Distribution and Age Composition of Red Snapper across the Inner Continental Shelf of the North-Central Gulf of Mexico

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Abstract

The Red Snapper *Lutjanus campechanus* is an economically and ecologically important species in the northern Gulf of Mexico, where it often dominates the reef fish community in shallow to mid water depths along the continental shelf. The affinity of Red Snapper for artificial and natural reefs is well established; however, this affinity appears to vary with age. We used a multigear survey that targeted all age-classes of Red Snapper to determine the distribution by age-class on artificial reefs, natural reefs, and unconsolidated mud–sand bottom across the shallow-water (<100 m) portion of the north-central Gulf of Mexico continental shelf. Bottom trawl, remotely operated vehicle (video), vertical longline, and bottom longline surveys were conducted in randomly selected 2-km × 2-km grids that were previously surveyed with side-scan sonar to yield a synoptic understanding of habitat use by age-class. Zero- and 1-year-old Red Snapper (collected from trawls) were found primarily in shallow water (~20–40 m deep) on unconsolidated muddy bottom in the northwestern portion of the survey area. Vertical longline catch per unit effort was highest at artificial reef sites, followed by natural reef sites and lastly sites with unstructured bottom. The vertical longline surveys collected 2–8-year-old Red Snapper near artificial and natural reefs, yet the mean age and size of these fish did not differ between the two habitats. Older Red Snapper (5–42 years old) were collected on bottom longlines, away from reef structures on unstructured bottom throughout all depth strata. Our results demonstrate ontogenetic changes in habitat use for Red Snapper (from unstructured bottom areas to artificial or natural reefs and back to unstructured bottom areas), but unlike the results from previous studies they do not show a strong trend toward increases in the prevalence of older Red Snapper with increasing depth.

The economic and cultural importance of Red Snapper *Lutjanus campechanus* in the northern Gulf of Mexico cannot be overstated. Since the 1980s, when federal regulations were adopted for the fishery, management of the stock has been controversial (Strelcheck and Hood 2007), and this controversy continues to escalate (Cowan et al. 2011). The species' affinity for structured habitats (Patterson et al. 2001b) facilitates exploitation by a growing fisher population that is equipped with increasingly sophisticated technology designed to locate such habitats. The long-lived nature of the species (50+ years; Wilson and Nieland 2001) and a fecundity-at-age relationship that does not approach an asymptote until well after 10 years, results in a long rebuilding time for Red Snapper when they are overexploited.

Currently, the stock is under a rebuilding plan until 2032 and is considered overfished but not currently experiencing overfishing (SEDAR 2014). Catch is allocated evenly between the recreational and commercial fisheries, with the commercial sector being managed under an

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individual fishing quota system that results in a year-round fishery. Recreational catch in federal waters is managed by means of annual seasons and daily bag limits. The length of the private recreational season has diminished over the last decade, from 194 d in 2007 to 11 d in 2016. This truncated season has resulted in tremendous disputes over the general approach to Red Snapper management as well as the science behind the current Red Snapper assessment (Powers and Anson 2016).

The consequences of overfishing the Gulf Red Snapper stock are evident in recent age composition data, which reveal low proportions of older age-classes of fish (10+ years; SEDAR 2014). The current stock assessment relies on age composition data acquired primarily from commercial and recreational fishery landings. A routine—but often ignored—research recommendation from stock assessments of many fished species is for expanded fisheries-independent data collection. For many species, such surveys can provide critical information on distribution, habitat use, and age structure. The outcomes of stock assessments are often influenced primarily by age composition data derived from fishery landings (fisheries-dependent data) because fisheries-dependent samples are easier to acquire than fisheries-independent samples. The potential disparity in age composition between fisheries-dependent and fisheries-independent data sources requires further investigation. For example, age composition data from the commercial Gulf of Mexico Red Snapper fishery revealed heavy exploitation of 5–6-year-old fish, which resulted in a stock assessment that predicts high fishing mortality (*F*; SEDAR 2014). Although the lack of age-5 and older Red Snapper may be attributed to heavy exploitation (see Cowan et al. 2011), it might also result from commercial fishers' behavior (i.e., their targeting of more marketable-sized fish) or from the selectivity of commercial gear. If older fish are present in the population at relatively high frequencies, then the current *F* terms may be overestimated; however, if older fish are rare, this age composition would accurately reflect the current stock status. Evidence for older fish is present in the National Marine Fisheries Service (NMFS) bottom longline survey (Mitchell et al. 2004), but that survey was designed to assess shark populations (Grace and Henwood 1997) and does not target areas of high Red Snapper abundance (e.g., shallow-water areas containing structured habitats; Karnauskas et al. 2017). Thus, targeted bottom longline surveys in areas exploited by the commercial and recreational fisheries would aid in assessing the true age composition of the Red Snapper stock.

A synoptic study of the age composition of Red Snapper across a representative section of the continental shelf of the Gulf of Mexico would provide a more complete understanding of habitat use by age. Gallaway et al. (2009), the most recent synthesis of Red Snapper life history, details the strong affinity of 2–8-year-old Red Snapper for artificial reefs and oil and gas production platforms and suggests that older Red Snapper occupy deeper-water natural reefs and open-ocean bottom. We conducted a 5-year (2011–2015) survey of the Alabama continental shelf (<100 m depth) to examine habitat use by age-class and evaluate the prediction that older Red Snapper would be more common at greater depths. When possible, we adopted gear types and methodologies similar or identical to those of the long-term fisheries-independent monitoring programs conducted by NMFS to allow for historical comparisons. Specifically, we used a combination of bottom trawls, remotely operated vehicles (ROVs), vertical longlines, and bottom longlines to obtain a complete snapshot of the age-classes across different habitats and life history stages.

METHODS

The benthic habitat in the northern Gulf of Mexico consists mainly of unstructured, soft-bottom sediments and sporadically distributed artificial and natural (hard-bottom) reefs. The Alabama Artificial Reef Zone (AARZ), the largest artificial reef zone in the country (1,030 mi^2 [2,668 km^2]), is located off the coast of Alabama and is comprised of five zones pre-permitted for the deployment of artificial reefs. The state of Alabama deploys many artificial reefs and publishes the coordinates for these locations, thereby making the reefs accessible to the public for fishing purposes. Alternatively, the general public may deploy reefs in the AARZ by obtaining a permit (for $25) and getting approval for the materials to be used from the state's Marine Resources Division. Coordinates for private reefs are not published. The quantity of artificial reefs deployed in the AARZ numbers in the thousands.

Smith et al. (2011) demonstrated that stratifying by habitat features (including reef structure, rugosity, and depth) was an efficient sampling strategy and an effective means of partitioning variability. Therefore, to define our study area, we first stratified the AARZ by depth (shallow [18.3–36.6 m], mid-depth [36.6–54.9 m], and deep [54.9–91.4 m]; Gregalis et al. 2012; Figure 1) and subsequently divided it into a series of 2-km × 2-km grids. A random subset of these grids was selected for sampling purposes. The selected grids were surveyed with side-scan sonar prior to synoptic sampling using trawl, ROV, vertical longline, and bottom longline methods (Figure 2). Sampling with these four gear types was conducted during two time periods annually: late spring (April–May) and late summer (August–September) from 2011 to 2015 (Table 1).

Habitat assessment.— Side-scan sonar was used to quantify habitat types across the survey area and identify targets to be sampled. Each year, randomly selected grids

(N = 24–56) were first surveyed using side-scan sonar, then by trawl, vertical longline, ROV, and bottom longline gears. Grids were selected to proportionally allocate sampling effort according to the total bottom area covered by each depth stratum, such that 50% of the total effort occurred in shallow water, 33% in mid-depth water, and 17% at greater depths. Additionally, nine grids located west of the AARZ were selected and mapped in 2014 and 2015 to quantify and describe structures outside of the permitted area. Each grid was surveyed using an Edgetech 4200 dual-frequency side-scan sonar (300/600 kHz) and a Biosonic echo sounder with a 200-kHz single-beam transducer. The side-scan towfish was deployed using a data-conducting winch equipped with a digital metering block from the A-frame of the survey vessel and towed approximately 15 m above the seafloor. A differential global positioning system (DGPS) receiver was attached directly above the metering block on the A-frame and provided position information for the vessel. All data (position, sonar, and cable-out) were recorded and integrated using Chesapeake Technology, Inc., SonarWiz.MAP 4 software running on a ruggedized laptop computer. This software was used to produce a real-time, fully georeferenced mosaic of the sonar data and to serve as a navigational aid for the vessel during the course of the survey. The single-beam transducer was deployed in a downward-looking configuration from a pole mount attached to the gunwale of the survey vessel. A series of paired parallel lanes ranging in distance from 2,300 to 2,500 m were steered by the survey vessel at speeds between 4 and 5 knots. The paired lanes were spaced 120 m apart, and lane pairs were spaced 240 m apart. This configuration permitted 100% coverage of the survey grid as long as 20 m of lane tolerance was maintained. Bottom targets visualized by the SonarWiz.MAP 4 program were captured and displayed on the chart plotter of the program. The positions of selected targets were then verified using the single-beam sonar. Typically,

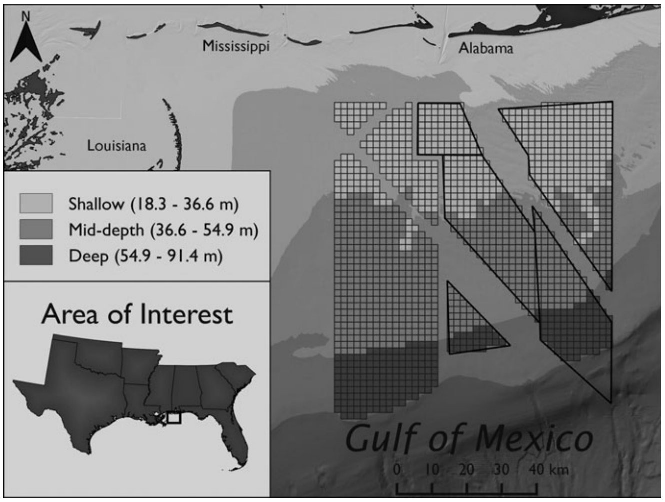

FIGURE 1. Map of the study location in the northern Gulf of Mexico showing the 4-km^2 sampling grids used in the current monitoring program, stratified by depth. Grids within the Alabama Artificial Reef Zone are enclosed within heavy lines.

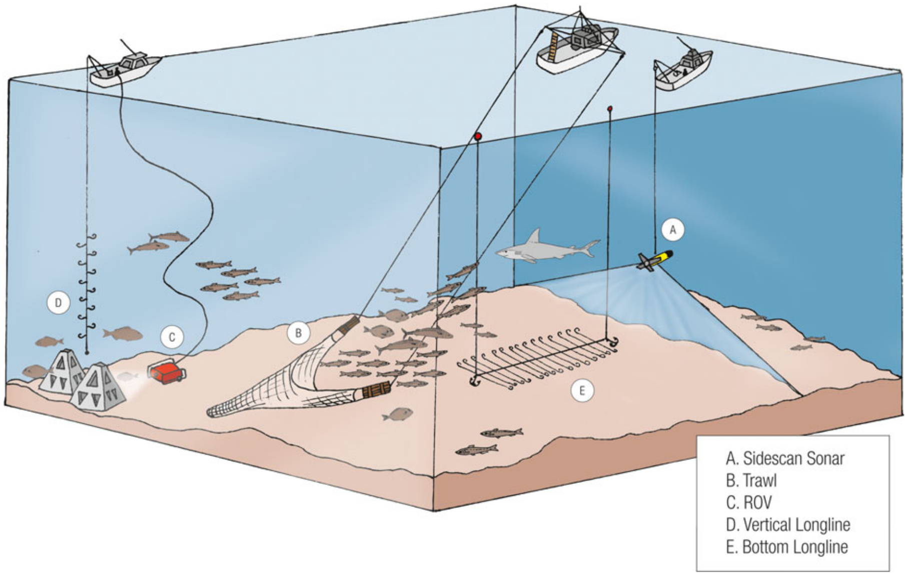

FIGURE 2. Artist's illustration of the approach to sampling reef fish communities in this article: a grid was randomly selected and all structure was mapped with high-resolution side-scan sonar, identifying natural and artificial reefs (A); a 12.5-m-wide bottom trawl was towed through the grid (B); ROV video of fish assemblages was taken on and off reefs (C); the sites were fished with a vertical longline (D); and finally, a 2-km, 100-hook bottom longline was fished (E).

TABLE 1. Sampling effort (sites) by collection period and gear type.

Year	Period	ROV	Trawl	Vertical longline	Bottom longline	Annual total
2011	Apr–May	18	16	49	8	166
	Aug–Sep	20	11	27	17	
2012	Apr–May	24	17	54	18	182
	Aug–Sep	18	12	27	12	
2013	Apr–May	18	11	39	17	170
	Aug–Sep	17	12	39	17	
2014	Apr–May	24	11	51	28	236
	Aug–Sep	24	18	49	31	
2015	Apr–May	61	27	87	27	409
	Aug–Sep	61	27	92	27	
All years		285	162	514	202	1,163

targets found in overlapping sonar data from parallel lanes were verified to aid in data alignment during post-processing.

Based on the side-scan sonar map of structures, a contact report was generated, giving the length, width, height, description, and coordinates (latitude and longitude) of each contact within each grid. Bottom contacts were broadly categorized as either qualifying structure (>4 m^2 of area and >0.5 m of vertical relief) or nonqualifying structure (<4 m^2 of area and <0.5 m of vertical relief; Gregalis et al. 2012). Two to three qualifying structures within each grid were randomly selected from the contact report and designated as sites for ROV and vertical longline sampling. If natural reefs were identified on the contact report, they were automatically selected as sites to be sampled. Given that natural reefs are relatively scarce off the Alabama coast (Gallaway et al. 2009), this strategy ensured that the maximum amount of natural reef was sampled. In addition, during one sampling event per depth stratum, an area with no structure was randomly chosen for sampling with ROV and vertical longline gears. In this way, both structured and nonstructured sites were fished within each depth stratum. After contacts were selected for the ROV and vertical longline sampling, the beginning and ending coordinates for the bottom trawl and bottom longline sampling were randomly generated.

Bottom trawl.— One bottom trawl was performed in each selected grid during each of the two sampling periods annually. The path of the trawl was preselected to avoid structured habitats that would snag the net. Trawl gear and protocols were standardized to those used by the NMFS Southeast Area Monitoring and Assessment Program (SEAMAP; Eldridge 1988). The trawl net was a 12.2-m semiballoon shrimp trawl with a 12.8-m headrope, wooden doors (2.4 m × 1 m), rollers, and a tickler chain. The net was composed of three sections: wings, an intermediate area, and a cod end, with mesh sizes of 5.08, 3.81, and 4.13 cm, respectively. All tows were conducted for 30 min at speeds ranging from 2.5 to 3 knots. After each tow, the entire catch was brought on deck and released onto a sorting table. Catch was sorted by species into 5-gal (19 L) buckets. Counts of all individuals were noted, and measurements (standard length, fork length, and stretch total length) and weight (kg) were recorded for all of the Red Snapper collected. With two exceptions, all Red Snapper were assigned an age of 0, 1, or 2 based on an age–length key (Patterson et al. 2001a).

Remotely operated video.— After completion of the side-scan sonar operations and data processing, video footage of the fish community was recorded at ~50% of the targeted sites (Table 1) using high-definition video on a four-thruster ROV. The ROV was equipped with sonar with a 75-m detection range and 360° viewing capabilities, allowing the operator to safely approach large structures. The ROV umbilical (250 m) was attached to a 4.5-kg depression weight, which reduced the umbilical's catenary. The terminus of the depression weight was maintained on the seafloor and was followed by 20 m of unweighted umbilical cable. At each site, the ROV was positioned ~5 m from the structure, with the cameras pointed at the structure. The ROV was maneuvered at approximately 0.25 m/s and 3–4 m from the bottom. Two minutes of video were recorded. The process was repeated on the opposite side of the structure for additional 2 min. After sampling both sides of the structure, the ROV was positioned approximately 1 m above it to record a 360° vertical view of the structure. The total time for video recording was approximately 10 min. When possible, fish measurements were estimated by using a pair of Digi-Key 5-mW red lasers that were aligned in parallel and separated by 3 cm as a frame of reference. Video imagery from the ROV was saved to a handheld high-definition recorder for later analysis. In the laboratory, fish visible in the ROV footage were identified to the lowest possible taxon, enumerated, and measured (when possible). Fish abundance was estimated using a minimum-count method known as MaxN (Schobernd et al. 2013), wherein the still frame with the most fish visible represents the minimum amount of fish present in the sampled area. This method was assumed to yield the most conservative estimate of population size.

Vertical longline.— Following the ROV operations at each site, three replicate vertical longlines (also known as handlines or bandit gear) were used to collect reef-associated fish. The main line of the vertical longline was 152 m of 300-lb (136 kg) test monofilament with a 6/0 Rosco snap swivel crimped onto the end. The backbone was 6.7 m of 400-lb (181 kg) test monofilament. The top of the backbone had a crimped loop to attach the 6/0 Rosco snap swivel from the main line, and the bottom of the backbone had a 2/0 Rosco snap swivel to attach a 4.5-kg sash weight. The crimps used at the top and bottom of the backbone were 2.2-mm double copper crimp sleeves. Ten gangions were attached to the backbone described above. Each gangion had a total length of 18 in (45.72 cm). The gangions were made by twisting 100-lb (45.36 kg) test camouflage monofilament together and terminated in one of three hook sizes: 8/0, 11/0, or 15/0. All gangions were baited with a piece of Atlantic Mackerel *Scomber scombrus* cut proportionally to the size of the hook. The vertical longline was fished for 5 min. After the 5-min soak period, the gear was brought to the surface via a manual crank reel and the status of each hook was recorded (species caught, bait present, or bait absent). All fish were removed from their respective hooks (1–10 [deepest to shallowest]), and length (standard length, fork length, and stretch total length) and weight (kg) were recorded. Otoliths were extracted for aging purposes. All fish were placed on ice for further processing at the lab. The second and third vertical longline replicates were fished simultaneously in an identical manner. The gear configuration and sampling procedure described above have been adopted by SEAMAP as a standardized method for vertical longline sampling throughout the Gulf of Mexico (see Gregalis et al. 2012 for a complete description).

Bottom longline.— One 100-hook bottom longline was deployed in each grid at a random start location. The gear was deployed without regard to bottom features or structures. The mainline was 2 km of 940-lb (426 kg) test monofilament and supported 100 gangions. The gangions consisted of 12 ft (3.66 m) of 730-lb (332 kg) test monofilament and a 15/0 circle hook, baited with Atlantic Mackerel. The main line was deployed through a series of blocks from the stern of the vessel at a speed of approximately 2 m/s. Bottom longlines were soaked for 1 h. All fish captured were enumerated by species, their lengths and weights were recorded, and otoliths were extracted. The configuration and the operation of the bottom longline were identical to the procedure used by NMFS in their Gulf-wide surveys (see Mitchell et al. 2004; Drymon et al. 2010).

Age determination.— Red Snapper were aged according to methodology adopted by the Gulf States Marine Fishery Commission. Specifically, ages were determined by sectioning the left otolith from each fish using a Hillquest petrographic saw and grinding wheel. This method is similar to the freehand technique described by VanderKooy and Guidon-Tisdel (2003) for processing Red Snapper otoliths. Each otolith core was marked and the anterior end of the otolith ground until the core and sulcus acusticus were visible though a magnifying glass. The anterior end was then polished to remove any scratches and mounted anterior end down on a slide using Flow-Texx mounting medium. After drying, the posterior end of the otolith was ground until the otolith was approximately 0.5 mm in thickness. The posterior side was polished, covered in Flow-Texx, and allowed to dry. The otolith sections were then placed under a dissecting microscope attached to an Image-Pro imaging system. A snapshot of the otolith was taken (50× magnification), the image enlarged, and the annuli enumerated. Each opaque zone on the dorsal side of the sulcus acusticus in the transverse plane was assumed to represent an annulus. To age each otolith, two readers independently read and enumerated annuli and determined a margin code. The results were then compared, and when the readers disagreed, they jointly examined the otolith in question. If a consensus was not reached, the otolith data for that fish were omitted from further analyses.

Data analysis.— Our primary focus across all our data analyses was to determine how abundance, age, and size varied by depth of capture and, when possible (through vertical longline and ROV data), by habitat type. To evaluate these factors, we utilized two-way and three-way analysis of variance (ANOVA) models. Year (2011–2015 [random effect]) and depth stratum (shallow, mid, and deep [fixed effect]) were included in all models. For data sets in which the habitat type fished (artificial, natural, or no structure) was available, habitat type was included as a fixed effect. We use a type III sum of squares to determine statistical significance at $P \leq 0.05$. Specifically, we tested the effects of year and depth stratum as well as their interaction on the CPUE of Red Snapper collected by trawls (number per tow-minute) and bottom longline (number·hook^{-1}·h^{-1}) and the mean size (TL [mm]) of Red Snapper collected by those gears. Additionally, we used a similar model to test the effects of year and depth stratum on the mean age (per set) of Red Snapper. Next, we tested the effects of year, depth stratum, and habitat type and their interactions on the CPUE of Red Snapper collected by vertical longline (number·hook^{-1}·5 min^{-1}) and observed on ROV video (MaxN count per reef) and the mean size of the Red Snapper collected/observed by the gear. For vertical longline (VLL)–captured Red Snapper, we were also able to analyze the mean age of the fish collected at a site by a similar three-way model. When analyzing VLL CPUE, we combined (averaged) the catches of the different hook sizes. Although each hook size has a different selectivity (Gregalis et al. 2012), we used the combined approach as a measure of relative abundance across the range of sizes because all three VLLs were fished as a unit at each site and their selectivities overlapped. The mean size or age from all hooks at a site was used as the dependent variable in analyses of size and age patterns to avoid pseudoreplication.

In most instances, the dependent variables failed to meet the assumptions of normality (Shapiro–Wilk test) and homogeneity of variance (Cochran's C test) of an ANOVA. After data transformation ($\log_{10} + 1$), size and age data met these assumptions ($P > 0.05$); however, the CPUE data (trawl, VLL, and bottom longline [BLL]) and MaxN counts (ROV), which were all zero inflated, failed to meet these assumptions. Because ANOVAs are robust to violations of normality and homogeneity of variances (Underwood 1997), we chose to perform the ANOVAs on CPUE data that were log transformed, recognizing that greater caution is needed in interpreting the significance of these tests. All post hoc contrasts of levels within significant main effects were performed by means of Games–Howell (GH) tests, which do not require the assumptions of equal variances or sample sizes (Day and Quinn 1989).

RESULTS

Between 2011 and 2015, our multigear survey sampled a wide range of size- and age-classes of Red Snapper in a variety of habitats across the shallow-water (<100 m) portion of the north-central Gulf of Mexico. In general, sampling effort increased every year, with a total of 1,163 sampling events being conducted during the study period (Table 1). Capture gears (trawl, vertical longline, and bottom longline) provided catch, size, and age data, whereas the ROV provided abundance and size without any potential effects resulting from hook selectivity (Table 2).

Bottom Trawl

The highest abundance of juvenile Red Snapper occurred between 20 and 40 m depth (Figures 3, 4A). Abundance was highest in the shallow stratum, followed by the mid-depth and deep strata (Table 3; GH tests: shallow > mid-depth > deep). The mean ± SD total length of trawl-collected Red Snapper was 132 ± 78 mm. Juvenile Red Snapper collected during the April–May period were larger (147 ± 79 mm; $N = 224$) than those collected during the September–October period (116 ± 75 mm; $N = 225$), although the CPUE between the two sampling periods was similar (0.81 ± 0.26 in April–May versus 0.82 ± 0.25 in September–October). Bottom trawls collected almost exclusively 0–2-year-old Red Snapper, primarily in shallow-water areas in the northwest section of the AARZ and in the nearby waters outside the permitted area (Figure 5A). Most fish were assigned an age of 0 ($N = 263$, size range = 30–170 mm stretch total length) or 1 ($N = 39$, size range = 175–297 mm). Six fish (size range = 320–360 mm) were assigned an age of 2, and two fish (727 and 767 mm) were not assigned an age (Figure 4C). Frequency plots of total length (Figure 6A) and age (Figure 7A) revealed that the trawl catch was dominated by 0- and 1-year-old Red Snapper.

TABLE 2. Summary of data collected by gear type; Y = yes, N = no.

	Gear			
Data collected	ROV	Trawl	Vertical longline	Bottom longline
Catch	Y	Y	Y	Y
Size	Y	Y	Y	Y
Age	N	Y	Y	Y

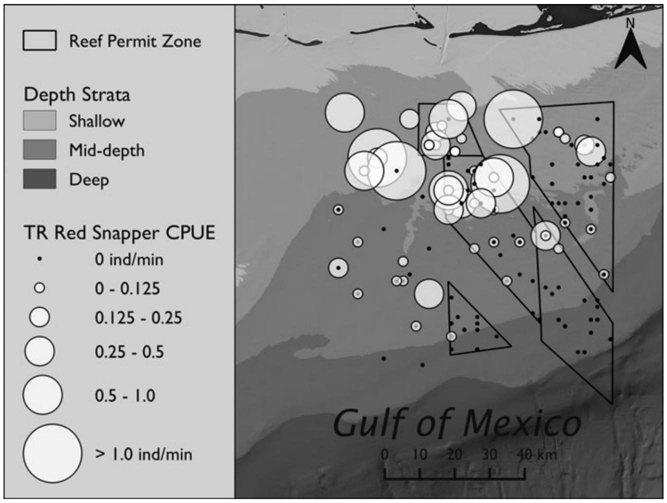

FIGURE 3. Distribution of trawl catch per unit effort (number of Red Snapper per minute) throughout the coastal waters of Alabama from 2011 to 2015.

ROV Video

ROV-based video observations were collected at 256 sites (205 artificial reefs, 30 natural hard-bottom sites, and 21 sites with no structure). The MaxN count of Red Snapper varied as a function of habitat type (Table 4). The number of Red Snapper was highest at artificial reefs (12.2 ± 9.5 [mean ± SD]), followed by natural reefs (2.7 ± 5.6) and unstructured areas (0 ± 0). In this regard, the GH tests showed that artificial reefs were significantly different from natural and no-structure areas, which did not differ from each other. Total lengths were

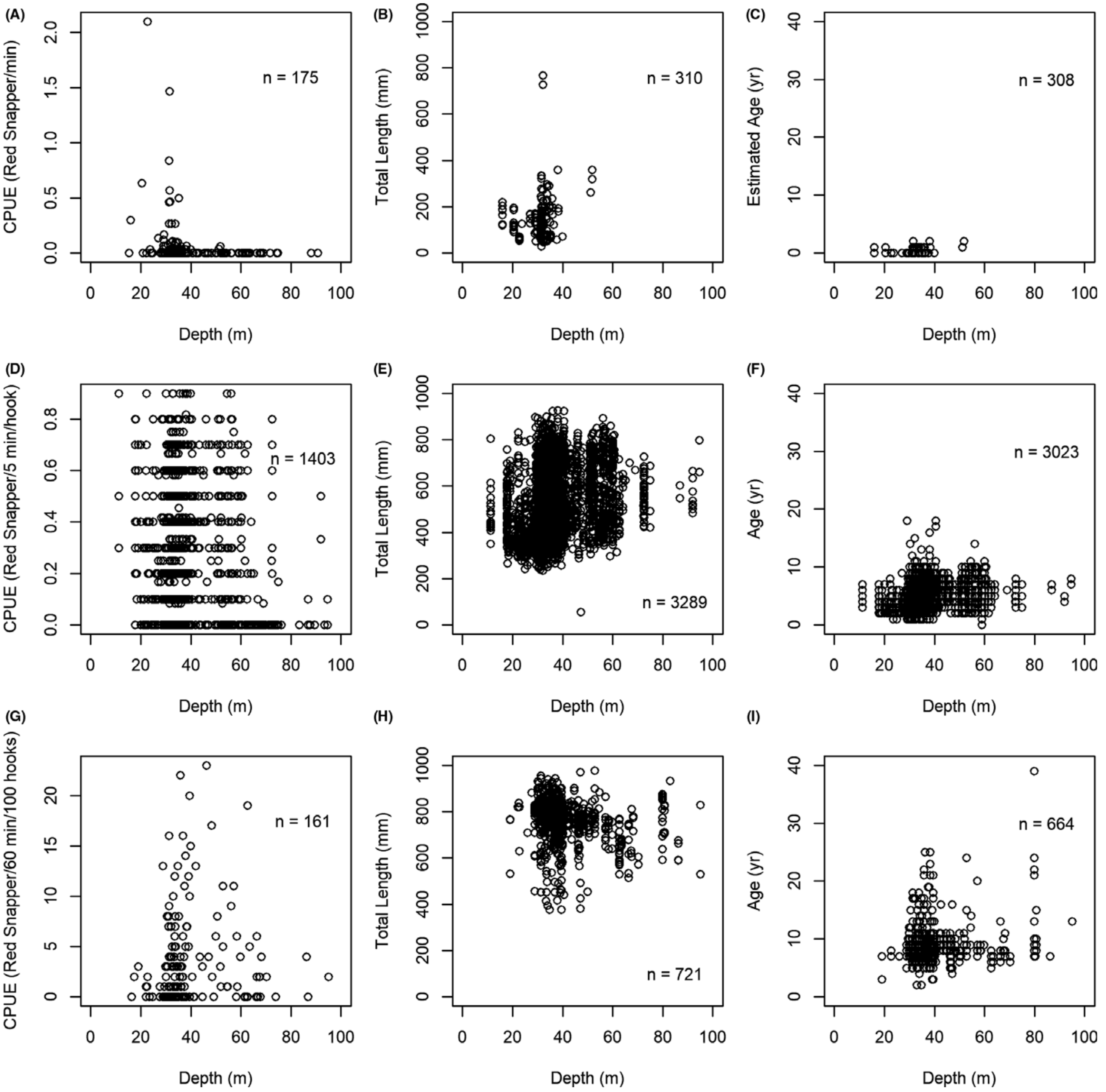

FIGURE 4. Scatterplots of Red Snapper catch per unit effort, total length, and age by depth of collection and gear: **(A)–(C)** trawl, **(D)–(F)** vertical longline, and **(G)–(I)** bottom longline. The number of sites/individual is represented on each panel. Trawl ages are based on age–length relationships. Two trawl-caught fish were very large (see panel B); because their estimated ages were simply >2, they are not shown in panel (C).

estimated for 1,007 Red Snapper on artificial reefs and 58 Red Snapper from natural reefs (Figure 6B). The mean total length of Red Snapper did not vary significantly between natural and artificial reefs (Table 4). A significant effect of mean size was detected for depth strata, with the Red Snapper observed in shallow depths being smaller than those observed in mid-depth and deepwater areas.

Vertical Longline

Vertical longlines set on artificial reefs, natural hard bottoms, and unstructured bottom revealed different

TABLE 3. Results of two-way ANOVA testing the effects of year (2011–2015) and depth stratum (shallow, mid, or deep) on the CPUE of Red Snapper and the mean size collected in bottom trawls. Bold italics indicates significance at the 0.05 level.

Dependent variable	Source	Type	df	Sum of squares	Mean square	*F*	*P*
CPUE	Year	Random	4	0.014	0.004	1.419	0.311
	Depth stratum	Fixed	2	0.038	0.019	7.415	***0.015***
	Year × depth stratum	Random	8	0.020	0.003	0.665	0.722
	Error		147	0.565	0.004		
Mean size (mm)	Year	Random	4	0.539	0.135	6.017	0.055
	Depth stratum	Fixed	1	0.027	0.027	1.227	0.330
	Year × depth stratum	Random	4	0.090	0.022	0.594	0.669
	Error		34	1.282	0.038		

CPUE by habitat (Table 5). For the 407 sites that could be assigned to one of the three habitat categories, count-based CPUE across all hook sizes on the vertical longline was highest at artificial reef sites (0.27 ± 0.19·hook^{-1}·5 min^{-1}; $N = 297$ sites), followed by natural reef sites (0.07 ± 0.15; $N = 38$ sites) and unstructured bottom (0.01 ± 0.06; $N = 73$ sites) (all levels differed significantly in the GH test). CPUE did not differ by depth (Table 5), although a trend ($P = 0.12$) was noticeable in the data, with CPUE being lower at greater depths than in mid-depth and shallow-water areas. Finally, male Red Snapper were slightly more common than females in the vertical longline catch (52% versus 48%).

The ANOVA for mean size captured by VLL revealed no significant effects among years, habitats, or depth strata (Table 5). Combining all hook sizes, the Red Snapper collected on the vertical longlines averaged 519 mm (SD, 116) in total length (Figure 6C); however, total length varied by hook size, with 8/0 hooks (448 ± 115 mm) capturing smaller Red Snapper than 11/0 (519 ± 137 mm) and 15/0 hooks (631 ± 131 mm) (Figure 6D–F). The ANOVA did indicate a trend ($P = 0.09$) with respect to depth stratum × year, with mean size tending to decrease over years in the shallow and mid-depth areas.

Age composition displayed a pattern similar to that of total length, with no effect of year, depth stratum, or habitat but a significant interaction with year × depth stratum (Table 5). The overall mean age of the Red Snapper collected on the vertical longline was 5.0 (SD, 2.2; Figure 7B). Age varied by hook size, with the Red Snapper collected on 8/0 hooks being younger (3.9 ± 1.7) than those collected on 11/0 (4.9 ± 1.4) and 15/0 hooks (6.5 ± 2.2) (Figures 7C–E, 8A). Combining all hook types, the Red Snapper collected from artificial reefs averaged 4.9 years (SD, 1.9), those collected on natural hard bottom 6.0 years (1.3), and those collected on unstructured bottom 8.6 years (1.1). The pattern of older Red Snapper being collected from deeper sites was evident in the spatial distribution of the mean age of Red Snapper across the depth strata of the AARZ (Figure 5B) and drove the interaction between depth stratum and year, with older fish being detected at greater depths in some years. Finally, the age composition of Red Snapper sampled on the vertical longline showed little interannual variation from 2011 to 2015 (Figure 9A).

Bottom Longline

The bottom longline sampled larger and older fish (Figure 6G, 7F) than the other gear types. The mean age of the Red Snapper collected on the bottom longline was 9.25 years (SD, 3.6), and the mean total length was 991 mm (92). The CPUE and mean size of the Red Snapper collected with bottom longlines varied by year and depth but not with the interaction of the two factors (Table 6). Red Snapper were caught in slightly greater numbers in the mid-depth stratum than in the shallow and deep strata; however, GH tests did not detect a significant difference between any of the depth strata. The bottom longline CPUE varied by year, with higher catches in 2012 and 2014 than in 2011, 2013, and 2015 (GH tests: 2012 = 2014 > 2011 = 2013 = 2015). Mean size was higher in shallow than in deep areas (GH test: $P < 0.05$), with no differences between sites in mid-depth areas and those in either shallow or deep areas (Figure 4H). The mean size of Red Snapper also increased with year (GH test: 2015 = 2014 > 2013 = 2012 = 2011). Neither the ANOVA model (Table 6) nor visual inspection of the distribution of the mean ages (Figure 4I) of Red Snapper collected on the bottom longline revealed any pattern with depth—older fish were captured throughout the study area. Similar to the pattern detected by the ANOVA for mean size, the mean age of Red Snapper collected on the bottom longline increased with year (Table 6; Figure 9). Examination of the cumulative frequency diagram by year indicates that this increase is likely caused by the progression of specific age-class(es) (2005 and 2006) of fish, as the curves shift right at an apparent annual step (Figure 8B). Finally, females were captured more frequently than males (56% versus 44%).

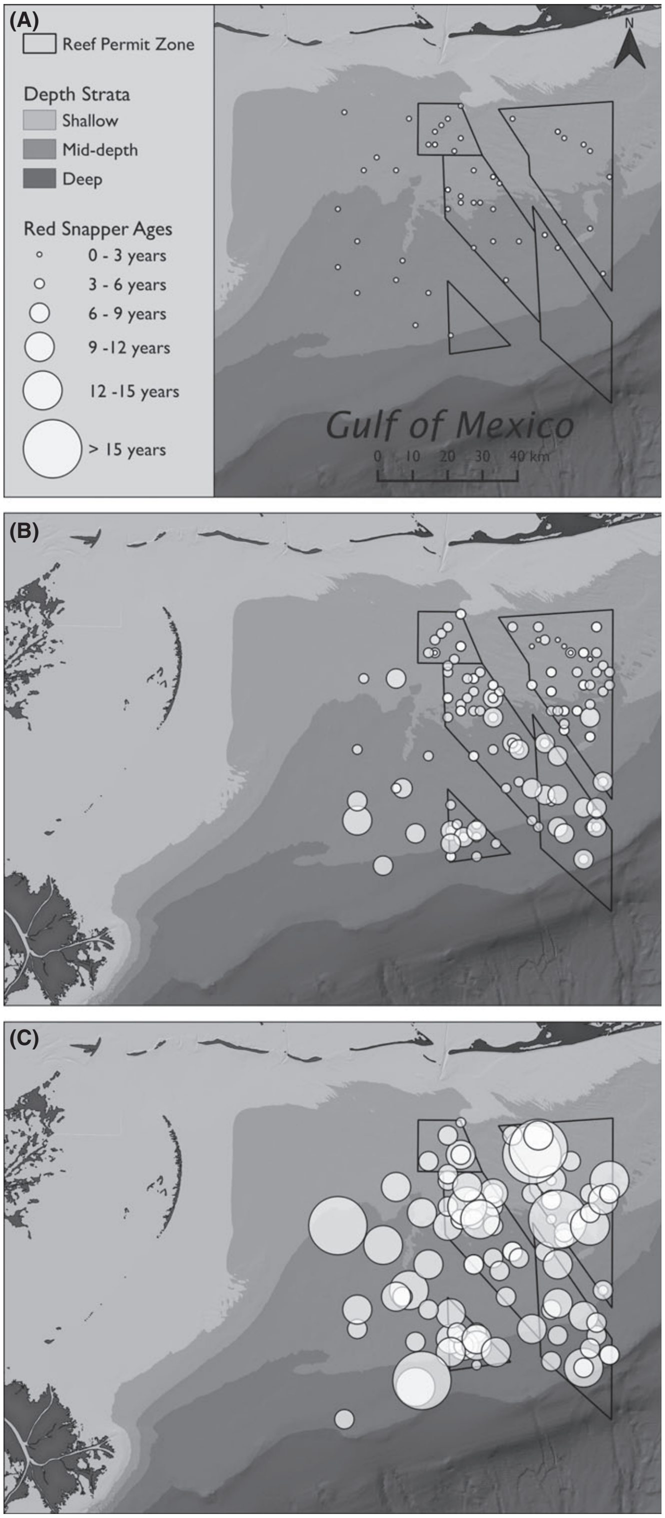

FIGURE 5. Average age of Red Snapper by sampling grid and gear: **(A)** bottom trawl, **(B)** vertical longline, and **(C)** bottom longline.

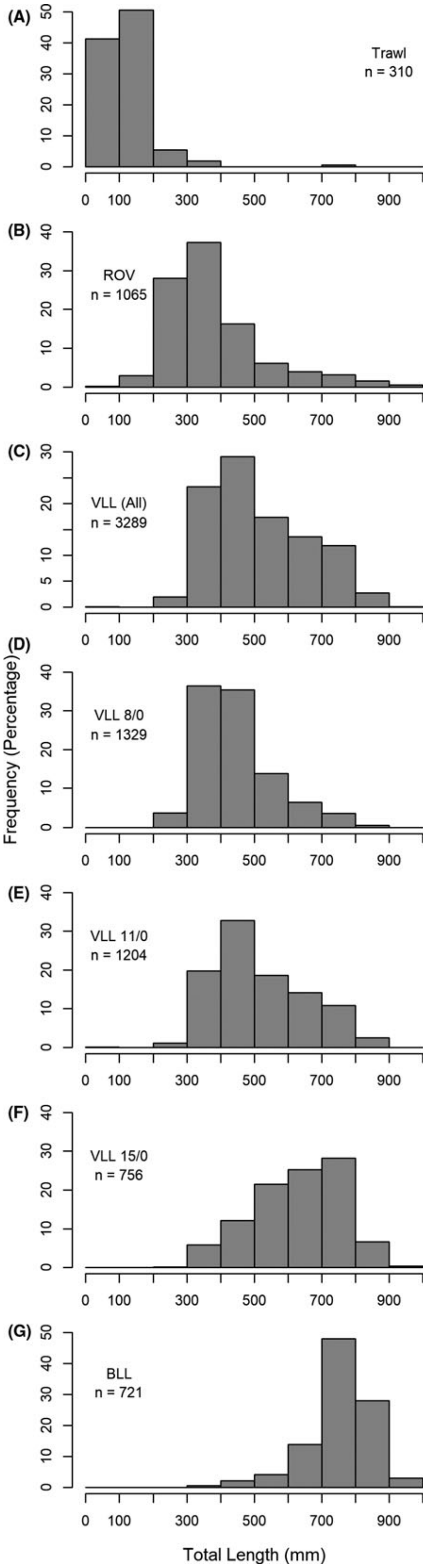

FIGURE 6. Length frequency distributions of Red Snapper by gear type and hook size (where applicable).

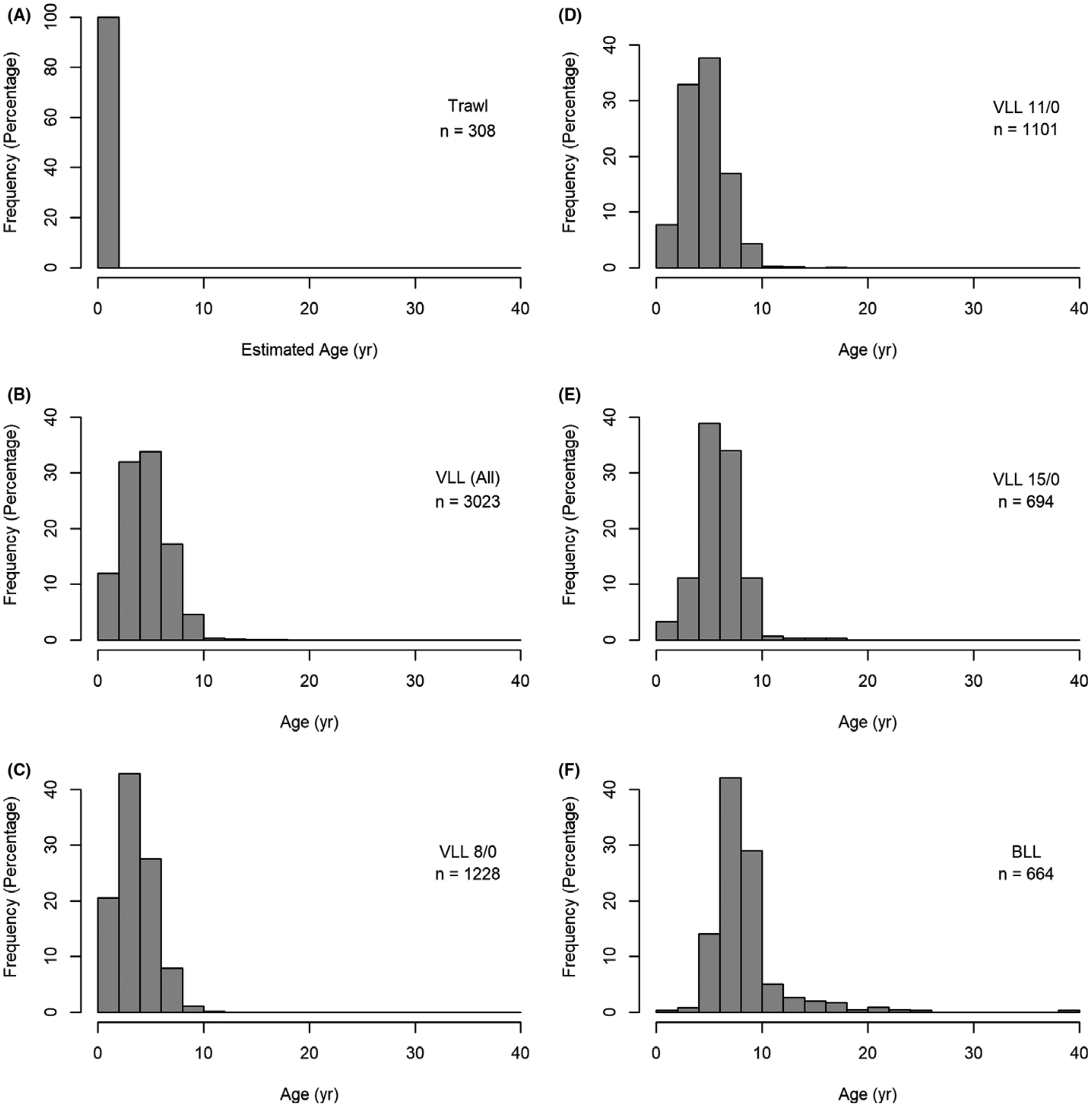

FIGURE 7. Age frequency distributions of Red Snapper by gear type and hook size (where applicable).

DISCUSSION

Red Snapper were common on artificial reefs, natural hard bottom, and unstructured bottom throughout our study area in the north-central Gulf of Mexico, and age differed by habitat area. Our study results generally agree with the life history model proposed by Gallaway et al. (2009), with some notable exceptions. Juvenile Red Snapper (25–240 mm in total length [ages 0 and 1]) are found primarily on inner-shelf, muddy-bottom habitats. Based on ROV video footage, Red Snapper begin to recruit to natural and artificial reefs at 200 mm TL and are fully recruited by 280 mm. The density of Red Snapper is four times higher on artificial reefs than on natural reefs. Red Snapper size and age did not differ between

TABLE 4. Results of three-way ANOVA testing the effects of year (2011–2015), habitat (artificial or natural reef), and depth stratum (shallow, mid, or deep) and their interactions on the max–min count of Red Snapper observed on ROV video. The interactions could not be resolved for mean size because of the low number of observations on natural reefs. Bold italics indicates significance at the 0.05 level.

Dependent variable	Source	Type	df	Sum of squares	Mean square	F	P
MaxN (log x +1)	Year	Random	5	1.572	0.314	0.414	0.833
	Habitat	Fixed	2	10.878	5.439	12.010	***0.004***
	Depth stratum	Fixed	2	3.799	1.900	3.965	0.059
	Year × habitat	Random	9	2.528	0.281	0.775	0.646
	Year × depth stratum	Random	10	3.071	0.307	0.847	0.605
	Habitat × depth stratum	Fixed	4	0.936	0.234	0.646	0.645
	Year × habitat × depth stratum	Random	8	2.899	0.362	1.903	0.059
	Error		348	66.280	0.190		
Mean size (log x + 1)	Year	Random	4	0.03	0.01	−1.30	***<0.001***
	Depth stratum	Fixed	2	0.14	0.07	6.96	***0.03***
	Habitat	Fixed	1	0.01	0.01	1.59	0.30
	Year × depth stratum	Random	6	0.06	0.01	0.48	0.82
	Year × habitat	Random	3	0.02	0.01	0.26	0.86
	Depth stratum × habitat	Fixed	0	<0.0001			
	Year × depth stratum × habitat	Random	0	<0.0001			
	Error		141	3.07	0.02		

TABLE 5. Results of three-way ANOVA testing the effects of year (2011–2015), habitat (artificial, natural, or deep), and depth stratum and their interactions on the CPUE of Red Snapper on vertical longlines. Bold italics indicates significance at the 0.05 level.

Dependent variable	Source	Type	df	Sum of squares	Mean square	F	P
CPUE (log x + 1)	Year	Random	4	0.10	0.03	0.36	0.84
	Depth stratum	Fixed	2	0.23	0.11	3.29	0.12
	Habitat	Fixed	2	2.08	1.04	29.43	***0.00***
	Year × depth stratum	Random	8	0.28	0.04	1.15	0.40
	Year × habitat	Random	8	0.29	0.04	1.18	0.38
	Depth stratum × habitat	Fixed	4	0.12	0.03	0.96	0.46
	Year × depth stratum × habitat	Random	12	0.37	0.03	0.97	0.48
	Error		406	12.93	0.03		
Mean size (log x + 1)	Year	Random	4	0.02	0.01	0.30	0.86
	Depth stratum	Fixed	2	0.04	0.02	1.13	0.41
	Habitat	Fixed	1	0.03	0.03	−4.17	1.00
	Year × depth stratum	Random	8	0.21	0.03	68.33	0.09
	Year × habitat	Random	2	0.00	0.00	2.32	0.42
	Depth stratum × habitat	Fixed	1	0.00	0.00	5.70	0.25
	Year × depth stratum × habitat	Random	1	0.00	0.00	0.05	0.83
	Error		306	2.47	0.01		
Mean age (log x + 1)	Year	Random	4	0.13	0.03	0.78	0.60
	Depth stratum	Fixed	2	0.16	0.08	2.10	0.26
	Habitat	Fixed	1	0.03	0.03	−1.25	1.00
	Year × depth stratum	Random	8	0.49	0.06	356.43	***0.04***
	Year × habitat	Random	2	0.00	0.00	9.66	0.22
	Depth stratum × habitat	Fixed	1	0.00	0.00	27.95	0.12
	Year × depth stratum × habitat	Random	1	0.00	0.00	0.01	0.93
	Error		296	6.68	0.02		

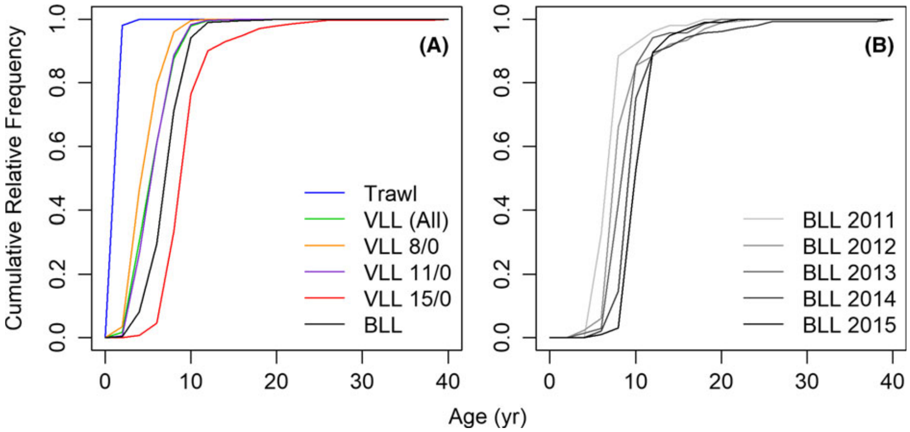

FIGURE 8. **(A)** Cumulative relative age frequencies of Red Snapper by gear type and hook size (where applicable) and **(B)** age frequencies of Red Snapper collected during the bottom longline survey, by year. The ages of trawl-caught fish are based on age–length relationships.

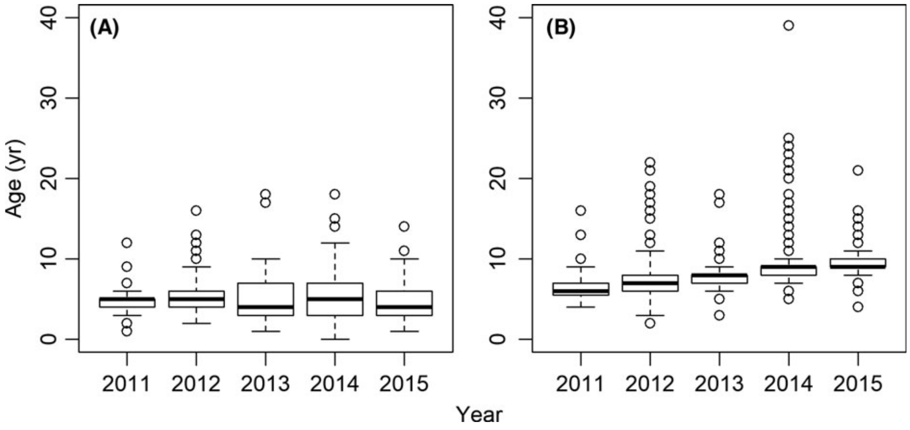

FIGURE 9. Boxplots of Red Snapper ages from **(A)** the vertical longline survey and **(B)** the bottom longline survey, by year of capture. Box plots represent median (horizontal line) and 1st and 3rd quartiles (interquartile range). Individual data points more than 1.5 times the interquartile range are shown in circles.

TABLE 6. Results of two-way ANOVA testing the effects of year (2011–2015) and depth stratum (shallow, mid, or deep) on the CPUE, mean size, and age of Red Snapper collected by bottom longlines. Bold italics indicates significance at the 0.05 level.

Dependent variable	Source	Type	DF	Sum of squares	Mean square	*F*	*P*
CPUE (log x + 1)	Year	Random	4	0.006	0.001	9.970	***0.003***
	Depth stratum	Fixed	2	0.002	0.001	5.563	***0.031***
	Year × depth stratum	Random	8	0.001	0.000	0.416	0.910
	Error		146	0.053	0.000		
Mean size (log x + 1)	Year	Random	4	0.036	0.009	5.305	***0.022***
	Depth stratum	Fixed	2	0.034	0.017	9.998	***0.007***
	Year × depth stratum	Random	8	0.014	0.002	1.241	0.282
	Error		108	0.149	0.001		
Age (log x + 1)	Year	Random	4	0.185	0.046	11.615	***0.002***
	Depth stratum	Fixed	2	0.008	0.004	0.961	0.422
	Year × depth stratum	Random	8	0.032	0.004	0.508	0.848
	Error		98	0.767	0.008		

artificial and natural reefs in our study. As Red Snapper age (>5–8 years), they spend less time near reef structure and more time in unstructured bottom habitats. Counter to previous suggestions, we found no strong trend of older or larger Red Snapper inhabiting deeper waters. Large Red Snapper appear to roam throughout waters deeper than 18 m (our study's shallow-water boundary) across the inner continental shelf.

The pattern of greater abundance of juvenile Red Snapper in shallow-water areas over unstructured bottom habitats is well established. In our study, the bottom trawl gear collected juvenile (0–1-year-old fish, based on length) Red Snapper throughout the Alabama coastal region, with juveniles being more common in water depths <40 m. Higher abundances were generally confined to the northwestern portion of the study area (where sediments consist more of mud) than in the northeastern portion (where sediments are dominated by sand). The occurrence of juvenile Red Snapper over muddy habitats has been documented in areas off the Texas (Rooker et al. 2004; Geary et al. 2007) and Alabama coasts (Szedlmayer and Lee 2004). Higher catches of recently settled Red Snapper have been reported over shell bottom than in open sand/mud habitats off the coast of Alabama (Szedlmayer and Conti 1999). In contrast, neither Rooker et al. (2004) nor Geary et al. (2007) found a preference for shell bottom over open mud/sand habitats in their studies off the coast of Texas. In fact, Geary et al. (2007) found higher densities of juvenile Red Snapper over mud habitats than over shell ridge habitats. The use of side-scan sonar as a gear type in our monitoring program provides considerable insight into habitat use by Red Snapper. These surveys revealed areas of both high and low reflectance in our study area. Trawl sites often crossed several features, so our trawl results do not permit fine-scale discrimination between bottom types; however, the northwest corner of the AARZ, where juvenile Red Snapper were caught in greater numbers, is an area of primarily low reflectance, which is indicative of muddier sediments.

The movement of juvenile Red Snapper from unstructured (mud/sand) or low-relief (shell ridge) bottoms to higher-relief natural and artificial reefs occurs during a critical stage of their life cycle and has important implications for fisheries exploitation. This transfer to higher-relief areas affords juvenile Red Snapper some protection from predators that forage in the vast expanse of open bottom in the northern Gulf of Mexico, but it also introduces them to a different suite of reef-associated predators. From a fisheries perspective, Red Snapper movement to artificial and natural reefs reduces their vulnerability to the trawl-based shrimp fishery (see Gallaway and Cole 1999) but increases their vulnerability to the hook-and-line-based commercial and recreational fisheries. Szedlmayer and Lee (2004) reported that Red Snapper migrated to structured reef habitat at 60 mm SL. Our study found a larger size at the time of resettlement from unstructured to structured habitat. While a few small Red Snapper (1 at 20 mm and 1 at 60 mm TL) were seen in ROV video footage, almost all Red Snapper in the footage were 180 mm TL or greater. Our larger size at reef occupancy agrees with the findings of several other studies, including Nieland and Wilson (2003) and Wells and Cowan (2007). It is possible that some Red Snapper recruit to the reefs at smaller sizes and the lack of these fish in our data is a function of gear selectivity. Although we do not have a measure of size selectivity for our ROV video survey, Wells and Cowan (2007) reported that their underwater camera array (four Sony digital video camcorders) greatly underestimated (by 10.5×) Red Snapper below 100 mm TL and modestly underestimated (by 1.4×) Red Snapper from 100 to 200 mm TL. While our video survey may underestimate the size of small Red Snapper to a degree, the appearance of 180–200-mm Red Snapper in our video surveys of reefs corresponds to a decline in the number of Red Snapper measuring more than 180 mm collected by our trawl surveys of known nursery grounds.

Comparison of the length frequencies derived from the ROV video footage and the vertical longline samples indicates selectivity of the hook-based collection gear. Vertical longlines collected a large size range of Red Snapper from artificial and natural reefs; combining the catches on all three hook sizes, Red Snapper from 200 to 920 mm TL were collected from artificial and natural reefs. The broader size range (180–1,000 mm) and smaller size recorded in the ROV footage indicates a higher proportion of smaller Red Snapper at reef sites than is suggested by the vertical longline data. Based on the ROV video, Red Snapper begin recruiting to reef habitats at approximately 180 mm TL; a peak in the distribution occurs between 260 and 400 mm. Decreases in the relative frequency of Red Snapper larger than 400 mm TL is likely a result of fishing pressure because ~400 mm (16 in) is the legal minimum size for retaining Gulf of Mexico Red Snapper. Alternatively, the decreasing frequency of larger Red Snapper may reflect ontogenetic movement of these fish from structured habitats to unstructured bottom. Based on our data, the use of dome-shaped selectivity for vertical longlines in the current stock assessment seems appropriate.

Based on the vertical longline survey, the abundance—but not the average size or age—of Red Snapper differed among the three habitat types (artificial reef, natural hard bottom, and unstructured bottom). Red Snapper (primarily 2–8-year-olds) were four times more abundant on artificial reefs than on natural reefs and 27 times more abundant on artificial reefs than on unstructured bottom. Similar patterns of higher abundance of young Red Snapper on artificial reefs than natural reefs have been reported by others (Karnauskas et al. 2017). The results of our analysis contrast with those of Gallaway et al. (2009), which suggest that as Red Snapper age and grow they seek out lower-relief natural reefs.

Larger and older Red Snapper were sampled away from artificial and natural reefs. The bottom longline surveys were conducted primarily away from reefs in the expanse of unstructured bottom area surrounding the scattered clusters of artificial reefs. The age structure of bottom longline–collected Red Snapper was significantly skewed toward older fish than those caught on the vertical longline on artificial and natural reefs. This pattern reflects an ontogenetic shift of Red Snapper from high-relief habitats at young ages to lower-relief habitats as they age (see Gallaway et al. 2009). Our sampling did not have a confounding effect of depth. Bottom longline surveys were performed across a range of depths, and no relationship was detected between depth and the average age of the Red Snapper collected. The age × depth interaction (Gallaway et al. 2009; Ajemian et al. 2015) found in other studies has been a cornerstone of the current understanding of the life cycle of Red Snapper. We found no such relationship; in fact, older Red Snapper (10+ years) were common at all depths. However, it should be noted that our bottom longline catches were dominated by fish younger than 20 years of age. It is possible that older fish normally occur at greater depths but that the high fishing pressure of recent decades has removed these fish from the population. Hence, continued monitoring of Red Snapper, which can live to 55 years of age (Baker and Wilson 2001; Fischer 2007), should continue until the stock is fully rebuilt.

The high frequency of older Red Snapper caught over unstructured bottom has important implications for accurately characterizing the dynamics of the stock. Because these fish are collected away from reef structure, they are less likely to be captured by anglers, who normally target structured habitats. The lower potential for capture suggests that older fish are less likely to be represented in fisheries-dependent age samples. Thus, these older Red Snapper might only be sampled through fisheries-independent sampling programs. Given that the appearance of older Red Snapper is a key metric of stock recovery, we encourage the expansion of bottom longline sampling across all depth strata, on unconsolidated bottom as well as near artificial and natural reefs. This approach would promote the capture of older Red Snapper and provide comprehensive age data for the stock that would, in turn, benefit the stock assessment process.

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