps utilized in this study may be duplicative and provide less information on Red Snapper than the currently used SERFS chevron traps, although a more thorough comparison of size selectivity between the two trap gears would be necessary to determine the size at which Red Snapper become fully available to each respective gear.

Although this study has demonstrated potential sampling gear that could be utilized in a fishery-independent survey for collecting data on the relative abundance of juvenile Red Snapper in the Atlantic, incorporating these efforts into a broadscale survey designed to characterize the interannual variability in recruitment strength of Red Snapper will require additional considerations. Most notably, survey efforts should encompass the entirety of possible Red Snapper nursery habitat in the Atlantic. To maximize the likelihood of success, our study focused efforts along the Florida shelf, where adult Red Snapper densities historically have been highest and where spawning activity has been observed (Moe 1963; White and Palmer 2004; Lowerre-Barbieri et al. 2015; SEDAR 2017). However, if Red Snapper are found to exhibit hyperstability (i.e., catch rates remain high even as the population declines), interannual fluctuations in recruitment strength within the historical center of distribution (SEDAR 2009; Mitchell et al. 2014) may not accurately represent population-level trends throughout their full range (Hilborn and Walters 1992; Wilberg et al. 2010). However, more research would be necessary to determine whether this is the case for the trawls and traps used during this study.

As Red Snapper populations have continued to rebuild, not only has overall abundance increased, but an increasing proportion of the population has been found in offshore waters off Georgia and the Carolinas (Ballenger and Smart 2015a, 2015b). Analyses of otolith microchemistry indicate that there are multiple nursery sources for Atlantic Red Snapper, although individuals tend to move northward as they age, indicating that nursery areas off northeast Florida may contribute strongly to populations at higher latitudes (Barnett et al. 2016). In addition, simulations of the transport and settlement of Red Snapper larvae in the Atlantic indicate that settlement can also occur as far south as West Palm Beach (Mandy Karnauskas, NOAA, Southeast Fisheries Science Center, personal communication), although important questions remain as to what percentage of these larvae originates from the Gulf or the Atlantic (Portnoy et al. 2022). Therefore, we recommend that any efforts to implement a survey of juvenile Red Snapper in the Atlantic should include waters to the north and south of our study area, at least until the value of these areas as nursery habitat has been fully assessed. Similar consideration should be given to the depth range of future sampling efforts. In the present study, age-0 Red Snapper were rarely collected in waters deeper than 30 m, although larvae apparently can settle in waters much deeper (Karnauskas, personal communication). Individuals settling in deeper waters may exhibit much higher rates of mortality and therefore may not contribute appreciably to recruitment strength; if so, sampling efficiency could be improved by restricting sampling effort to sites shallower than 30 m. It is impossible to determine at present whether the general lack of juvenile Red Snapper in deeper waters is consistent throughout the remainder of the Atlantic, although this is not the case in the northern Gulf (Gallaway et al. 1999; Switzer et al. 2015).

Our results provide a foundation for a fishery-independent survey targeting juvenile Red Snapper (<150 mm TL) in the Atlantic. Given the ongoing limited availability of data for monitoring the status and recovery of this economically important species in the Atlantic, we contend that such efforts warrant strong consideration.

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