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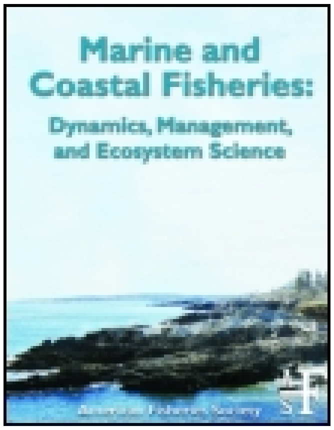

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ARTICLE

Depth-Related Distribution of Postjuvenile Red Snapper in Southeastern U.S. Atlantic Ocean Waters: Ontogenic Patterns and Implications for Management

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Abstract

For the economically and ecologically important Red Snapper *Lutjanus campechanus*, depth distribution patterns across ontogeny are not well understood, particularly in the southeastern U.S. Atlantic Ocean (SEUSA). Using data derived from two fishery-independent surveys targeting hardbottom habitats, we examined patterns of age- and length-specific depth distributions of postjuvenile (age 1+) Red Snapper in the SEUSA. We also compared age and length distributions between fishery-independent surveys and commercial hook-and-line catches to make inferences about gear-specific age and size selectivity, which could have implications for gear-specific interpretations of Red Snapper depth distribution patterns and for determining selectivity functions used in stock assessments. Older, larger Red Snapper were generally distributed throughout all depths, whereas the younger and smaller Red Snapper occurred disproportionately in relatively shallow waters. For Red Snapper equal to or larger than 50 cm FL, we found no evidence of a positive relationship between depth and age or length. Additionally, age and length distributions of Red Snapper $\geq$ 50 cm FL did not differ between fishery-independent surveys and the commercial hook-and-line fishery. These results provide no support for assertions of greater abundances of older and larger Red Snapper in deeper SEUSA waters. As observed in this study for Red Snapper in SEUSA waters, we suggest that patterns of increasing age and size with depth for multiple reef-associated fish species in SEUSA and Gulf of Mexico waters may be driven by younger and smaller fish occurring in shallower waters, and older and larger fish being distributed more equally across depths. Analyses to test this hypothesis for multiple species would be informative for their assessment and management and are recommended.

Foraging requirements, competitive interactions, and predation risk vary throughout an animal's lifetime (i.e., ontogeny) due to increases in body size and changes in behavior (Werner and Gilliam 1984; Ludwig and Rowe 1990). Ontogenic habitat shifts are commonly observed for mobile species and are especially well documented for marine species (Dahlgren and Eggleston 2000; Etherington et al. 2003; Snover 2008; Jones et al. 2010). For example, many marine reef fish species have larvae that settle from pelagic waters to inshore benthic habitats that serve as nurseries (Parrish 1989; Nagelkerken et al. 2000;

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Adams et al. 2006) and gradually shift to offshore habitats as older juveniles and adults (Deegan 1993; Lindeman et al. 2000).

Successful assessment and management of marine fish species is predicated in part upon a clear understanding of ontogenic shifts in distribution patterns, driven, for example, by changing habitat affinities with ontogeny. For instance, unknown levels of immigration into, or emigration from, the unit stock during ontogeny would be a clear violation of most parameterizations of stock assessment models (Hilborn and Walters 1992; Walters and Martell 2004). Moreover, changes in distribution patterns during an individual's lifetime can also result in a pattern of spatial overlap between fish and fishers that varies across ontogeny, resulting in some ages or life stages of a species being less vulnerable to fishing (i.e., subject to lower selectivity) than other ages would (Bacheler et al. 2010). Incorrect assumptions or estimates of the selectivity patterns of a fishery can result in highly erroneous estimates of stock abundance and harvest rate (Myers and Hoenig 1997).

Red Snapper *Lutjanus campechanus* is an economically and ecologically important species in the Gulf of Mexico (GOM) and in southeastern U.S. Atlantic Ocean waters (SEUSA). In the SEUSA, where Red Snapper depth distribution patterns across ontogeny are not well understood, the Red Snapper fishery experienced a complete closure in 2010 due to assessment results that suggested an unsustainable harvest and low spawning biomass (SEDAR 2009, 2010). Some SEUSA stakeholders have asserted that relatively old and large Red Snapper are disproportionately distributed in relatively deep waters (see SEDAR 2010), which has implications for fishing sector-specific selectivity functions used in recent Red Snapper stock assessments. For example, if older and larger Red Snapper were disproportionately distributed in relatively deep waters, but the recreational or commercial hook-and-line fishery was centered in shallower waters, then a dome-shaped selectivity pattern (which assumes that the largest, most fecund fish escape capture), as used for Red Snapper in the GOM (Cowan 2011), might be more appropriate than a flat-top selectivity pattern (in which selectivity plateaus with increasing age or length; Thorson and Prager 2011).

Here we examine patterns of age- and length-specific depth distributions of postjuvenile (age 1+) Red Snapper in the SEUSA to inform future Red Snapper stock assessments and, more generally, broaden understanding of the ecology of this economically and ecologically important species. Specifically, we used two fishery-independent data sets (both targeting hardbottom habitats) to assess patterns of depth- and latitude-related variation in ages, lengths, and CPUE for Red Snapper in SEUSA waters. Additionally, to make inferences about gear-specific age and size selectivity, we compared age and length distributions from the two fishery-independent surveys with distributions from the commercial hook-and-line fishery. Finally, because relatively old and large Red Snapper are thought to become progressively less associated with hardbottom habitats (Szedlmayer 2007; Gallaway et al. 2009; Cowan 2011), we assessed the sparse Red Snapper catch history and depth information available from a fishery-independent survey that included sampling of unstructured (nonhardbottom) habitats in SEUSA waters.

METHODS

Trap survey.—The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program of the South Carolina Department of Natural Resources has used chevron fish traps to index reef fish abundance in the SEUSA since the late 1980s (McGovern et al. 2002), supplemented with funding from Southeast Area Monitoring and Assessment Program-South Atlantic (SEAMAP-SA) beginning in 2009. We analyzed MARMAP/SEAMAP-SA data from 1990 to 2011, during which time chevron-fish-trap sampling was conducted in a consistent manner (described below). In 2010, the National Marine Fisheries Service (NMFS) created the SouthEast Fishery-Independent Survey (SEFIS) to work cooperatively with MARMAP and SEAMAP-SA to increase fishery-independent sampling in the SEUSA; we also included 2010–2012 SEFIS data in our analyses because sampling methods were identical between the two survey programs. Hereafter, the MARMAP–SEAMAP-SA–SEFIS chevron trap survey is referred to as the "trap survey."

Hardbottom sampling stations included in the analyses were selected for sampling in one of three ways. First, most sites were randomly selected from the MARMAP–SEAMAP-SA–SEFIS sampling frame between Cape Hatteras, North Carolina, and Port St. Lucie, Florida. Second, some stations in the sampling frame were sampled opportunistically even though they were not randomly selected for sampling in a given year. Third, new hardbottom stations were added during the study period using information from fishers, charts, and historical survey information. These locations were investigated using vessel echosounders or drop cameras and sampled if hardbottom was present. Sampling for the trap survey occurred during daylight hours on one of four primary research vessels: MARMAP–SEAMAP-SA used the RV *Palmetto* (1990–2011), while SEFIS used the RV *Savannah* (2010–2012), the NOAA Ship *Nancy Foster* (2010), and the NOAA Ship *Pisces* (2011).

Chevron fish traps were deployed at each station sampled in the trap survey. Chevron traps were constructed from plastic-coated, galvanized, 12.5-gauge wire (mesh size = 3.4 cm^2), and were shaped like an arrowhead that measured 1.7 × 1.5 × 0.6 m and had a total volume of 0.91 m^3 (see Collins 1990). Each trap was baited with 24 menhaden *Brevoortia* spp. and was typically deployed in a group of six traps. The minimum distance between individual traps was 200 m to provide some measure of independence among traps. A soak time of 1.5 h was targeted for each trap, and only those soaking for 0.8–2.5 h were included in the analyses. Also, only traps deployed between 28°N and 32°N were included, which encompassed the historical "heart" of the SEUSA Red Snapper fishery (SEDAR 2009) and is consistent with the geographic coverage of the longline survey described below. Traps were deployed in spring through fall at depths

TABLE 1. Cruise information for trap deployments in the MARMAP–SEAMAP-SA–SEFIS chevron trap survey that occurred south of 32°N, 1990–2012, used to elucidate the depth distribution of Red Snapper.

Year	Number of traps	Start date	End date	Latitude (°N)	Depth (m)
1990	34	10 Jul	12 Jul	30.42–31.69	26–62
1991	35	30 Jul	15 Aug	30.42–31.69	27–55
1992	14	19 May	20 May	30.42–31.69	27–62
1993	107	21 Jul	12 Aug	30.43–31.74	16–57
1994	119	12 Jul	26 Oct	30.74–31.74	16–53
1995	180	17 Apr	26 Oct	29.94–31.74	16–55
1996	102	9 May	24 Jul	28.78–31.74	26–69
1997	139	22 Jul	28 Aug	28.27–31.74	16–74
1998	162	2 Jun	29 Jul	28.28–31.98	16–81
1999	56	13 Jul	6 Oct	29.93–31.39	15–60
2000	136	23 May	19 Oct	28.95–31.74	15–61
2001	79	10 Jul	24 Oct	30.52–31.64	14–67
2002	172	18 Jun	5 Nov	28.95–31.74	13–70
2003	65	3 Jun	11 Jun	28.95–31.54	34–62
2004	110	18 May	28 Oct	29.99–31.64	14–70
2005	127	14 Jun	20 Oct	28.95–31.74	15–69
2006	84	6 Jun	19 Oct	28.94–31.74	15–69
2007	115	26 Jun	13 Sep	28.95–31.74	15–73
2008	90	5 Jun	29 Sep	28.52–31.69	14–66
2009	158	2 Jun	8 Oct	28.52–31.74	15–70
2010	615	5 May	27 Oct	28.50–31.74	14–83
2011	492	21 May	26 Oct	28.08–31.74	14–85
2012	554	24 Apr	26 Sep	28.08–31.74	17–84
Overall	3,745	17 Apr	5 Nov	28.08–31.98	13–85

between 13 and 85 m (Table 1; Figure 1A). For some analyses, trap sets were grouped into three depth strata to be consistent with longline sampling (see below), defined as <29.0 m, 29.0–48.9 m, and ≥49.0 m. The shallow and intermediate depth strata represented continental shelf waters, and the deep depth stratum represented shelf-break and deeper waters.

Upon capture, all Red Snapper were measured for FL and otoliths were removed and retained for aging. Sagittal otoliths were sectioned and aged using standard methodologies (Cowan et al. 1995; McInerny 2007; Stephen et al. 2011). Red Snapper captured by the trap survey in 2012 were not aged in time to be included here, so only lengths from 2012 Red Snapper were included.

Georgia–Florida (GA-FL) longline survey.—This survey occurred in 2010 and early 2011. Protocols of longline sampling were developed cooperatively by NMFS biologists and advocates from the commercial fishing community. Two commercial fishers were contracted to perform longline sampling using their respective fishing vessels (referred to as fishing vessels A and B). Each vessel was required to have at least one crew member during all surveys who possessed a demonstrated history (e.g., logbook data) of conducting bottom longline trips targeting Red Snapper in the study area. A NMFS Bottom Longline Observer Program fisheries observer was present for all trips to ensure agreed-upon sampling methodologies were followed and to lead data and sample collection efforts.

Longline sets targeting Red Snapper were allocated across three depth strata in federal waters, defined a priori as <29.0 m, 29.0–48.9 m, and ≥49.0 m (Table 2; Figure 1B), and eight latitudinal "bands" defined by half-degree increments between 28°N and 32°N (Figure 1B). Four longline sets were completed within each depth × latitude combination, for a total of 96 longline sets. Hardbottom habitats were targeted, with the specific location of each longline set chosen by the vessel captain. To maximize consistency across depth strata within a latitude band, the same vessel and crew sampled all 12 sets within each band. Sampling occurred between September 24, 2010, and February 2, 2011.

Contract vessels were rigged for bottom longline fishing according to specifications agreed upon by NMFS biologists and contracted fishers. Mainlines were constructed of 3.2-mm-diameter stainless steel cable and were sufficiently long to drop from surface floats to the sea floor, accommodate 150 gangions at 9.1–12.2-m spacings along the sea floor, and rise from the

TABLE 2. Cruise information for the Red Snapper longline study, 2010–2011. Number of sets is the number of longline deployments made during each research cruise.

Vessel	Year	Number of sets	Start date	End date	Latitude (°N)	Depth (m)
A	2010	10	24 Sep	26 Sep	30.1–30.2	20–75
A	2010	2	27 Sep	27 Sep	30.2–30.3	14–22
A	2010	12	25 Oct	28 Oct	30.5–30.8	19–72
A	2010	10	8 Nov	12 Nov	31.1–31.4	18–88
A	2010	14	17 Nov	20 Nov	31.4–31.9	18–75
B	2010	3	9 Dec	10 Dec	29.0–29.2	20–29
B	2010	9	16 Dec	18 Dec	28.8–29.3	19–52
B	2010	2	22 Dec	22 Dec	28.7–28.8	38–43
B	2011	5	5 Jan	6 Jan	29.2–29.3	31–76
B	2011	8	15 Jan	17 Jan	28.2–29.0	30–71
B	2011	9	18 Jan	20 Jan	28.1–28.5	23–76
B	2011	12	30 Jan	2 Feb	29.5–29.7	17–72
	Overall	96	24 Sep	2 Feb	28.1–31.9	14–88

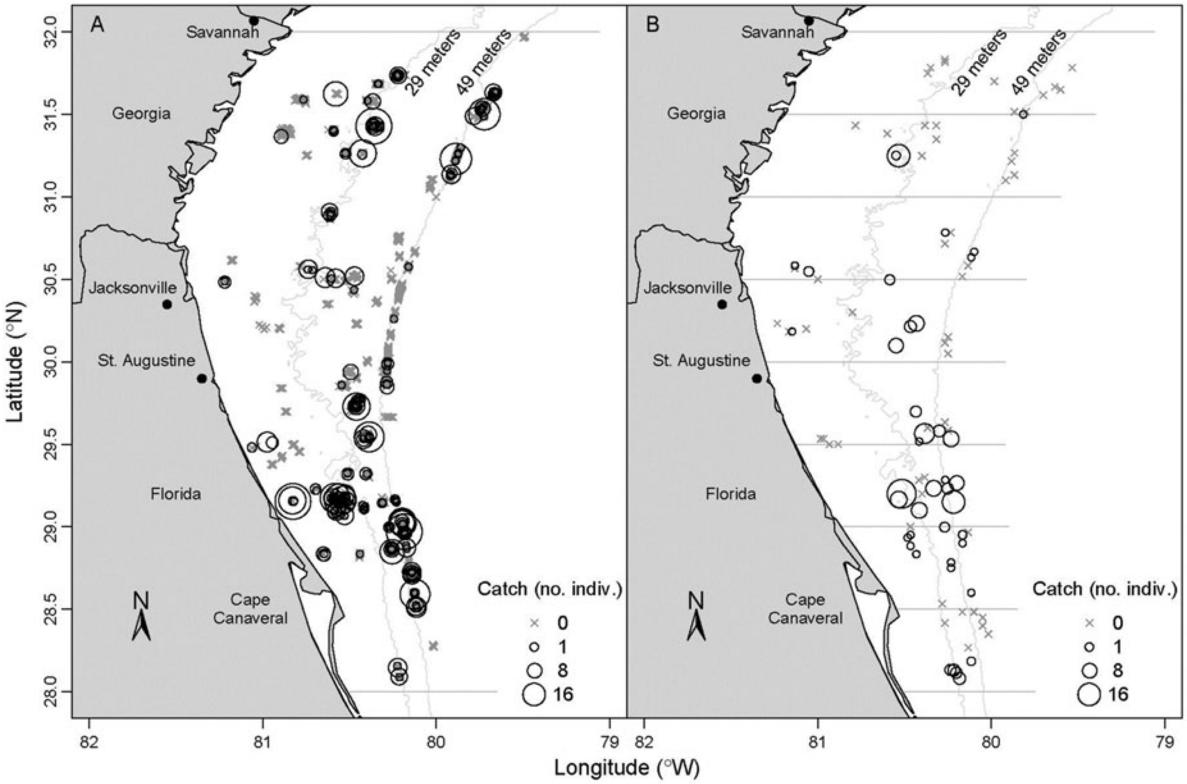

FIGURE 1. Study area in Georgia and Florida showing catches of Red Snapper in (**A**) the trap survey in 1990–2012 and (**B**) the longline survey in 2010–2011. Catch of Red Snapper is shown as either the number of individuals caught per trap or the number of individuals caught per longline set (150 hooks) and is represented by the open circles. Trap or longline sets where no Red Snapper were caught are shown by a gray × symbol. Gray lines are isobaths of 29 and 49 m deep (corresponding to depth strata used in analysis) and horizontal lines delineate latitudinal bands (0.5°N) used in stratification of longline sampling effort.

sea floor to a second set of surface floats (total bottom longline length ≈ 1,500 m). Gangions originated in a medium snap clip connected to a 4/0 swivel and were composed of 4.6 m of 300-lb-test (136 kg) monofilament line that was crimped at the snap clip and snelled to the hook. Hooks were offset circle hooks of sizes 13/0, 14/0, and 15/0 (Mustad 39965, Mustad, Gjövik, Norway) and were fished in a systematically alternating pattern along the mainline (e.g., 13/0, 14/0, 15/0, 13/0, . . .). Hooks were baited with a mixture of imported Indian Oil Sardine *Sardinella longiceps* and Atlantic Mackerel *Scomber scombrus*. Soak time was defined as the elapsed time between the last hook deployed and the first hook retrieved, and was limited to 2 h. All sets were initiated (i.e., first hook deployed) between 0.5 h before sunrise and 0.5 h after sunset.

Trained fisheries observers recorded station-level information and characteristics of the catch, and collected biological samples (e.g., otoliths). All Red Snapper were measured for FL. Otoliths were extracted, processed, and read as described above for Red Snapper captured by the trap survey. However, the number of opaque zones was used as the unadjusted age of the fish from which the otolith was sampled, since longline sampling occurred during the fall and winter when no annuli were being deposited (Baker et al. 2001; Allman et al. 2005).

Commercial hook-and-line data.—The third data source included in our analyses was the Trip Interview Program (TIP), which provided information on commercial fishery landings in the SEUSA. The TIP program is a cooperative effort between NMFS and the various state fisheries agencies in the SEUSA. The TIP program uses port agents to sample the commercial catch from fish being unloaded or already in storage containers at fish houses. Port agents collect length and weight information from randomly selected individuals, as well as obtain biological samples such as otoliths or spines for aging. Moreover, port agents collect information regarding each fishing trip, including the general area and depth ranges where fishing occurred, and the type and quantity of fishing gear used. Here, we focused on commercial hook-and-line catches of Red Snapper caught during a time period (1992–2009) when TIP sampling methods were generally consistent and during which minimum size limits were in place for the commercial fishery. The hook-and-line catches included samples between 28°N and 32°N to be consistent with the geographic range of the trap and Georgia–Florida (GA-FL) longline surveys. Where available, depth ranges spanned the duration of a trip and were not specific to the location where a fish was caught. Often range was not available and only minimum depths were reported.

NMFS-SEFSC annual longline survey.—The NMFS Southeast Fisheries Science Center (NMFS-SEFSC) Mississippi Laboratories has conducted standardized bottom longline surveys in the GOM, Caribbean, and SEUSA waters since 1995 (see Mitchell et al. 2004; Ingram et al. 2005) to generate fisheries-independent data for stock assessment purposes for multiple taxa, including shark, snapper, and grouper species. While survey protocols have varied over time (Ingram et al. 2005), the survey typically has employed 100-hook sets of baited, large (∼15/0) hooks in depths ranging from 9 to 366 m during July–September (Mitchell et al. 2004). The survey does not target specific bottom types or bottom features; however, randomly selected set locations are examined with echosounders prior to gear deployment and if the bottom profile appears prohibitive for survey operations (e.g., containing hardbottom with vertical relief) the set location is moved within 0.93 km of the original location or the station is eliminated if suitable bottom is not found. Thus, gear deployment typically occurs partially or completely over unstructured bottom habitat. We assessed total longline survey effort and Red Snapper catch from SEUSA waters from 1995 to 2012.

Statistical analysis.—We investigated patterns in Red Snapper age, length, and catch over the predictor variables of depth, latitude, gear type, and habitat type. Of the four described data sources, two presented data issues and were not used in all analyses. Specifically, given the nonspecific nature of depths included in the TIP database, commercial hook-and-line data from TIP were only used to analyze age- and length-frequency distributions. Due to low Red Snapper sample size (see Results), data from the NMFS-SEFSC annual longline survey were only used to make inferences about Red Snapper habitat utilization.

For trap and GA-FL longline surveys, we assessed patterns of age- and length-specific depth distributions of Red Snapper using two statistical methods. First, Kolmogorov–Smirnov (KS) two-sample tests were used to determine whether the age or length distributions of Red Snapper caught in traps or on GA-FL longlines were different among the three depth strata (shallow: <29.0 m; middle: 29.0–48.9 m; deep: ≥49.0 m) sampled in this study. Kolmogorov–Smirnov tests are advantageous because they are sensitive to differences in location, dispersion, and skewness of two samples (Sokal and Rohlf 1995). Because only two samples can be compared at a time, three KS tests were used to compare Red Snapper ages (shallow versus deep, middle versus deep, and shallow versus middle) and three additional tests were used for Red Snapper lengths for each gear. We also used two-sample KS tests, separately for traps or GA-FL longlines, to test for differences across depth strata in age and length distributions of smaller (<50 cm FL) and larger (≥50 cm FL) Red Snapper. The 50-cm length was chosen as a cutoff between smaller and larger fish because it approximates the minimum size limit (20 in [51 cm] TL) for Red Snapper in SEUSA waters prior to the 2010 fishery closure. Significance was accepted at $P \leq 0.05$ for all statistical tests; a Bonferroni correction was not used to correct for multiple comparisons due to concerns about the corresponding reduction in power to detect significant effects (Perneger 1998).

Second, linear models were used to test whether the mean age or length of Red Snapper caught in each trap or on each GA-FL longline was related to depth or latitude. Mean age or length for each trap and longline set was used in these analyses due to the potential lack of independence of fish caught in a single collection. Mean age or length was used as the response variable and depth and latitude were included as continuous predictor variables. Only traps or longlines that caught Red Snapper were included in these analyses.

Linear models were also used to test whether Red Snapper catch rates from traps or GA-FL longlines varied as a function of depth and latitude. The response variables were the log-transformed number of Red Snapper caught per trap or longline. Catch per trap or longline (hereafter, CPUE) was not standardized by soak time because preliminary linear models indicated no relationship between soak time and catch per trap ($P = 0.07$) or longline ($P = 0.52$). Depth and latitude were included in both linear models as predictor variables. Depth was included as a categorical variable with three levels (shallow, middle, or deep), and latitude was included as a continuous variable. We also tested for interactions in Red Snapper CPUE between depth and latitude to determine whether Red Snapper depth distribution varied by latitude.

To make inferences about gear-specific age and length selectivities, KS tests were used to compare age and length distributions of Red Snapper collected in the trap survey, GA-FL longline survey, and commercial hook-and-line fishery. Because the commercial hook-and-line fishery data excluded fish smaller than the regulatory minimum size limit (most recently, ~50 cm), we limited comparisons to fish ≥ 50 cm FL.

Finally, to make inferences about the extent to which Red Snapper occurred in association with unstructured (nonhardbottom) habitats, we assessed the number of Red Snapper collected by the NMFS-SEFSC annual longline survey (1995–2012; $N = 789$ longline sets) in SEUSA waters.

RESULTS

A total of 3,745 chevron traps were deployed south of 32°N in the trap survey in 1990–2012 (Table 1; Figure 1). Mean ± SE soak time was 1.64 ± 0.02 h and depths ranged from 13 to 85 m. In terms of GA-FL longline sampling, a total of 96 sets were completed in 2010–2011 (Table 2; Figure 1). Vessel A sampled the northern four latitude bands earlier in the study than Vessel B, which sampled the southern four latitude bands (Table 2). Longlines were set in waters 14–88 m deep (Table 2). Mean soak time was 0.40 ± 0.02 h, and no sets had soak times that exceeded 2 h. From the TIP sampling database, we included 253 commercial hook-and-line fishing trips from 1992 to 2009 that caught at least one Red Snapper (catch: 8.8 ± 0.8 [mean ± SE]; range, 1–71). A total of 668 Red Snapper were caught in the trap survey, 220 were caught in the GA-FL longline study, and 2,233 were sampled from the commercial hook-and-line fishery.

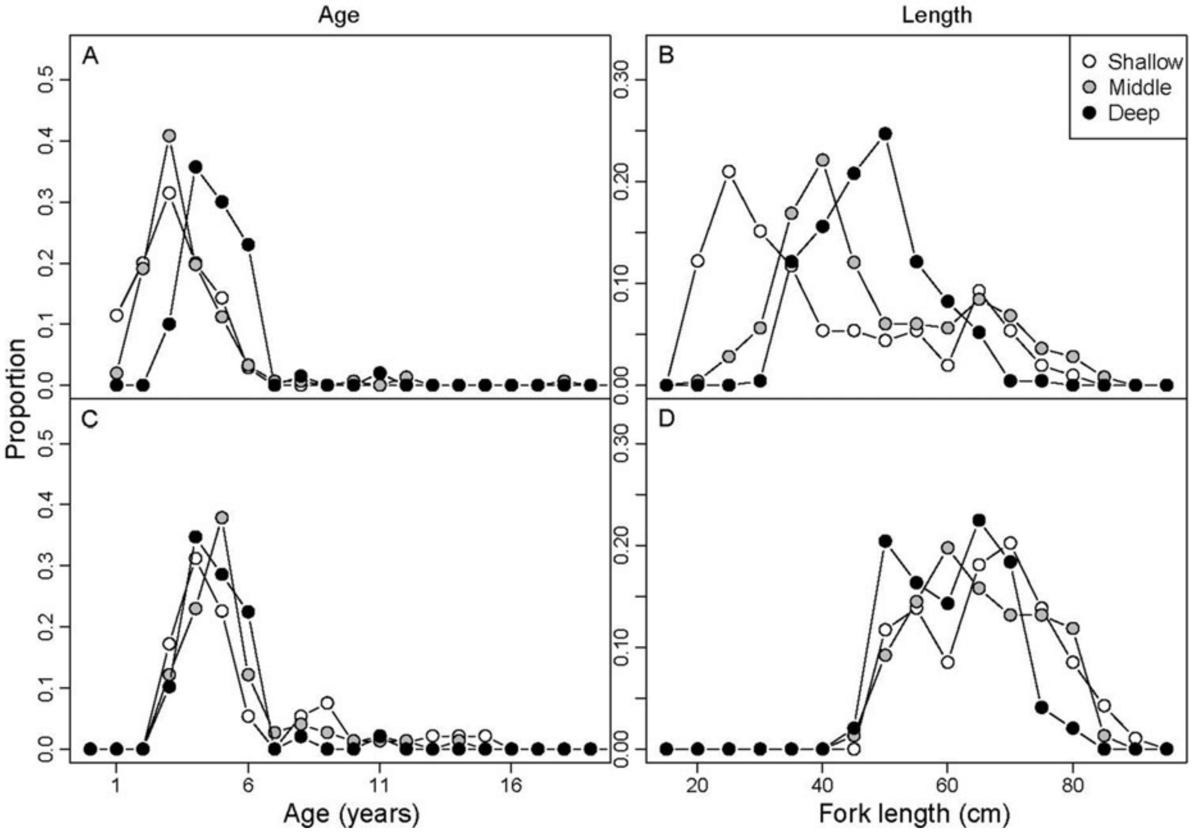

FIGURE 2. (**A**, **C**) Age and (**B**, **D**) length of Red Snapper caught in shallow (<29.0 m; open circles), middle (29.0–48.9 m; gray circles), or deep (≥49.0 m; black circles) depth strata by (**A**, **B**) the trap survey in 1990–2012 and (**C**, **D**) the longline survey in 2010–2011.

There was an effect of depth on Red Snapper age and length distributions in the trap survey, but not in the GA-FL longline survey (Figure 2). In the trap survey, age distributions were significantly different between the middle and deep depth zones (one-tailed KS two-sample distribution tests: $P < 0.01$), but not between the shallow and deep zones or shallow and middle zones (KS tests: $P > 0.05$). Length distributions from traps were significantly different for all depth-zone combinations (KS tests: $P < 0.001$). For both ages and lengths, older and larger fish collected in the trap survey occurred in higher proportions in the deep depth zone compared with the shallow and middle depth zones (Figure 2A, B). In contrast, there was no evidence that Red Snapper caught in the deep stratum were older or larger than those from the shallow or middle strata in the GA-FL longline survey (KS tests: $P > 0.80$; Figure 2C, D).

For smaller (<50 cm FL) Red Snapper, age distributions of fish collected in the trap survey were significantly different between shallow and middle depth zones, and between shallow and deep depth zones, and greater proportions of younger fish were found in the shallow zone (Figure 3A). For smaller Red Snapper collected by GA-FL longline, limited samples sizes ($n = 0$ collected in the shallow depth zone and $n = 1$ collected in each of the middle and deep zones; Figure 3C) prohibited informative statistical comparisons of age distributions as a function of depth zones. For smaller Red Snapper caught in traps, there were significant differences in length distributions across the three depth zones (KS test: $P < 0.001$); the smallest Red Snapper occurred in higher proportions in the shallow depth zone than in the middle and deep depth zones (Figure 4A). For smaller (<50 cm FL) Red Snapper caught in the GA-FL longline survey, length distributions did not differ across depth zones as no fish < 45 cm FL were caught (Figure 4C).

For larger (≥50 cm FL) Red Snapper, age and length distributions across the three depth zones were similar in both the trap (KS tests: $P > 0.50$) and GA-FL longline surveys (KS test: $P > 0.80$) (Figures 3B, D and 4B, D). Using the linear modeling approach, there was no effect of depth on mean age or length of Red Snapper caught in either the trap or GA-FL longline survey ($P > 0.05$ for all tests; Figure 5). Mean age and length of Red Snapper were positively related to latitude in the GA-FL longline survey ($P < 0.01$), but not in the trap survey ($P > 0.05$).

The CPUE of Red Snapper was variable (Figure 6), ranging from 0 to 28 in the trap survey (0.18 ± 0.02 [mean ± SE]) and from 0 to 19 in the GA-FL longline survey (2.4 ± 0.4). Overall, 270 traps (7%) caught Red Snapper, whereas 41 GA-FL

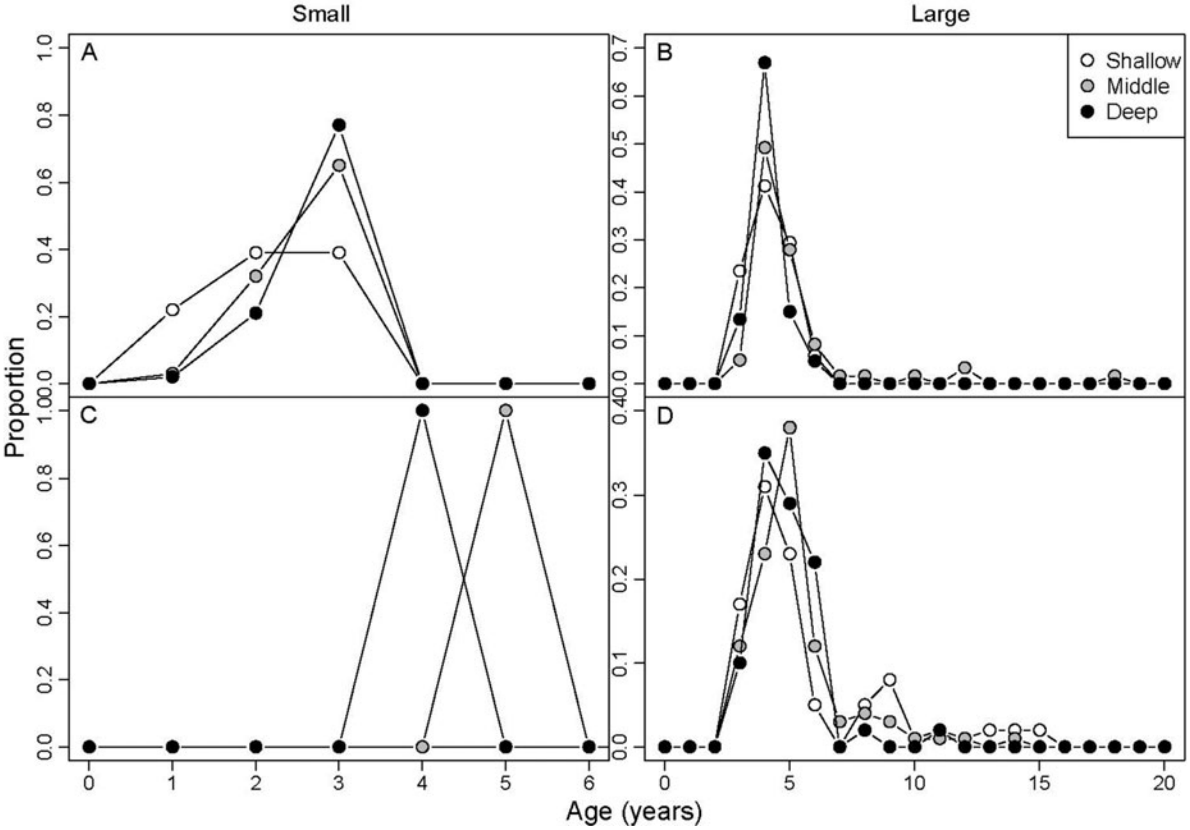

FIGURE 3. Age frequency histograms for (**A**, **C**) smaller (<50 cm FL) or (**B**, **D**) larger (≥50 cm FL) Red Snapper caught in shallow (<29.0 m; open circles), middle (29.0–48.9 m; gray circles), or deep (≥49.0 m; black circles) depth strata by (**A**, **B**) the trap survey in 1990–2012 or (**C**, **D**) the longline survey in 2010–2011.

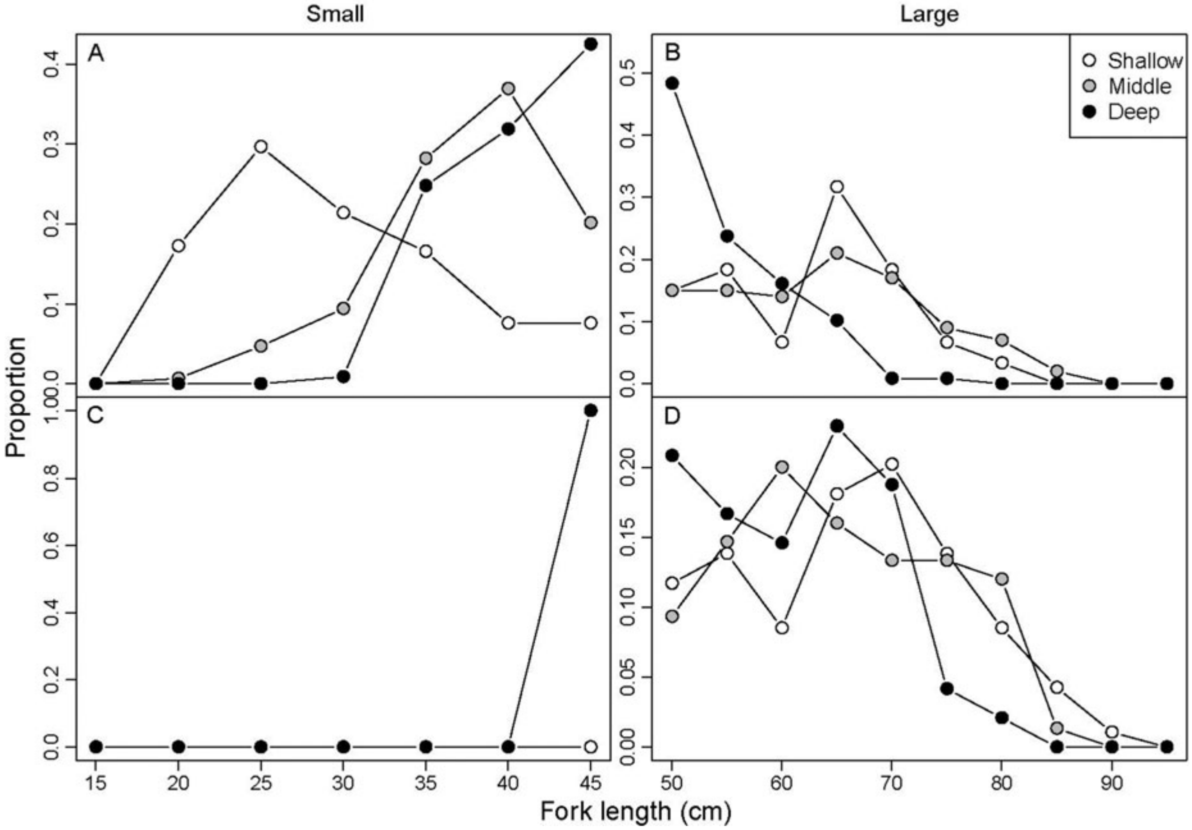

FIGURE 4. Length frequency histograms for (**A**, **C**) smaller (<50 cm FL) or (**B**, **D**) larger (≥50 cm FL) Red Snapper caught in shallow (<29.0 m; open circles), middle (29.0–48.9 m; gray circles), or deep (≥49.0 m; black circles) depth strata by (**A**, **B**) the trap survey in 1990–2012 or (**C**, **D**) the longline survey in 2010–2011.

longlines (43%) caught Red Snapper. Highest CPUE in both surveys occurred just north of Cape Canaveral between 28.5° and 29.5°N (Figure 1). Log-transformed Red Snapper CPUE was not related to depth in either survey ($P > 0.05$), but was significantly and negatively related to latitude in both surveys ($P < 0.01$). Although differences in CPUE were not statistically significant across depth zones, mean CPUE was 30% higher in shallow depths than in deep depths in the trap survey and 94% higher in the GA-FL longline survey (Figure 6).

Red Snapper caught in the trap survey (age: 3.6 ± 1.5 years [mean ± SE]; length: 48 ± 10 cm FL) were generally younger and smaller than those caught by the commercial hook-and-line fishery (age: 4.8 ± 3.9 years; length: 59 ± 10 cm FL) or the GA-FL longline survey (age: 5.4 ± 2.4 years; length: 66 ± 10 cm FL; Figure 7). However, the reason for the difference in mean age or size appeared to be due to traps catching a higher proportion of younger, smaller Red Snapper than the other gears, as opposed to traps missing the older, larger fish (Figure 7). Age and length distributions of fish ≥ 50 cm FL did not differ between the trap survey, GA-FL longline survey, and the commercial hook-and-line fishery (KS test; $P > 0.80$ for all comparisons).

The NMFS-SEFSC annual longline survey database (1995–2012; $N = 789$ longline sets) contained records of 16 Red Snapper collected in SEUSA waters (age range, 2–27 years; length range, 55–90 cm FL; depth of capture range, 31–80 m; depth range sampled, 6–232 m; Figure 8).

DISCUSSION

We found evidence of depth-related variation in Red Snapper age, length, and CPUE in SEUSA waters; greater proportions of older and larger fish occurred in deeper waters and CPUE decreased nominally with depth. However, the depth-related variation in Red Snapper age and length was driven by younger and smaller fish occurring disproportionately in shallower waters, as opposed to older and larger fish occurring disproportionately in deeper waters. In essence, younger and smaller fish (<50 cm FL, approximating the minimum size limit for Red Snapper in SEUSA waters before the 2010 fishery closure) occurred predominantly in relatively shallow waters. For Red Snapper ≥ 50 cm FL, we found no evidence of a positive relationship between depth and Red Snapper age or length. Thus, within the depths where surveys occurred (to 85 m for the hardbottom-targeted trap survey, 88 m for the hardbottom-targeted GA-FL longline survey, and 232 m for the nonhardbottom-targeted NMFS-SEFSC annual longline survey), these results provide no support for assertions of greater abundances of older and larger Red Snapper in deeper

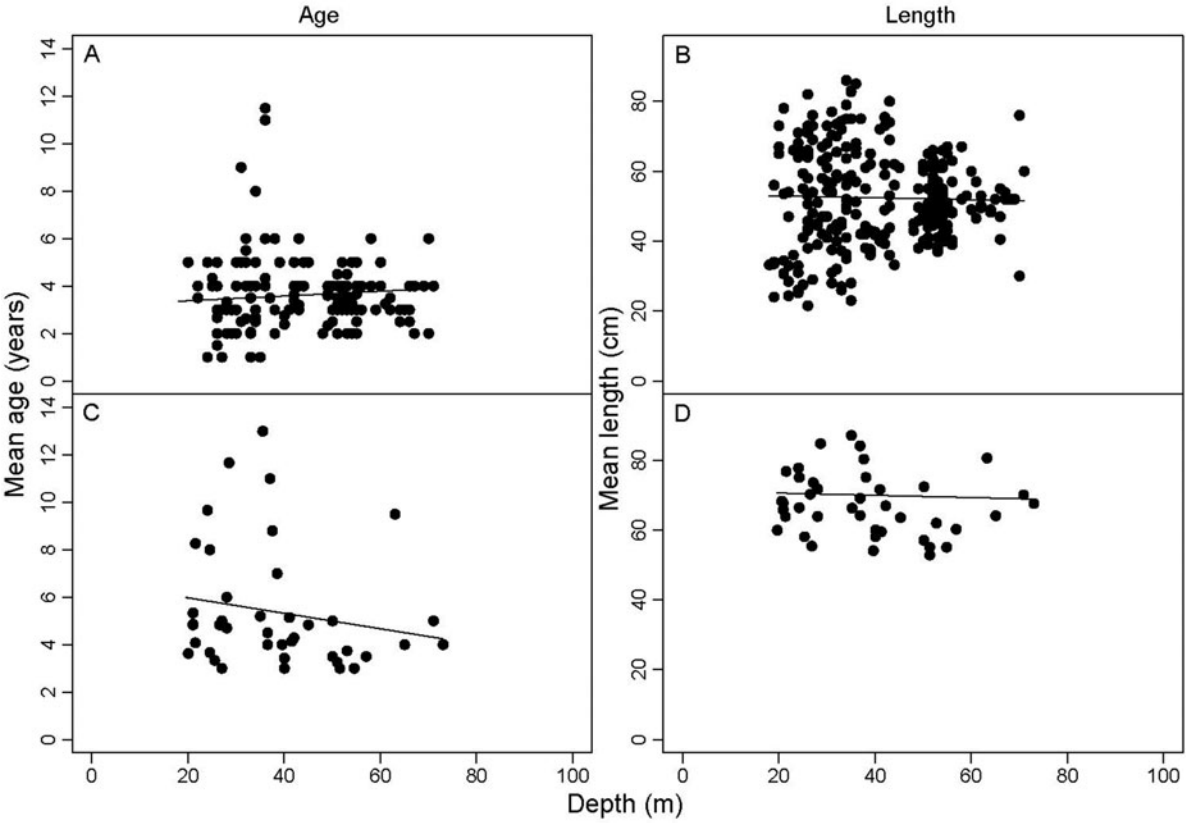

FIGURE 5. (**A**, **C**) Mean age and (**B**, **D**) fork length of Red Snapper caught in various depths in (**A**, **B**) the trap survey in 1990–2012 or (**C**, **D**) the longline survey in 2010–2011. Mean age and fork length were calculated for each trap or longline collection to avoid pseudoreplication, and trend lines indicate linear regression fit.

SEUSA waters. It is possible that relatively older and larger Red Snapper inhabit SEUSA hardbottom habitats in waters deeper than 88 m, and thus the depths sampled by the trap and GA-FL longline surveys were insufficient to document older and larger fish. However, we believe this possibility to be unlikely given that (1) the commercial fishers who performed the GA-FL longline survey essentially had an objective of identifying older and larger Red Snapper in deeper waters, and yet chose to sample in depths no greater than 88 m, (2) the NMFS-SEFSC annual longline survey did not record a significant abundance of Red Snapper in SEUSA waters deeper than 88 m, as was common in the GOM sampling (Mitchell et al. 2004), and (3) Red Snapper have been only infrequently observed in deep-water (>50 m) studies off SEUSA coasts (see Quattrini and Ross 2006; Sedberry et al. 2006; Harter et al. 2009).

Our findings on the relationship between depth and Red Snapper age or length are consistent with conclusions reported in SEDAR 2010 (see their Figure 2.9.1a, b) based on analyses of age- and length-with-depth data pooled from multiple SEUSA fishery-independent and fishery-dependent data sources, but potentially contrast with patterns exhibited by Red Snapper in the GOM. In the GOM, shallower continental shelf waters, particularly in association with artificial habitat, are dominated by relatively young (age 2–4) fish (Gitschlag et al. 2003; Szedlmayer 2007; Gallaway et al. 2009), while older, larger fish are captured more frequently in deeper (>50 m) habitats farther from shore (Mitchell et al. 2004; Henwood et al. 2005; Allman and Fitzhugh 2007; Gallaway et al. 2009). The apparent lack of a positive age- or length-with-depth relationship for larger (exploited size) Red Snapper in the SEUSA could be a natural phenomenon, perhaps due to the narrow width of the continental shelf in SEUSA waters (∼55–75 km off Florida and Georgia coasts), or to a greater availability of reef habitat on the SEUSA continental shelf relative to the GOM (Cowan 2011). Alternatively, the lack of an age- or length-with-depth relationship for larger Red Snapper could be a result of fishing exploitation, in which a majority of older, larger individuals have been removed from the population, precluding the observation of a positive age- or length-with-depth pattern that would be apparent if a greater proportion of older and larger individuals existed (Lindeman et al. 2000). The truncated age distribution of the Red Snapper landed during the study was consistent with the findings of SEDAR (2010), in which a majority of fish were assigned to ages 3, 4, 5, or 6, and few older fish (Figure 2). Given that Red Snapper are a relatively long-lived species (maximum reported age in the study area = 54 years: SEDAR 2010), these

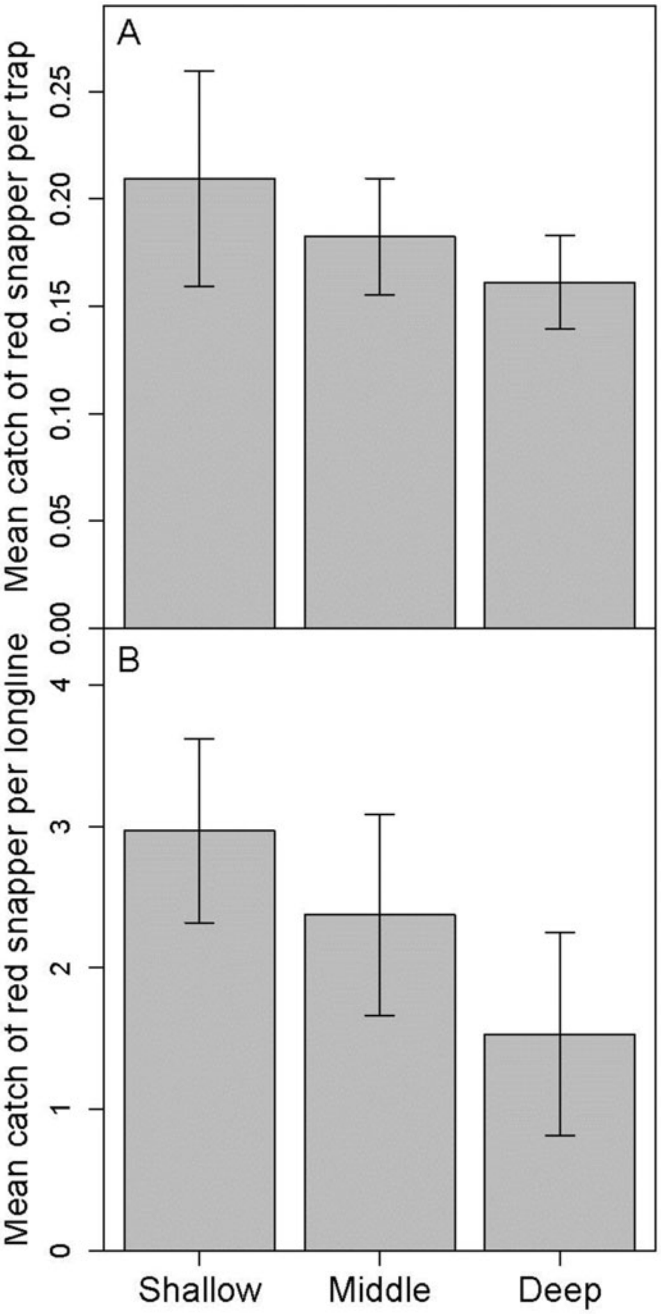

FIGURE 6. Mean catch (number of fish) of Red Snapper in shallow (<29.0 m), middle (29.0–48.9 m), and deep (≥49.0 m) depth strata from (**A**) the trap survey in 1990–2012 and (**B**) the longline survey in 2010–2011. Error bars indicate ± 1 SE.

results are consistent with age-truncation patterns expected in heavily exploited populations (Hsieh et al. 2006). Repeating this study in subsequent years, following increases in SEUSA Red Snapper population size and age structure anticipated to result from the current fishery closure, should allow differentiation between the competing, but not mutually exclusive, explanations of habitat availability versus fishing exploitation underlying the apparent lack of a positive age- or length-with-depth relationship for larger Red Snapper in SEUSA waters.

Importantly, the trap survey and GA-FL 2010 longline survey, which were used to assess age and length distributions, targeted hardbottom habitats. In the GOM, older and larger Red Snapper are thought to become progressively less associated with hardbottom habitats, venturing instead over nonstructured, soft-sediment habitats (Szedlmayer 2007; Gallaway et al. 2009; Cowan 2011). Thus, Red Snapper are regularly collected in GOM waters by the NMFS-SEFSC annual longline survey, which occurs partially or entirely over nonstructured habitats, to an extent that Red Snapper annual abundance indices are generated from that survey for use in GOM stock assessments (Ingram and Pollack 2012). (Note that catch rates in the GOM vary spatially between the eastern and western regions such that rates are considerably lower in the eastern GOM, although catches appear to have increased in recent years [Ingram and Pollack 2012; Figures 1, 2]). In contrast to GOM sampling efforts, only 16 Red Snapper were collected by the NMFS-SEFSC annual longline survey in SEUSA waters over an 18-year period during which 789 longline sets were completed. That the NMFS-SEFSC annual longline survey effectively targets Red Snapper in GOM waters but rarely catches them in SEUSA waters could be explained by (1) regional (GOM versus SEUSA) differences in Red Snapper ontogenic habitat utilization patterns, such that Red Snapper in SEUSA waters do not become less affiliated with hardbottom or structured habitats as they increase in age or size, (2) fewer Red Snapper per unit of preferred habitat area in SEUSA versus GOM waters, in which density-dependent processes cause Red Snapper to use nonreef habitats disproportionately in GOM (relative to SEUSA) waters, (3) a general dearth of older and larger fish in SEUSA waters relative to GOM waters (Cowan 2011), or (4) some combination thereof. Nevertheless, these results suggest that Red Snapper were not widely distributed over nonstructured, soft-sediment habitats in SEUSA waters. Thus, the hardbottom-targeted surveys from which data were analyzed for this study were appropriate for assessing patterns of depth- and latitude-related variation in ages, lengths, and CPUE for Red Snapper in SEUSA waters.

Our ability to make inferences about patterns of age- and length-specific depth distributions of Red Snapper is a function of the fishery-independent gears (chevron trap and longline) used in the surveys we utilized, as well as the seasonality of those surveys and the depths over which they occurred. From a gear standpoint, longlines are used in the GOM to survey Red Snapper (Mitchell et al. 2004; Henwood et al. 2005) and, in outer shelf and upper slope depths, generally sample greater proportions of older fish than do other gears (SEDAR 2005). The GA-FL longline gear used in this study was chosen at the specific recommendation of industry members, with a reasoning that the gear had been successful historically in targeting relatively large Red Snapper in SEUSA continental shelf-break waters. Thus, we believe the combination of longline and trap gears we employed (the latter of which more effectively sampled

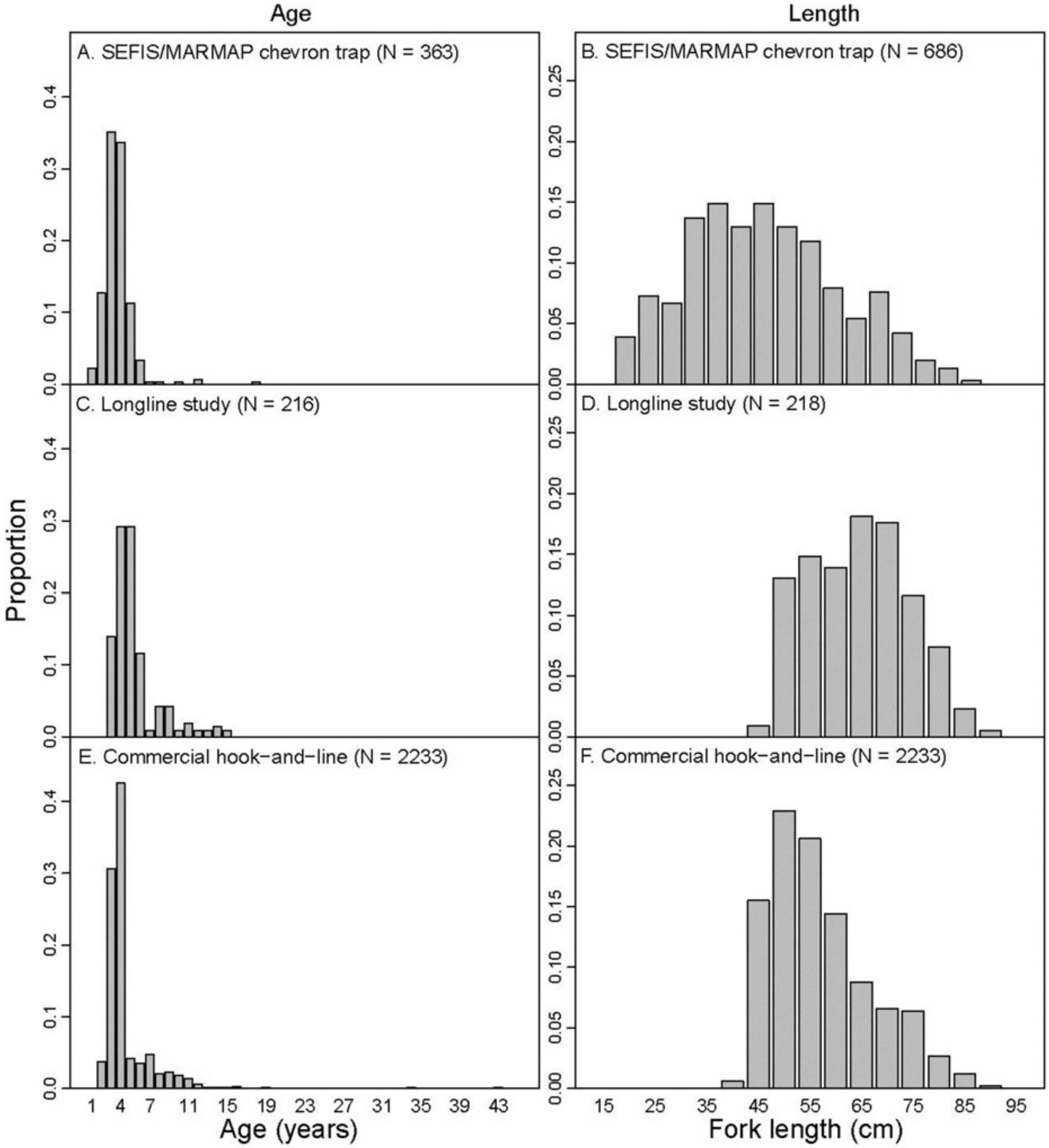

FIGURE 7. Histograms of (**A**, **C**, **E**) ages and (**B**, **D**, **F**) lengths of Red Snapper caught across all depths and latitudinal bands by (**A**, **B**) the trap survey in 1990–2012, (**C**, **D**) longline survey in Georgia and Florida in 2010–2011, and (**E**, **F**) commercial hook-and-line sampling in 1992–2009.

smaller fish than did longlines) was appropriate for assessing patterns of age- and length-specific depth distributions of Red Snapper over the depths covered in the surveys. From a seasonality standpoint, sampling in the trap (April–November) or GA-FL longline (September–February) survey occurred during all months but March. Given the similarity in patterns of age- and length-specific depth distributions generated from each survey and the generally differing seasonality of those surveys, it is unlikely that patterns of Red Snapper age- and length-specific depth distributions vary considerably by season in SEUSA waters, and thus, it is unlikely our results were biased by the seasonality of the fishery-independent surveys we used. From a depth standpoint, while it is possible that relatively high abundances of relatively old and large Red Snapper occur in waters deeper than those covered by the surveys we used (13 to 88 m for the hardbottom-targeted trap and GA-FL longline surveys and up to 232 m for the nonhardbottom-targeted NMFS-SEFSC annual longline survey), surveys in the GOM indicate that a majority of

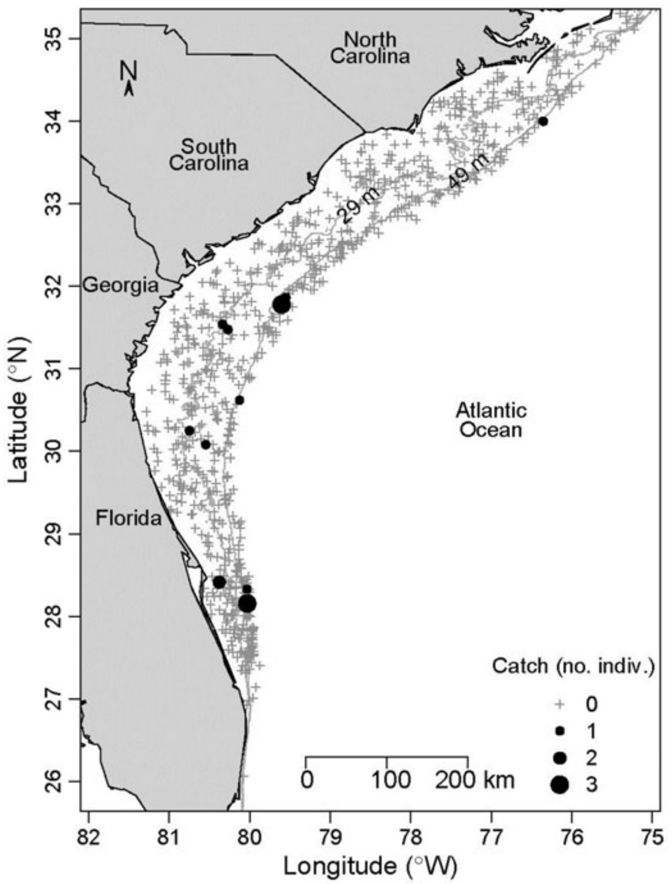

FIGURE 8. Number of Red Snapper caught per gear deployment in the NMFS-SEFSC annual longline survey, 1995–2012; $N = 789$ longline sets.

Red Snapper are caught in depths shallower than 92 m (Mitchell et al. 2004), suggesting the depths covered in this study were appropriate for assessing patterns of age- and length-specific depth distributions of Red Snapper in SEUSA waters.

While assessing depth variation in gear-specific CPUE was not a main objective of this study, we noted that the high variability of CPUE values generated in this study was likely a result of multiple factors, including potential Red Snapper schooling behavior (e.g., McDonough and Cowan 2007) and variability in habitat quality and quantity within the study area. The significant latitudinal trend in CPUE observed in the GA-FL longline survey, in which greater CPUE values occurred in the southern end of the study area, was consistent with prior observations of a SEUSA Red Snapper population centered off north-central Florida (SEDAR 2010).

From a selectivity standpoint, our comparison of age and size distributions between the commercial hook-and-line sector and the trap and GA-FL longline surveys suggests that larger Red Snapper are not underselected by the commercial hook-and-line sector, thus providing no justification for the use of a dome-shaped selectivity function for the Red Snapper commercial hook-and-line sector in SEUSA waters, such as was used in stock assessments for Red Snapper in GOM waters (Cowan 2011). Similarly, our finding of no evidence of a positive relationship between depth and larger (exploited size) Red Snapper age or length provides no support for the use of a dome-shaped selectivity function for Red Snapper in any hook-and-line fishery sector (e.g., commercial, recreational, for-hire) in waters where those sectors are focused. However, given that younger and smaller Red Snapper appear to occur disproportionately in shallower waters (Figures 3, 4), while older and larger Red Snapper appear to be distributed equally throughout the depth range assessed in this study, it is possible that a spatial focus of sector-specific fishing pressure in shallower waters (e.g., as likely occurs for the recreational and for-hire sectors) could result in decreased overall selectivity of older and larger fish (given lower fishing pressure on the fish in deeper depths). This could potentially contribute to a dome-shaped selectivity pattern. Additionally, if the lack of an age- or length-with-depth relationship for larger Red Snapper in the SEUSA is a result of fishing exploitation (in which older and larger Red Snapper have been selectively removed from deeper waters by fishing), then increases in SEUSA Red Snapper population size and age structure expected to occur due to ongoing South Atlantic Fishery Management Council actions could result in dome-shaped selectivity functions becoming more appropriate.

Finally, in terms of ontogeny, it is generally accepted that many marine fish species exhibit shifts to deeper depths (and habitats) as they increase in age and size, resulting in positive relationships between depth and mean age and size. Within the SEUSA and GOM, such ontogenic shifts occur for multiple species with estuarine juvenile phases (e.g., Spot *Leiostomus xanthurus*, Atlantic Croaker *Micropogonias undulatus*, paralichthyid flounders, and Gag *Mycteroperca microlepis*: SEDAR 2006a, 2006b), for at least one fully marine species (Hogfish *Lachnolaimus maximus*: Collins and McBride 2011), and potentially for Red Porgy *Pagrus pagrus* (DeVries 2005). In this study, we found no evidence of a positive relationship between depth and Red Snapper age or length once smaller fish were excluded from the analyses, suggesting that ontogenic depth or habitat shifts cease to occur once a critical age or size is reached. We suggest this phenomenon (cessation of increasing depth with ontogeny once a critical age or size is obtained) may be common and perhaps widespread for reef-associated fish species in SEUSA and GOM waters—e.g., snappers (Lutjanidae), groupers (Serranidae), and grunts (Haemulidae)—and recommend analyses of existing data sets, where possible, to test this hypothesis. Examining populations in which age truncation due to harvest does not occur may be particularly useful.

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