

ARTICLE

Absolute Abundance Estimates for Red Snapper, Greater Amberjack, and Other Federally Managed Fish on Offshore Petroleum Platforms in the Gulf of Mexico

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Abstract

Offshore petroleum platforms provide habitat utilized by an array of reef fish that are valuable to both commercial and recreational fishers. However, thousands of offshore platforms have been decommissioned in the Gulf of Mexico over the past decade, with many of the removals being accomplished using explosive severance methods. Here, we estimate the impact of platform removal in the Gulf of Mexico on five stocks of federally managed reef fish based on the percentage of each stock that is resident on platforms. We conclude that the gulfwide impact of removal will be relatively minor (1% to 8% of the estimated stock abundance) for four species, Red Snapper *Lutjanus campechanus*, Gray Triggerfish *Balistes caprisus*, Vermilion Snapper *Rhomboplites aurorubens*, and Cobia *Rachycentron canadum*. In contrast, losses for the Greater Amberjack *Seriola dumerili* stock would potentially represent 45% of the known stock. An alternative explanation is that the actual abundance of Greater Amberjack is much larger than the most recent stock size estimate; in either case, we suggest this issue needs further examination. Removal impacts could also be significant for reef-fish fisheries (especially the Red Snapper fishery) in areas where platforms are presently abundant but other high-relief natural or artificial reefs are not present. Removal of the platforms from these areas will greatly impact the local fisheries.

It has been long recognized that offshore petroleum platforms in the Gulf of Mexico serve as aggregation points for large numbers of fish representing an array of species (e.g., Gallaway and Lewbel 1982; Stanley and Scarborough-Bull 2003; Stanley and Wilson 2003; Versar 2008; Ajemian et al. 2015; Bolser et al. 2020; Egerton et al. 2021). These aggregations include 25 species of federally managed reef fish that have commercial and/or recreational value, the most valuable of which is the focal species of our study, the Red Snapper *Lutjanus campechanus* (GMFMC 2015). The magnitude of the value of petroleum platforms (and other artificial reefs) as

compared to the value of natural reefs to the Red Snapper population has been frequently debated with no settled resolution (e.g., Gallaway et al. 2009; Cowan and Rose 2016; Karnauskas et al. 2017). In contrast, the value of these platforms to the Red Snapper fishery is much less contentious. In areas of the Gulf of Mexico where platforms (and other artificial reefs) are present, a large but unquantified portion of the Red Snapper landings come from these habitats (Gallaway et al. 2009; Shipp and Bortone 2009; Karnauskas et al. 2017). Karnauskas et al. (2017) noted that for younger year-classes, catch rates on artificial structures were 20 times higher than on natural

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reefs. The platforms are easily located by fishers, Red Snapper densities are high, and the fish remain in close proximity to the structure. As a consequence, they exhibit high rates of fishing mortality on relatively young fish (Everett et al. 2020).

In 2007, there were between 3,500 and 4,000 standing platforms in the Gulf of Mexico. However, the total numbers of offshore platforms began a steep decline after that year (LGL 2017). The reason for the net decline is explained by platform removals (on the order of 200 platforms are being removed each year), and many of these removals used explosives to sever the platforms. As of 2017 and 2018, only 1,260 and 1,171 standing fixed-leg platforms or well protectors were present in the Gulf of Mexico.

In 2016, the U.S. Department of the Interior's Bureau of Ocean Energy Management (BOEM) and Bureau of Safety and Environmental Enforcement initiated an assessment to reevaluate the impacts of explosive platform removals on federally managed commercial and recreational fish and fisheries. Gitschlag et al. (2000, 2003) noted that the explosive removals typically resulted in massive fish kills. While they estimated that the population-level impacts on Red Snapper resulting from platform removal mortality was low, reports of hundreds to thousands of floating dead Red Snapper following the removal explosions are an especially sensitive topic given the limits the government has set on fishery seasons and catch.

The estimates by Gitschlag et al. (2000, 2003) were obtained from a sample of nine platforms, with five of these located in water depths less than 20 m and only one (32 m deep) site was located in water deeper than 30 m. To obtain defensible estimates of platform removal effects on federally managed fish stocks and the associated fisheries, BOEM determined that a larger sample size covering a wider array of depths was necessary. The first step in this process was to obtain absolute estimates of abundance of Red Snapper and other reef fish residing on the platforms, and this paper provides those estimates.

The Red Snapper was selected as the focal species of the study because it is one of the most economically valuable fisheries in the U.S. Gulf of Mexico (Karnauskas et al. 2017). The trends in fishing activities in the past 150 years have led to a depleted stock, which is now under a rebuilding plan (e.g., SEDAR 2013). While Red Snapper was the focal species, four other federally managed fish species were also evaluated in detail as described below. Absolute abundance estimates on offshore petroleum platforms in the Gulf of Mexico in 2017 and 2018 are provided herein for Red Snapper, Cobia *Rachycentron canadum*, Vermilion Snapper *Rhomboplites aurorubens*, Gray Triggerfish *Balistes caprisacus*, and Greater Amberjack *Seriola dumerili*. These data are used to evaluate impacts based on the percentage of the total stock that is resident on platforms.

METHODS

Study area.—Our study area extended from the Alabama–Florida border westward to the Texas–Mexico border (Figure 1). During 2017, a total of 1,260 offshore platforms were present in the study area, and by 2018, the number of platforms had been reduced to 1,171 (Gallaway et al. 2020). Our goal was to sample a total of 30 platforms during each year of the study, 2017 and 2018. Selection of the study sites was based on a stratified-random sampling approach where each stratum was weighted by the number of platforms present. The strata we selected were state Red Snapper management areas (Texas, Louisiana, Mississippi, Alabama) subdivided by depth zone (depths of 10–17, 18–30, 31–90, and 91–300 m). Depth zones were chosen based upon historical patterns of platform fish community distributions (Gallaway and Lewbel 1982). State management area boundaries for Red Snapper were established by the Gulf of Mexico Fishery Management Council in 2019. In this action, the Gulf of Mexico Fishery Management Council delegated management authority of the private angling component for recreational Red Snapper fishing to each Gulf Coast state; that is, each state now manages both federal and state waters for Red Snapper (GMFMC 2019). The total number of platforms for each year, state management zone, and depth zone is shown in Figure 1 and Table 1. The distribution of the randomly selected sites for 2017 and 2018 is shown in Figure 2 and Table 1.

Key species selection.—A total of 246 species of fish have been documented on petroleum platforms in the Gulf of Mexico (Versar 2008). Only 25 of the federally managed species are known to occur on platforms in the Gulf of Mexico (GMFMC 2015), and of those, only 9 fish species have stock assessments available from the Southeast Data Assessment and Review (SEDAR; see Table 2). Since our study period corresponded to the May-to-October season, during which nearly all decommissioning activity takes place, we eliminated King Mackerel *Scomberomorus cavalla* and Spanish Mackerel *Scomberomorus maculatus* because they have only short-duration residence times during the summer months (Gallaway et al. 1981). The Yellowtail Snapper *Ocyurus chrysurus* is not common in the western Gulf (SEDAR 2003, 2020) and was thus not included. Very few groupers were observed in our study, and they were also not included as key species. Hence, we selected five key species for consideration: Red Snapper, Gray Triggerfish, Vermilion Snapper, Greater Amberjack, and Cobia.

Stock assessments for the five focal species have been completed within the past 8 years, and the total numbers at age 2+ for each species in the most recent year available serve as the basis for the comparative analyses presented in this study (Table 3). Numbers at each age across all ages for each species are provided in Appendix 1 of LGL (2019). All five of the focal stocks were overfished at some point in the past and are therefore presently under

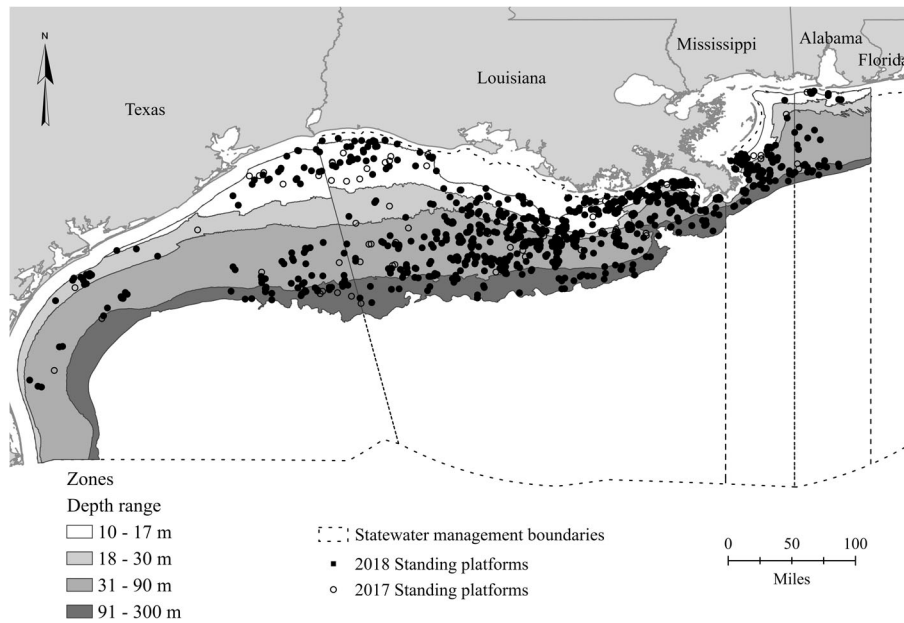


FIGURE 1. The distribution of standing platforms in the Gulf of Mexico by year, private recreational Red Snapper state management area, and depth zone.

TABLE 1. Number of standing platforms and randomly selected study sites (values in parentheses) for fish abundance in the Gulf of Mexico study area by state and depth zone in 2017 and 2018. The data were obtained from the 2019 Bureau of Ocean Energy Management database.

2017					
Depth zone (m)	Total	TX	LA	MS	AL
10–17	374 (7)	30 (1)	297 (6)	39 (0)	8 (0)
18–30	247 (7)	26 (1)	198 (5)	20 (0)	3 (1)
31–90	520 (13)	50 (3)	386 (8)	67 (2)	17 (0)
91–300	119 (3)	31 (0)	66 (3)	13 (0)	9 (0)
Total	1,260 (30)	137 (5)	947 (22)	139 (2)	37 (1)
Percent	100 (100)	11 (17)	75 (73)	11 (7)	3 (3)
2018					
Depth zone (m)	Total	TX	LA	MS	AL
10–17	346 (2)	26 (1)	275 (1)	39 (0)	6 (0)
18–30	229 (10)	23 (2)	186 (8)	17 (0)	3 (0)
31–90	484 (17)	47 (5)	356 (9)	66 (0)	15 (3)
91–300	112 (0)	26 (0)	65 (0)	13 (0)	8 (0)
Total	1,171 (29)	122 (8)	882 (18)	135 (0)	32 (3)
Percent	100 (100)	10 (3)	75 (62)	12 (0)	3 (10)

rebuilding plans. Four of the five focal stocks (Red Snapper, Gray Triggerfish, Vermilion Snapper, and Cobia) have recovered to the point that the most recent assessment concluded that the stocks were not overfished, nor was overfishing occurring (Table 4). By contrast, Greater

Amberjack was still considered overfished and undergoing overfishing at the time of the most recent assessment (SEDAR 2016; Table 4).

Species abundance estimates.—Species abundances were estimated using hydroacoustic surveys coupled with

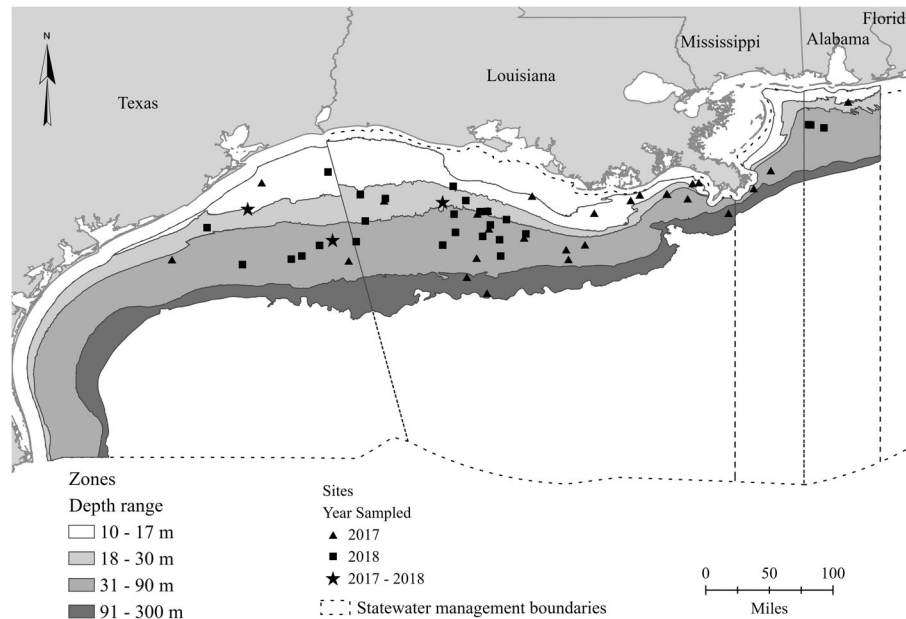


FIGURE 2. The distribution of randomly selected study platforms in the Gulf of Mexico by year, private recreational Red Snapper state management area, and depth zone.

submersible rotating video (SRV) camera surveys and measurement of physical properties of the water column. At each site, hydroacoustic surveys were conducted first, followed by measurement of water column properties and SRV surveys. Additionally, weather conditions (wind strength, wind direction, wave height, current strength and direction) were recorded for each site. The detailed protocols for these surveys are described in LGL (2018a). In addition to these methods, we also conducted hook-and-line sampling at all surveyed sites to obtain specimens of Red Snapper and other reef fish. Determination of length, weight, and sex were recorded for all reef fish collected; age based on otoliths was also determined for Red Snapper. Gallaway et al. (2020) provide details of the methods used and results of this sampling effort. Hook-and-line sampling events also included synoptic SRV and water column property surveys as described below. Some of the age, length, and weight data gathered in the sampling efforts and reported in Gallaway et al. (2020) are used here to clarify age composition and biomass estimates.

Hydroacoustic surveys.—A Simrad EK80 split beam echosounder with a 120-kHz transducer (circular beam width of 6.8°; pulse duration = 0.128 ms; specified ping rate = “max”) was used for the hydroacoustic surveys. Detailed survey methods are also described in Egerton et al. (2021). The echosounder transducer was pole mounted over the starboard side of the survey vessel using a customized bracket, with the transducer face 1 m under the surface of the water aimed directly downwards. Prior to each survey event, the EK80 echosounder was

calibrated using standard methods and a tungsten carbide sphere (Foote et al. 1987). Any offsets between the actual and expected acoustic response from the sphere were applied during data processing.

In hydroacoustic fish surveys, adequate coverage of the survey area is needed to achieve a reliable estimate of fish abundance. Degree of coverage (Λ) is defined as $\Lambda = D/\sqrt{A}$, where D is the cruise track length (m), and A is the size of the planned survey area (m^2). Empirical data from Aglen (1989) showed that adequate coverage requires a ratio of 6:1 or greater. Appropriate total transect lengths were planned for each site to achieve this degree of coverage ratio. While it is important to cover enough area during hydroacoustic surveys, there is always the chance that fish can be counted more than once due to their mobile nature. This cannot be directly accounted for but is an important caveat when conservatively considering results.

The hydroacoustic surveys followed a spiral pattern, commencing as close to the platform as possible and then approximately 20 m further out on each pass, out to a distance of 100 m. Additional transects, towards and away from the platform, were conducted perpendicular to the spiral transects. When possible, the vessel was navigated under the platform (e.g., under walkways) to quantify fish abundance within the structure. A radius of 100 m around a platform was chosen to give confidence that the entire platform-associated fish community was assessed, as previous studies have found that fish densities further than 50 m from platforms were similar to background levels (Stanley and Wilson 1996, 1997, 2000). This resulted in a

TABLE 2. Federally managed Gulf of Mexico species fish species, with those observed on petroleum platforms, those with stock assessments, and species chosen for our study of impacts of platform removal.

Common name	Scientific name	Observed on platforms	With stock assessments	Chosen for impact analysis
Almaco Jack	<i>Seriola rivoliana</i>	X		
Atlantic Goliath Grouper	<i>Epinephelus itajara</i>	X		
Banded Rudderfish	<i>Seriola zonata</i>	X		
Black Grouper	<i>Mycteroperca bonaci</i>			
Blackfin Snapper	<i>Lutjanus buccanella</i>			
Bluefish	<i>Pomatomus saltatrix</i>	X		
Blueline Tilefish	<i>Caulolatilus microps</i>			
Cero	<i>Scomberomorus regalis</i>			
Cobia	<i>Rachycentron canadum</i>	X	X	X
Cubera Snapper	<i>Lutjanus cyanopterus</i>			
Dolphinfish	<i>Coryphaena hippurus</i>	X		
Gag	<i>Mycteroperca microlepis</i>	X	X	
Goldface Tilefish	<i>Caulolatilus chrysops</i>			
Gray Snapper	<i>Lutjanus griseus</i>	X		
Gray Triggerfish	<i>Balistes capriscus</i>	X	X	X
Greater Amberjack	<i>Seriola dumerili</i>	X	X	X
Hogfish	<i>Lachnolaimus maximus</i>	X		
King Mackerel	<i>Scomberomorus cavalla</i>	X	X	
Lane Snapper	<i>Lutjanus synagris</i>	X		
Lesser Amberjack	<i>Seriola fasciata</i>	X		
Little Tunny	<i>Euthynnus alletteratus</i>	X		
Mutton Snapper	<i>Lutjanus analis</i>			
Queen Snapper	<i>Etelis oculatus</i>			
Red Drum	<i>Sciaenops ocellatus</i>	X		
Red Grouper	<i>Epinephelus morio</i>	X		
Red Snapper	<i>Lutjanus campechanus</i>	X	X	X
Scamp	<i>Mycteroperca phenax</i>	X		
Silk Snapper	<i>Lutjanus vivanus</i>	X		
Snowy Grouper	<i>Hyporthodus niveatus</i>			
Spanish Mackerel	<i>Scomberomorus maculatus</i>	X	X	
Speckled Hind	<i>Epinephelus drummondhayi</i>			
Tilefish	<i>Lopholatilus chamaeleonticeps</i>			
Vermilion Snapper	<i>Rhomboplites aurorubens</i>	X	X	X
Warsaw Grouper	<i>Hyporthodus nigrilus</i>			
Wenchman	<i>Pristipomoides aquilonaris</i>	X		
Yellowedge Grouper	<i>Hyporthodus flavolimbatus</i>			
Yellowfin Grouper	<i>Mycteroperca venenosa</i>	X		
Yellowmouth Grouper	<i>Mycteroperca interstitialis</i>			
Yellowtail Snapper	<i>Ocyurus chrysurus</i>	X	X	
<i>n</i> = 39		<i>n</i> = 25	<i>n</i> = 9	<i>n</i> = 5

survey area of 31,400 m² at each site. When a site consisted of multiple joined platforms, it was necessary to survey within a 200-m radius circle (125,600 m²) to encompass all the joined structures.

Hydroacoustic data processing.—Acoustic data were analyzed in cells 20 m long and 10 m deep, chosen as a balance between spatial resolution and including adequate

fish single echoes in each cell for robust calculations. The width of the cells was dependent upon the water depth as it is a function of the spreading of the beam of sound, and the software algorithms normalize for this (Egerton et al. 2021). In each of these cells, fish density was calculated via echo integration (*Sv*/*TS* scaling). In this approach, the backscattering coefficient per volume of

TABLE 3. Gulfwide total numbers at age (0+ and 2+) for five focal species at the most recently assessed year. Eastern and western Gulf data are also provided for Red Snapper. Southeast Data Assessment and Review (SEDAR) reports are given as references.

Species	Area	Total number of age 2+	Total number of age 0+	Year estimated	Reference and year
Red Snapper	Gulfwide	36,738,000	256,277,000	2016	SEDAR 52, 2018
Red Snapper	Eastern Gulf	13,095,000	72,231,000	2016	SEDAR 52, 2018
Red Snapper	Western Gulf	23,643,000	184,046,000	2016	SEDAR 52, 2018
Vermilion Snapper	Gulfwide	30,184,024	63,736,924	2014	SEDAR 45, 2014
Gray Triggerfish	Gulfwide	2,822,750	10,872,330	2013	SEDAR 43, 2015
Greater Amberjack	Gulfwide	695,549	2,674,016	2015	SEDAR 33 update, 2016
Cobia	Gulfwide	423,955	2,054,265	2011	SEDAR 28, 2013

TABLE 4. Stock status for the five focal species in the Gulf of Mexico as reported in their most recent Southeast Data Assessment and Review (SEDAR) assessments.

Species	Undergoing overfishing (Y/N)	Overfished (Y/N)	Year estimated	Reference and year
Red Snapper	N	N	2016	SEDAR 52, 2018
Vermilion Snapper	N	N	2014	SEDAR 45, 2014
Gray Triggerfish	N	N	2013	SEDAR 43, 2015
Greater Amberjack	Y	Y	2015	SEDAR 33 update, 2016
Cobia	N	N	2011	SEDAR 28, 2013

water (S_v) is divided by the target strength (TS) from individual fish. It is relatively straightforward to obtain S_v values per cell; however, acquiring reliable TS is more challenging. In a mixed-species situation such as this, where the species (and size) structures within each acoustic cell is unfeasible to ascertain, the approach was to use in situ mean TS of the fish (derived from the single echoes) within that cell (20×10 m). When no single fish echoes were available to calculate a mean TS per cell, or when the TS estimate was compromised by “multiple echoes” (see Sawada et al. 1993), then the mean TS was smoothed from adjacent cells using the “ $X \times Y$ statistic” operator in Echoview (version 8) with values of 21 “samples” (pings) by 999 “rows” (equating to approximate distances of 5×5 m). Using in situ TS makes the necessary assumption that TS signals in a cell are representative of the schools in that same cell that are scaled via echo integration. Smoothing mean TS signals attempts to reduce the risk of including a mix of species. Other approaches (e.g., using ex situ TS) carry equivalent risks, and established TS -length equations do not exist for the majority of the species encountered in these assemblages. To deal with the absorption of sound through water, time-varied gain (TVG) corrections of $40 \log(R)$ for TS values and $20 \log(R)$ for S_v values were used. R equates to range or distance. A bottom exclusion layer of 1 m was applied, and data from within this layer were not included in the analysis due to the acoustic dead zone (Ona and Mitson, 1996).

Similarly, a surface exclusion of 3 m was applied to the data to remove surface noise from bubbles under the transducer face. Data were conservatively held at a threshold of at -56 dB for S_v values and -50 dB for TS values to discern fish from other particulate material.

Fish density from the Echoview (version 8) processing was given in number of fish per m^3 for each cell. Multiple fish density estimates occurring within a single area were averaged. Fish per ha^3 was calculated by multiplying fish/ m^3 by $10,000 m^3/ha^3$. The center point of the cell data was then plotted using GIS (QGIS version 2.18.9). Polygons were defined by a buffer zone of increasing distance from the platform (e.g., 0–25, 25–50, 50–75, and 75–100 m) and then divided into the four quadrants (north, east, south, and west). Fish volumetric densities were converted into abundance by multiplying mean density values per polygon by the volume of water investigated in that polygon. These abundances were calculated for each 10-m depth interval.

Submersible rotating video surveys.—We adapted the Koenig and Stallings (2015) SRV camera methods to estimate fish species assemblage structure (i.e., the proportion of the total each species represented). The SRV surveys used the following protocol. First, the SRV camera was lowered at each site in a location close to the platform where safe positioning was possible (normally downcurrent). The echosounder was used to avoid areas where the camera could become entangled with the platform legs. A total of 5 min of footage was recorded at each 10-m depth

stratum at prescribed depths at all sites (e.g., near surface, 10 m, 20 m, 30 m). The 5-min time frame was initially selected based on Bohnsack and Bannerot (1986) who noted that the number of new species observed tended to level off after 5 min of observation. The camera was set to complete two 360° rotations every minute, allowing for at least 10 full rotations at a depth. At 30 frames per s, the 5-min rotation yielded 9,000 frames for analysis per depth layer. The largest number of fish within a single frame for each species was recorded for each camera rotation. This resulted in up to 10 values per species per depth layer at a given platform.

As a precaution against artificially inflating estimates of total abundance for the species of interest, when hydroacoustic surveys identified significant aggregations of fish in areas away from the primary SRV sampling point, those fish were directly targeted for an additional SRV deployment. Start and end times of the drops at each depth interval were recorded on every occasion. Data from these surveys targeting specific aggregations of fish were integrated with the other SRV data by using whichever video's data had the higher maximum number for a given species at a given depth. This additional effort was conducted to avoid the overextrapolation of high-density schools to fishes not present in these school.

A generally accepted approach for conservatively estimating the relative abundance of a species is to use the metric MaxN, which is defined as the maximum number of a certain species seen in any single frame of the video record within that depth zone (Campbell et al. 2015). The benefit of this approach is that it ensures that no fish are double counted (Priede et al. 1994; Campbell et al. 2015). However, there is some disagreement in the literature as to whether MaxN is the most appropriate metric. Schobernd et al. (2014) advocate for use of MeanCount, which is estimated by averaging across a series of randomly or systematically selected video frames and was shown to be linearly related to true abundance (TA). However, Campbell et al. (2015) recommends MaxN, arguing that its non-linearity with TA causes nominal bias. Both acknowledge that MaxN from a single frame of a one-directional video seems to exhibit a nonlinear power relationship with TA. Causation was assigned to "screen saturation"; that is, only so many individuals can be seen in a single frame. Therefore, the fraction of individuals counted by MaxN declines exponentially as TA increases. It is therefore possible that highly abundant species may be more undercounted by MaxN than lesser abundant species, causing its proportion in an assemblage structure estimate to be biased low and the other species to be biased high.

Schobernd et al. (2014) used a simulation, a laboratory experiment, and an environmental study to show that MaxN was nonlinearly related to TA as a power function in all three cases, providing increasingly dampened

estimates of abundance with increasing TA (i.e., hyperstability). They concluded, therefore, that MaxN may result in positively biased indices of abundance for declining fish stocks or negatively biased abundance indices when fish stocks are increasing. Alternatively, their MeanCount was suggested to be approximately linearly related to TA and its variability similar to MaxN.

Campbell et al. (2015) further evaluated the performance of these abundance indices applied to a large data set (300 sites/year, 1993–2007). Their study was intended to reveal the potential trade-offs between the two metrics and explore the underlying mechanisms driving their relationships to TA. The most common modeling technique for such data is the delta-lognormal model, whereby the proportion of positive values are modeled with a binomial model and the positive values with a lognormal model; the two model outputs are combined to render the final estimate. Campbell et al. (2015) found the MeanCount metric to underestimate the proportion positively, especially for highly mobile, schooling species, hence biasing this index of abundance low. Conversely, MaxN is more likely to undercount such species when they occur in high abundance due to screen saturation. Ultimately, they found that there was high correspondence between the standardized indices produced through the years analyzed independent of the species evaluated.

However, as one reviewer pointed out, these studies assessed the accuracy and precision of MaxN versus MeanCount in the context of a single species. That is, for a given species, how closely did each index come to estimating TA? In the current study, the response of interest was assemblage structure (i.e., relative abundances of all species sum to one) based on MaxN counts from the SRV survey data. While other studies have used MaxN to estimate species assemblage structures (e.g., Schulz et al. 2012; Asher et al. 2017), to our knowledge no study has addressed the potential for bias in species' proportions due to screen saturation. To address this question, we generated hypothetical species assemblage structures varying in abundance magnitudes across species and compared how well MaxN estimated true species proportions (Appendix).

In short, MaxN rendered assemblage structure estimates that were nominally biased from the true structures despite simulated screen saturation. As these findings are tangential to our overall study, we relegate details on these methods and results to the Appendix for simplicity of presentation. Our core findings are based on the MaxN metric as in a number of other recent studies (e.g., Parsons et al. 2016; Reynolds et al. 2018; Jones et al. 2021; Smith et al. 2021).

To estimate overall abundance from the SRV data, the MaxN counts for each species per platform and depth zone were converted to species proportions, and these proportions were applied to the total fish abundance (estimated from the hydroacoustic surveys) within

that site–depth layer to estimate the abundance of each species.

Data sonde surveys.—At each study site, the physical properties of the entire water column were collected with an EXO3 data sonde. Recorded parameters included turbidity (Formazin Nephelometric Units), total suspended solids (mg/L), temperature (°C), specific conductivity (µS/cm), salinity (ppt), total dissolved solids (mg/L), optical dissolved oxygen (% saturation), dissolved oxygen (mg/L), pressure (psi), and depth (m). Water temperature and salinity data were also used to calculate the speed of sound through water, a necessary step in the calibration of an echosounder.

Statistical analyses and modeling.—The abundance estimation approach combining hydroacoustic and SRV data had to be carefully evaluated. For example, at a given site an estimation of Red Snapper abundance could be accomplished by combining total fish abundance estimated from the hydroacoustic survey with species relative abundances estimated concurrently with an SRV (Koenig and Stallings 2015). This abundance estimate would be wrong if either the total fish abundance or the proportion attributed to Red Snapper was in error. For instance, the hydroacoustic density estimate may have accurately estimated a total abundance of 2,000 fish and was unknowingly comprised of 1,000 Atlantic Bumper *Chloroscombrus chrysurus* and 1,000 Red Snapper. However, if the SRV sample only recorded 10 fish because of poor visibility, for example, nine of which were Atlantic Bumper and only one was a Red Snapper, then the Red Snapper abundance estimate would be biased low (i.e., 200 instead of 1,000). Thus, at a given site, error in the species apportionment would be magnified by the respective estimated total abundance. Averaging across site-specific estimates could then result in a biased overall estimate if an especially egregious apportionment error were unduly weighted by a large total abundance estimate for one of the sites. For this reason, site-specific estimates were not reported. Instead, we modeled the average assemblage structure for a given depth zone and vertical depth layer given average environmental variables and used this output to apportion the corresponding model output of average total fish abundance. In so doing, random errors in species apportionment had a greater chance of canceling each other across sites before being multiplied by the total abundance estimates. The same was true for site-specific errors in the total abundance estimates.

Variables quantifying the number of legs descending from the surface and categorizing a given platform as manned/unmanned were considered but were not used in the final model. The number of legs did not capture the number of total pipes descending to the ocean floor or the complexity of cross structures beneath the surface. We reasoned that the fish assemblage on a manned platform would be exposed more to fishing pressure. However,

during field activities, crew boats were sometimes observed tied to and actively fishing platforms designated as “unmanned” in the BOEM database. For these reasons, these variables were considered poor descriptors and were ultimately dismissed as misleading.

Below we describe how assemblage structure and total fish abundance were modeled separately. For each depth-zone and layer combination, predictions from both models were combined to provide species abundance estimates with confidence intervals. Species abundances were predicted for what we term an “average platform” within each depth zone. One could argue that given the variabilities in substrate type, physicochemical variables, bottom depth, platform complexity, distance from fishing ports, etc., an average platform does not exist. While our estimates may not apply to any single platform within a depth zone, we argue that our average platform estimates yield unbiased expanded abundances when multiplied by the total number of platforms within a given depth zone because they were based on random samples spanning the ranges of the variabilities just mentioned.

Assemblage structure from SRV surveys.—At each site, a survey of assemblage structure was available from the SRV MaxN count observations for each vertical depth layer. That is, the relative abundance of a given species was estimated as its MaxN counts divided by the sum of the MaxN counts for all species. In essence, this response, “assemblage structure,” can be characterized as a nominal multinomial distribution, which we modeled using a generalized logit link function:

$$\log_e \left[\frac{\Pr(y=j|x_i)}{\Pr(y=k|x_i)} \right] = \alpha_{jk} + x_i \beta_{jk}, \quad (1)$$

where, all j th nominal species categories were referenced to a particular species category k (we used the most numerically dominant species for k), x_i is the vector of fixed effects explanatory variables for the i th sample, and α_{jk} and β_{jk} are parameters specific to the j th category and referenced to k . Hence, we modeled the log odds of a fish in the assemblage structure being in the j th category rather than being in the reference category, k , and allowed this relationship to change with the explanatory variables. The likelihood (l_i) for each i th observation was given as

$$l_i = \sum_{j=1}^J y_{ij} \log_e(\lambda_{ij}), \quad (2)$$

where, J is the total number of species in the analysis, y_{ij} is the observed number of individuals in the j th species and i th sample, and λ_{ij} is the predicted number of individuals in the j th species and i th sample. Fixed-effect variables included the categorical variable DepthZone (10–17, 18–30, 31–90, or 91–300 m) and the covariates Layer (vertical

depth bands: 3–12 m [labeled as 1], 13–22 m [labeled as 2], and so on), temperature, and dissolved oxygen (DO). These last two covariates were included as extraneous/nuisance variables to reduce noise and confounding influences; furthermore, they were converted to standard normal deviates (z -scores) within each DepthZone–Layer combination before analysis. Layer was entered as a covariate to allow change in assemblage structure along the vertical depth gradient. Ignoring subscripts and parameters for the right side of the equation, fixed effects for the final model were specified as follows:

$$\lambda_{ij} = \text{DepthZone} | \text{Layer} + \text{Temperature} + \text{DO}, \quad (3)$$

where the operator “|” indicates an interaction of two or more terms and all of the corresponding main effects. We attempted to let the intercept and covariates Temperature and DO vary randomly across subjects defined, with the categorical variable Site nested within each Year–DepthZone combination. Model convergence could not be achieved with this specification so Site could not be modelled as a random variable. Thus, all effects remained fixed. This specification formed a generalized linear model (GLM) for which we estimated parameters with the GLIMMIX procedure in the statistical software SAS 9.4 TS Level 1M5 (SAS Institute 2016).

Total fish abundance from hydroacoustic surveys.—The hydroacoustic surveys provided observations of total fish abundance (TFA) for each site–layer combination. This response was assumed to be from a lognormal distribution, which we modeled with the log link function:

$$\log_e(\text{TFA}_i) = \alpha + x_i\beta + z_ib, \quad (4)$$

where TFA_i = predicted total fish abundance for the i th sample, α is the intercept, x_i is the vector of fixed-effects explanatory variables for the i th sample, β is their corresponding vector of coefficients, and Z_i and b are the random effects and coefficients. The likelihood (l_i) for each i th observation was given as:

$$l_i = -\frac{1}{2} \left\{ \frac{\log[y_i] - \mu_i}{\sigma_i^2} + \log[\sigma_i^2] + \log[2\pi] \right\}, \quad (5)$$

where y_i is the observed total fish abundance for the i th sample, μ_i and σ_i^2 are the respective predicted mean and variance parameters for the log-transformed observations, and π is the constant pi. The same fixed effects variables were used as was described above for modeling assemblage structure. However, as the pattern of fish abundance throughout the water column did not appear to be linear, the term Layer was fit using a cubic B-spline (splLAYER) with three equally spaced knots positioned between the

minimum and maximum values. Ignoring subscripts and parameters for the right side of the equation, fixed effects for the final model were specified as follows:

$$\mu_i = \text{DepthZone} | \text{splLayer} + \text{Temperature} + \text{DO}. \quad (6)$$

The intercept and covariates Temperature and DO were allowed to vary randomly across subjects defined, with the categorical variable Site nested within each year–DepthZone combination. This specification formed a generalized nonlinear mixed model (GNLMM) whose parameters were also estimated with the GLIMMIX Procedure in SAS.

Species abundance and associated variance propagation.—Abundance of each species was predicted by Layer for an average platform within each depth zone as the product of their predicted proportions from the assemblage structure model output and the predicted total fish abundance from the TFA model output. The arithmetic variance of TFA ($\text{Var}[\text{TFA}]$) was given by the method of moments estimator:

$$\text{Var}[\text{TFA}] = e^{2\mu + \sigma^2} (e^{\sigma^2} - 1). \quad (7)$$

Variances from TFA and assemblage structure were then combined using Goodman's (1960) variance of products estimator:

$$\text{Var}[\lambda * \text{TFA}] = \lambda^2 \text{Var}[\text{TFA}] + \text{TFA}^2 \text{Var}[\lambda] - \text{Var}[\text{TFA}] * \text{Var}[\lambda]. \quad (8)$$

RESULTS

A total of 36 taxa were observed and included in our GLM that produced an estimate of abundance for each of these species at an “average platform” in the four depth zones (Table 5). We observed 7, 26, 32, and 13 species (36 total) at study platforms within the depth zones 10–17, 18–30, 31–90, and 91–300 m, respectively. The modeled abundance estimates for the species identified in SRV surveys constituted from 97% to 99% of the total estimated abundance that was modeled for all 36 species within the four depth zones (Table 5).

Model diagnostics for the hydroacoustic predictions of TFA indicated no pattern in the residuals, and the average predicted values agreed well with those observed (Appendix 4 in LGL 2019). Likewise, the predicted values were similar to those observed from SRV counts (Appendix 4 in LGL 2019); however, residuals are not available for multinomial responses. The interaction of DepthZone and Layer (modeled as spline) was significant for the hydroacoustic model of TFA as was the random covariate effect of DO, while Temperature was not statistically significant (Appendix 4 in LGL 2019). All fixed-effect terms

TABLE 5. Model estimates of the median abundance of fish at the "average platform" in the four depth zones defined in this study of fish abundance at Gulf of Mexico petroleum platforms. An asterisk denotes taxa present verified by submersible rotating video observation. SRV = submersible rotating video.

Common name	Scientific name	Depth zone (m)			
		10–17	18–30	31–90	91–300
Almaco Jack	<i>Seriola rivoliana</i>	5 (1–25)	16 (8–32) *	129 (90–183) *	111 (–)
Angelfish sp.	<i>Pomacanthidae</i> sp.	0.4 (0–5)	2 (1–6) *	47 (18–122) *	0.7 (0–3)
Atlantic Bumper	<i>Chloroscombrus chrysurus</i>	4,362 (1,105–17,216) *	6,227 (3,507–11,054) *	841 (585–1,210) *	324 (171–612)
Atlantic Moonfish	<i>Selene setapinnis</i>	19 (4–82)	514 (261–1,011) *	97 (68–138) *	23 (11–47)
Atlantic Spadefish	<i>Chaetodipterus faber</i>	1,815 (463–7,117) *	926 (457–1,876) *	481 (323–716) *	60 (31–115)
Bar Jack	<i>Carangoides ruber</i>	1 (0–9)	4 (2–10)	13 (7–24) *	178 (42–745)
Bermuda Chub	<i>Kyphosus sectatrix</i>	39 (8–179)	162 (89–293) *	838 (545–1,288) *	1,405 (521–3,787)
Black Jack	<i>Caranx lugubris</i>	0.1 (0–4)	0.2 (0–2)	0.1 (0–1)	23 (10–55)
Blue Runner	<i>Caranx chrysos</i>	622 (152–2,539) *	1,712 (956–3,063) *	3,971 (2,805–5,622) *	691 (343–1,390)
Bluefish	<i>Pomatomus saltatrix</i>	2 (0–14)	4 (2–9) *	0.6 (0–1)	0.6 (0–2)
Butterflyfish sp.	<i>Chaetodontidae</i> sp.	0.1 (0–3)	0.4 (0–2)	8 (–) *	0.2 (0–2)
Cobia	<i>Rachycentron canadum</i>	57 (14–230) *	13 (6–26) *	24 (16–36) *	1.4 (0–5)
Crevalle Jack	<i>Caranx hippos</i>	16 (3–76)	148 (83–263) *	326 (234–456) *	2,074 (941–4,571)
Dog Snapper	<i>Lutjanus jocu</i>	0.2 (0–5)	0.1 (0–1)	0.5 (0–2) *	0.05 (0–1)
Filefish sp.	<i>Monacanthidae</i> sp.	– (–)	– (–)	0.2 (0–1) *	– (–)
Gray Snapper	<i>Lutjanus griseus</i>	137 (35–528) *	400 (255–710) *	491 (345–698) *	37 (19–70)
Gray Triggerfish	<i>Balistes capricus</i>	1.3 (0–11)	13 (6–26) *	63 (40–101) *	2 (1–6)
Great Barracuda	<i>Sphyræna barracuda</i>	4 (1–24)	27 (14–51) *	75 (50–113) *	478 (206–1,107)
Greater Amberjack	<i>Seriola dumerili</i>	14 (3–60)	32 (17–59) *	487 (176–1,347) *	587 (313–1,099)
Grouper sp.	<i>Epinephelinae</i> sp.	0.2 (0–5)	0.7 (0–3)	16 (–) *	0.3 (0–2)
Guaguanché	<i>Sphyræna guachancho</i>	3 (0–19)	32 (17–60) *	22 (14–33) *	2 (1–8)
Gulf Menhaden	<i>Brevoortia patronus</i>	67 (17–266)	2,876 (1,642–5,039) *	169 (120–239)	105 (56–197)
Horse-eye Jack	<i>Caranx latus</i>	3 (1–20)	19 (10–37) *	86 (56–133) *	416 (187–925)
King Mackerel	<i>Scomberomorus cavalla</i>	4 (1–23)	81 (45–146) *	38 (26–57) *	5 (2–12)
Leatherjack	<i>Oligoplites saurus</i>	26 (6–106)	105 (59–187)	706 (475–1,051) *	45 (23–86)
Lookdown	<i>Selene vomer</i>	3 (1–16)	26 (14–50) *	107 (72–159) *	8 (5–13)
Ocean Triggerfish	<i>Canthidermis sufflamen</i>	0.6 (0–9)	1 (0–4)	10 (5–17) *	20 (10–42)
Rainbow Runner	<i>Elagatis bipinnulata</i>	13 (3–67)	266 (133–529) *	53 (36–78) *	405 (178–924)
Red Drum	<i>Sciaenops ocellatus</i>	0.1 (0–2)	4 (1–13) *	0.2 (–)	0.2 (–)
Red Snapper	<i>Lutjanus campechanus</i>	359 (94–1,367) *	1,015 (541–1,904) *	2,980 (875–10,152) *	133 (72–246)
Sheepshead	<i>Archosargus probatocephalus</i>	0.3 (0–3)	19 (9–39) *	6 (–) *	1 (–)

TABLE 5. Continued.

Common name	Scientific name	Depth zone (m)			
		10–17	18–30	31–90	91–300
Spanish Hogfish	<i>Bodianus rufus</i>	0.1 (0–2)	0.3 (0–1)	2 (–)*	0.1 (0–1)
Spanish Mackerel	<i>Scomberomorus maculatus</i>	0.2 (0–6)	– (–)*	0.1 (0–1)*	– (–)
Unidentified Fish		142 (39–520)*	250 (140–446)*	276 (196–389)*	13,090 (5,363–31,952)
Vermilion Snapper	<i>Rhomboplites aurorubens</i>	45 (11–180)	118 (67–210)	3,506 (428–28,743)*	57 (30–109)
Yellow Jack	<i>Carangoides bartholomaei</i>	0.8 (0–11)	0.9 (0–3)*	7 (4–13)*	0.5 (0–3)
Total		7,764 (1,975–30,517)	15,014 (8,593–26,234)	15,877 (6,349–39,700)	20,284 (10,169–40,459)
Total taxa verified by SRV observation		7	26	32	13
Total number verified by SRV observation		7,494	14,784	15,707	19,611
Percent of model abundance verified by SRV		96.5	98.5	98.9	96.7

were statistically significant (at $\alpha=0.05$) for the SRV model (Appendix 4 in LGL 2019).

The dominant species at the average platforms within the shallow coastal zone (depth of 10–17 m) were, in order of abundance, Atlantic Bumper (4,362), Atlantic Spadefish (1,815), Blue Runner (622) and Red Snapper (359). These four species comprised 92% of the total number of individuals at the average shallow coastal platform. Numerically dominant species at an average platform in the deeper Coastal Zone (depth of 18–30 m) included Atlantic Bumper (6,227), Gulf Menhaden (2,876), Blue Runner (1,712), Red Snapper (1,015), Atlantic Spadefish (926), Atlantic Moonfish (514), and Gray Snapper (400). Collectively, these species comprised about 91% of the fish present (13,670 of 15,014; Table 5). The dominant species predicted to be associated with the average platform within each of the coastal zones (10–17 m deep and 18–30 m deep) were remarkably consistent with the historical findings (LGL 2017), albeit with one major exception (Atlantic Bumper; see Discussion).

At the average Offshore/Bluewater Platform (depth of 31–90 m) 10 species comprised 93% of the numerical abundance. The 10 dominant species were Blue Runner (3,971), Vermilion Snapper (3,506), Red Snapper (2,980), Bermuda Chub (838), Gray Snapper (491), Leatherjack (706), Atlantic Bumper (841), Greater Amberjack (487), Atlantic Spadefish (481), and Crevalle Jack (326). Again, the results are consistent with historical knowledge (LGL 2017) with the exception of Atlantic Bumper as noted above.

We documented 13 species to occur at shelf edge platforms (depth of 91–300 m) based on SRV surveys (Table 5). Unidentified “baitfish” dominated the estimates of total abundance (13,090 of 20,284 total fish), but the deep platforms, on average, were characterized by Crevalle Jack (2,074) and Bermuda Chub (1,405). Other notable species present included Greater Amberjack (587), Great Barracuda (478), Horse-eye Jack (416), Rainbow Runner (405), and Red Snapper (133). The 13 documented species comprised 97% of the total abundance.

Below, we discuss the five selected species in order of their overall study stock size estimates for age-2+ fish. Red Snapper has the largest stock of our selected species (36.8 million fish), followed by Vermilion Snapper (30.1 million fish), Gray Triggerfish (2.8 million fish), Greater Amberjack (696,000 fish), and Cobia (424,000 fish).

Red Snapper

The Red Snapper is one of the most, if not the most, valuable finfish in the Gulf of Mexico recreational and commercial fisheries (SEDAR 2018). It occurs throughout the Gulf of Mexico and consists of two stocks divided at the mouth of the Mississippi River. The Gulf-wide stock of age-2+ fish is estimated to at nearly 37 million

individuals, with 13 million fish occurring in the eastern Gulf of Mexico and 24 million fish occurring in the western Gulf of Mexico (see Table 3). In our study, Red Snapper ranked fourth in overall abundance (Table 5).

Red Snapper were most abundant at offshore platforms within the bottom depth range of 31–90 m (2,980 fish typically present with a 95% confidence limit [CL] of 875 to 10,152; Table 5), followed by platforms in the bottom depth range of 18–30 m, where 1,015 fish (95% CL: 541 to 1,904) were typically present. About 359 (95% CL: 94 to 1,367) Red Snapper were estimated at shallow platforms (bottom depth of 10–17 m). At deeper platforms (bottom depth of 91–300 m), 133 fish were predicted (95% CL: 72 to 246). Using the median abundance levels calculated by year (2017 and 2018), bottom depth, and state management zone in conjunction with the corresponding number of platforms present by bottom depth and state management zone in 2017 and 2018 (Table 1), we estimated that about 5.3% of the total age-2+ Red Snapper stock resided on platforms in 2017 and 4.9% in 2018 following the removal of 89 platforms (Table 6). Approximately 75% of the age-2+ Red Snapper estimated to occur on offshore platforms in the Gulf of Mexico occurred in the Louisiana management zone.

Vermilion Snapper

The Vermilion Snapper population is centered in the Gulf of Mexico but ranges north to North Carolina and south to Brazil (Grimes et al. 1982). This species occurs in moderately deep (40–300 m) waters, most commonly over rock, gravel, or sand bottoms near the edge of the continental shelf. Vermilion Snapper are generalist predators that feed on benthic and pelagic fishes, shrimp, crabs, polychaetes, cephalopods, and other invertebrates (Sedberry and Cuellar 1993). Vermilion Snapper share similar habitats and diets as Red Snapper, though Red Snapper are more voracious predators. In our study, the Vermilion Snapper ranked fifth in overall abundance of fish present on offshore platforms during 2017 and 2018. Vermilion Snapper were present at all depth zones but were most abundant at platforms within the depth range of 31–90 m. Within this depth range, the average platform harbored 3,506 Vermilion Snapper (95% CL: 428 to 28,743), as shown in Table 5. Using the abundance levels from Table 5 and the numbers of platforms present by bottom depth and state management zone in 2017 and 2018 (Table 1), we estimated that about 6.2% of the total age-2+ Vermilion Snapper resided on platforms in 2017 and a similar percentage, about 5.8%, was estimated for 2018 (Table 7). Given the numbers of platforms in each state management and depth zone, approximately 75% of the total Vermilion Snapper on platforms occurred in offshore Louisiana. Within the water column, this species was most abundant at depths

between 13 and 72 m as compared to shallower and deeper depths.

Gray Triggerfish

The Gray Triggerfish was reported by Gallaway et al. (1981), Gallaway and Lewbel (1982), Stanley and Wilson (2003), and Gitschlag et al. (2000) as being one of the more abundant species associated with platforms at bottom depths greater than 20 m. In this study, Gray Triggerfish were not abundant (ranked 22nd in overall abundance), ranging from about only 1 to 63 fish at the “average platform” over all depths (Table 5). We suspect that this might reflect a discrepancy between our SRV sampling protocol and fine-scale habitat selection of this species. It seems plausible that more Gray Triggerfish were present at our study sites but were within the structure itself where they could not be detected. Based on our estimates, only about 1.0% of the age-2+ Gray Triggerfish stock occurred at platforms (Table 8).

Greater Amberjack

Greater Amberjack ranked 10th in overall abundance in our study (Table 5). The “average platform” within the 31–90-m bottom depth zone was characterized by 487 (95% CL: 176 to 1,347) Greater Amberjacks, and similar numbers were estimated to occur on the average platform within the 91–300-m bottom depth zone (median = 587 fish, 95% CL: 313 to 1,095). A total of 30 Greater Amberjacks were collected by hook-and-line at platforms in the 31–90-m bottom depth zone, and almost all were relatively large fish, averaging over 12.6 kg (28 lb) each. Considering only age-2+ fish, a total of 336,210 fish were at offshore platforms in 2017 and 313,602 fish were present at these habitats in 2018 (Table 9). The estimates suggest that about 48% of the stock resided on platforms in 2017, and that number was reduced to 45% in 2018 due to the removal of 89 platforms. The vast majority of the Greater Amberjack occurred in the Louisiana state management zone where deep platforms are most abundant (Table 9).

Cobia

Cobias are usually thought of as being solitary but are also common in pairs and/or small groups ranging up to eight or more fish. Cobias ranked 21st in total abundance in our study. The numbers of Cobias present on an “average platform” in water depth ranges of 10–17, 18–30, 31–90, and 91–300 m were 57 (95% CL: 14 to 230), 13 (95% CL: 6 to 26), 24 (95% CL: 16 to 36), and 1.4 (95% CL: 0 to 5) fish, respectively (Table 5). Collectively, these numbers, used in combination with the total number of platforms within each depth zone, suggest that 37,045 Cobias were present on platforms in 2017 and 34,350 Cobias were present in 2018 following the removal of 89 platforms between years (Table 10). Approximately 8% to 9% of the

TABLE 6. Estimated abundance of age-2+ Red Snapper (with lower 95% confidence limit [LCL] and upper 95% confidence limit [UCL]) at platforms within each of our four bottom depth zones in 2017 and 2018 and by state and bottom depth zone in 2017 and 2018.

Age 2+ Red Snapper by year and depth zone (median estimates with confidence limits)						
Depth zone (m)	2017			2018		
	LCL	Median	UCL	LCL	Median	UCL
10–17	35,156	134,247	511,258	32,524	124,197	472,982
18–30	133,627	250,774	470,288	123,889	232,499	436,016
31–90	455,000	1,549,523	5,279,040	423,500	1,442,249	4,913,568
91–300	6,835	8,568	24,570	6,433	8,064	23,125
Total		1,943,113			1,807,008	
Age 2+ Red Snapper by state and depth zone, 2017 (median estimates)						
State	Depth zone (m)				Total	
	10–17	18–30	31–90	91–300		
TX	10,769	26,397	148,993	2,232		188,390
LA	106,608	201,025	1,150,223	4,752		1,462,609
MS	13,999	20,306	199,650	936		234,891
AL	2,872	3,046	50,657	648		57,223
				2017 platform total		1,943,113
				Gulf of Mexico stock size		36,738,000
				Percent of stock on platforms		5.3
Age 2+ Red Snapper by state and depth zone, 2018 (median estimates)						
State	Depth zone (m)				Total	
	10–17	18–30	31–90	91–300		
TX	9,333	23,351	140,053	1,872		174,609
LA	98,711	188,842	1,060,827	4,680		1,353,061
MS	13,999	17,260	196,670	936		228,865
AL	2,154	3,046	44,698	576		50,473
				2018 platform total		1,807,008
				Gulf of Mexico stock size		36,738,000
				Percent of stock on platforms		4.9

Gulf of Mexico Cobia stock occurs on platforms, mostly in Louisiana, where platforms are the most numerous (SEDAR 2013).

DISCUSSION

Species Assemblage Structure

Our findings indicate that oil and gas platforms harbor a large number and high density of fish species. The basic structure of fish communities by depth was found to be similar to historical descriptions (e.g., Gallaway and Lewbel 1982). Platforms in the Gulf of Mexico continue to harbor large numbers of Atlantic Spadefish, Bluefish, Blue Runner, Lookdown, Atlantic Moonfish, and Red

Snapper. The major exception was Atlantic Bumper. This species was observed in our study to be the most abundant species at coastal platforms in the depth range of 10–30 m (Table 5). It was not listed by Gallaway and Lewbel (1982) as even being present on Gulf of Mexico platforms, nor was it listed as being seen at coastal platforms in the northern Gulf of Mexico by Stanley and Wilson (1997, 2003) or by Stunz et al. (2016) for platforms offshore of southern Texas. In contrast, Reeves (2015), Munnely (2016), and Reeves et al. (2019) observed that Atlantic Bumper were abundant at coastal platforms offshore of Louisiana by the mid-2000s.

Chesney et al. (2000) noted that Gunter (1936) reported that Atlantic Bumper ranked 22nd in abundance in shrimp trawl bycatch in the 1930s, but by the mid-1990s,

TABLE 7. Estimated abundance of age-2+ Vermilion Snapper (with lower 95% confidence limit [LCL] and upper 95% confidence limit [UCL]) at platforms within each of our bottom depth zones in 2017 and 2018 and by state and bottom depth zone in 2017 and 2018.

Age 2+ Vermilion Snapper by year and depth zone (median estimate with confidence limits)						
Depth zone (m)	2017			2018		
	LCL	Median	UCL	LCL	Median	UCL
10–17	4,114	16,708	67,320	3,806	15,457	62,280
18–30	16,549	29,242	51,870	15,343	27,111	48,090
31–90	222,560	1,823,235	14,946,360	207,152	1,697,011	13,911,612
91–300	3,570	6,783	12,971	3,360	6,384	12,208
Total		1,875,967			1,745,963	
Age 2+ Vermilion Snapper by state and depth zone, 2017 (median estimate)						
State	Depth zone (m)				Total	
	10–17	18–30	31–90	91–300		
TX	1,340	3,078	175,311	1,767		181,496
LA	13,268	23,441	1,353,401	3,762		1,393,872
MS	1,742	2,368	234,917	741		239,768
AL	357	355	59,606	513		60,831
				2017 platform total		1,875,967
				Gulf of Mexico stock size		30,184,024
				Percent of stock on platforms		6.2
Age 2+ Vermilion Snapper by state and depth zone, 2018 (median estimate)						
State	Depth zone (m)				Total	
	10–17	18–30	31–90	91–300		
TX	1,161	2,723	164,792	1,482		170,159
LA	12,285	22,020	1,248,214	3,705		1,286,225
MS	1,742	2,013	231,411	741		235,906
AL	268	355	52,593	456		53,673
				2018 platform total		1,745,963
				Gulf of Mexico stock size		30,184,024
				Percent of stock on platforms		5.8

Atlantic Bumper ranked 7th in abundance in the shrimp trawl bycatch (Adkins 1993). Many possible factors may have contributed to this and other changes in faunal assemblages. Chesney et al. (2000) focused on eutrophication and hypoxia as being possible factors accounting for Atlantic Bumper increases over time but also suggested that installation of offshore oil and gas platforms may have been a contributing factor. Whatever the reason, the Atlantic Bumper, a forage species, has become the dominant species on coastal platforms in the northern Gulf of Mexico in recent years (since about 2015). Apparently, it was not abundant or even present on platforms from the 1970s to the early 2000s.

In 2018, the last year of our study, offshore petroleum platforms harbored 4.9% of the total age-2+ Red Snapper stock in the Gulf of Mexico, 5.8% of the age-2+ Vermilion Snapper stock, 1.2% of the age-2+ Grey Triggerfish stock, and 8.1% of the age-2+ Cobia stock. In contrast, 45.1% of the total Gulf of Mexico age-2+ Greater Amberjack stock was estimated to occur on offshore petroleum platforms in 2018. We provide additional detail for Red Snapper and Greater Amberjack below.

Red Snapper

Karnauskas et al. (2017) estimated that only about 2.3% of the total Red Snapper stock occurred on

TABLE 8. Estimated abundance of age-2+ Gray Triggerfish (with lower 95% confidence limit [LCL] and upper 95% confidence limit [UCL]) at platforms within each of our bottom depth zones in 2017 and 2018 and by state and bottom depth zone in 2017 and 2018.

Age 2+ Greater Amberjack by year and depth zone (median estimates with confidence limits)						
Depth Zone (m)	2017			2018		
	LCL	Median	UCL	LCL	Median	UCL
10–17	42	485	4,114	39	449	3,806
18–30	1,482	3,174	6,311	1,374	2,943	5,851
31–90	20,800	32,973	52,520	19,360	30,690	48,884
91–300	119	251	714	112	236	672
Total		36,883			34,318	
Age 2+ Greater Amberjack by state and depth zone, 2017 (median estimates)						
State	Depth zone (m)				Total	
	10–17	18–30	31–90	91–300		
TX	39	334	3,170	65		3,609
LA	385	2,544	24,476	139		27,545
MS	51	257	4,248	27		4,583
AL	10	39	1,078	19		1,146
				2017 platform total		36,883
				Gulf of Mexico stock size		2,822,750
				Percent of stock on platforms		1.3
Age 2+ Greater Amberjack by state and depth zone, 2018 (median estimates)						
State	Depth zone (m)				Total	
	10–17	18–30	31–90	91–300		
TX	34	296	2,980	55		3,364
LA	357	2,390	22,574	137		25,458
MS	51	218	4,185	27		4,481
AL	8	39	951	17		1,014
				2018 Platform Total		34,318
				Gulf of Mexico stock size		2,822,750
				Percent of stock on platforms		1.2

platforms and that ages 1 and 2 were the dominant age-classes present in these habitats. However, their platform surveys were restricted in time (about 12 d in late August and early September of 2007) and space (Alabama to Louisiana, 87°W to 92°W). Sampling this late in the season resulted in the collections containing a high proportion of age-1 fish (~65 of 138 aged fish) in the catch followed in abundance by age-2 fish (~55 of 138 aged fish). The samples we summarize here were obtained from May to October in both 2017 and 2018, with effort distributed over the area from southern Texas to Alabama (see Figure 1). We concur with Karnauskas et al. (2017) that the fraction of the total Red Snapper stock that occurs on platforms is small (5% in this study and 2% in

the Karnauskas et al. [2017] study). However, contrary to Karnauskas et al. (2017), we found that composition was not predominantly young fish at all depths. Age increased by depth. Red Snapper that were 2–3 years old were the dominant age-group for the 10–17-m depth zone, age 3 was the dominant age-group for the 18–30-m depth zone; and age 5 was the dominant age-group for the depth zone between 31 and ≥90 m (Figure 3). Late age-1 recruits were relatively scarce over time and area sampled as described by Gallaway et al. (2020).

At one time, based on early total stock size estimates and estimates of Red Snapper abundance on platforms, we believed that 70% to 80% of the age-2 Red Snapper stock occurred on platforms, assuming that both the

TABLE 9. Estimated abundance of age-2+ Greater Amberjack (with lower 95% confidence limit [LCL] and upper 95% confidence limit [UCL]) at platforms within each of our bottom depth zones in 2017 and 2018 and by state and bottom depth zone in 2017 and 2018.

Age 2+ Greater Amberjack by year and depth zone (median estimates with confidence limits)						
Depth Zone (m)	2017			2018		
	LCL	Median	UCL	LCL	Median	UCL
10–17	1,122	5,226	22,440	1,038	4,835	20,760
18–30	4,199	7,910	14,573	3,893	7,334	13,511
31–90	91,520	253,279	700,440	85,184	235,744	651,948
91–300	37,247	69,795	130,781	35,056	65,689	123,088
Total		336,210			313,602	
Age 2+ Greater Amberjack by state and depth zone, 2017 (median estimates)						
State	Depth zone (m)				Total	
	10–17	18–30	31–90	91–300		
TX	419	833	24,354	18,182		43,787
LA	4,150	6,341	188,011	38,710		237,212
MS	545	640	32,634	7,625		41,444
AL	112	96	8,280	5,279		13,767
				2017 platform total		336,210
				Gulf of Mexico stock size		695,549
				Percent of stock on platforms		48.3
Age 2+ Greater Amberjack by state and depth zone, 2018 (median estimates)						
State	Depth zone (m)				Total	
	10–17	18–30	31–90	91–300		
TX	363	737	22,893	15,249		39,242
LA	3,843	5,956	173,399	38,123		221,321
MS	545	544	32,147	7,625		40,861
AL	84	96	7,306	4,692		12,178
				2018 Platform Total		313,602
				Gulf of Mexico stock size		695,549
				Percent of stock on platforms		45.1

stock size and platform abundance estimates were correct (Gallaway et al. 2009). As described by Karnauskas et al. (2017), it was subsequently determined that the stock sizes estimated in SEDAR (2005), the estimate that was available to Gallaway et al. (2009), had been greatly underestimated. Using the revised estimates of age-2 stock size found in SEDAR (2013; 4.3 million fish) and the same approach used by Gallaway et al. (2009), Karnauskas et al. (2017) determined that only about 25% of the age-2 Red Snapper stock occurred on platforms. Notably, the SEDAR (2018) Red Snapper stock assessment further decreased the age-2 stock size estimate present at the beginning of 1992 to 3.5 million

fish. If this estimate is used, then 28% of the age-2 stock occurs on platforms.

Nevertheless, 25% to 28% of the age-2 population occurring on platforms is disproportionate to the relative amount of habitat in the Gulf of Mexico. Offshore petroleum platforms at their maximum number provided only about 12.1 km² of high-relief reef habitat compared to about 1,578 km² of natural reef habitat (Gallaway et al. 2009). Thus, 25% to 28% of the age-2 population occurs on <1% of the habitat. On a per area basis, that translates into 1 km² of platform habitat harboring about 43 times more Red Snapper than 1 km² of natural reefs.

TABLE 10. Estimated abundance of age-2+ Cobia (with lower 95% confidence limit [LCL] and upper 95% confidence limit [UCL]) on platforms within each of our bottom depth zones in 2017 and 2018 and by state and bottom depth zone in 2017 and 2018.

Age 2+ Cobia by year and depth zone (median estimates with confidence limits)						
Depth zone (m)	2017			2018		
	LCL	Median	UCL	LCL	Median	UCL
10–17	5,236	21,365	86,020	4,844	19,765	79,580
18–30	1,598	3,216	6,391	1,482	2,981	5,925
31–90	8,320	12,303	18,720	7,744	11,451	17,424
91–300	21	162	595	20	152	560
Total		37,045			34,350	

Age 2+ Cobia by state and depth zone, 2017 (median estimates)					
State	Depth zone (m)				Total
	10–17	18–30	31–90	91–300	
TX	1,714	338	1,183	42	3,277
LA	16,966	2,578	9,133	90	28,766
MS	2,228	260	1,585	18	4,091
AL	457	39	402	12	910
				2017 platform total	37,045
				Gulf of Mexico stock size	423,955
				Percent of stock on platforms	8.7

Age 2+ Cobia by state and depth zone, 2018 (median estimates)					
State	Depth zone (m)				Total
	10–17	18–30	31–90	91–300	
TX	1,485	299	1,112	35	2,932
LA	15,709	2,421	8,423	88	26,642
MS	2,228	221	1,562	18	4,028
AL	343	39	355	11	748
				2018 Platform Total	34,350
				Gulf of Mexico stock size	423,955
				Percent of stock on platforms	8.1

Karnauskas et al. (2017) also stated that, in some areas of the Gulf of Mexico, a large portion of the Red Snapper landings comes from artificial reefs. They

specifically mentioned that this was true for the Alabama Artificial Reef Zone, where artificial structures were estimated to contain approximately 80% of the total Red Snapper biomass in the area. They also noted that in other locations, platforms can provide most structure for age-1 and age-2 Red Snapper. They state, however, that given the low fraction of the Red Snapper population associated with artificial structures overall, the potential for population-level effects (either positive or negative) from harvest of Red Snapper from these habitats is relatively low. While we concur with this general assessment, we provide the caveat that the effects can be highly significant on a regional fishery basis.

Gallaway et al. (2020) show that 95% (1,115 of 1,171) of the offshore platforms remaining in the Gulf of Mexico in 2018 were within a 160.9-km (100 mi) radius of a major fishing port. Ultimately, the loss of these habitats will affect local directed reef-fish fisheries, especially those in the Louisiana and Mississippi state management areas (Figures 1 and 2). Hard-substrate habitat within the Louisiana management area (not including pipelines and pipeline crossings) consists of 866 offshore platforms (plus 161 caissons and 4 well protectors); 372 toppled oil platforms and bases located in 91 permitted artificial reef areas; and, based on analysis of existing natural bank topography data, 448 km² of natural bank habitat. While large in area, the natural banks consist of only 13 discrete or named banks, mostly located well offshore at the shelf edge. On a numerical basis, offshore platforms (including caissons and well protectors) thus constitute about 72% of the known, discrete reef habitats (1,031 of 1,363 sites). The loss of 72% of the known fishing sites in the Louisiana management area would likely have significant impacts on the local fisheries. The same is presumably true for Mississippi; Texas and Alabama fisheries would be less impacted.

For example, in Figure 4, we show a large area offshore of western Louisiana that is dominated by mud and sand sediments and contains no gravel (an index of age-0 and age-1 juvenile rearing habitat) or rock substrates (an index of natural high-relief habitats for age-2 to age-10 Red Snapper; Buczkowski et al. 2006). Our study site platforms are shown as stars, and dark circles represent other platforms present in the area. Each of the 312 platforms within this polygon, on average, was populated by 1,220 age-2+ Red Snapper. The average weight of these fish was 2.02 kg. Thus, a total of 768,893 kg (1.7×10^6 lb) of Red Snapper were present in this area that would otherwise not have been present in the absence of any platforms. There were no natural adult habitat areas within the depicted soft-bottom polygon, or within 6–8 km of the polygon border. The Louisiana total recreational harvest of Red Snapper in 2016 was estimated to

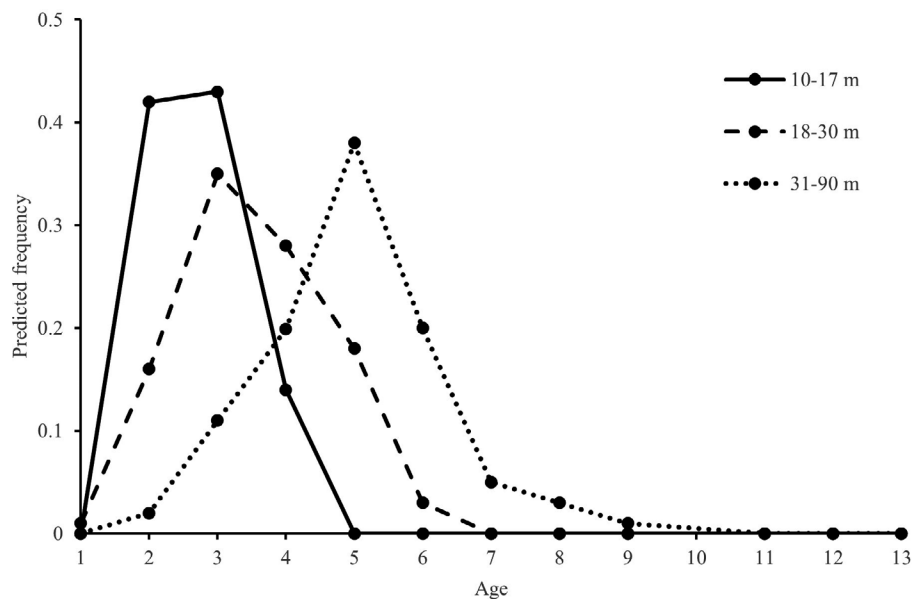


FIGURE 3. Age distribution of Red Snapper at offshore platforms in the Gulf of Mexico grouped by depth zone (10 to 17 m, 18 to 30 m, and 31 to ≥ 90 m). The source of data is Figure 7 in Gallaway et al. (2020).

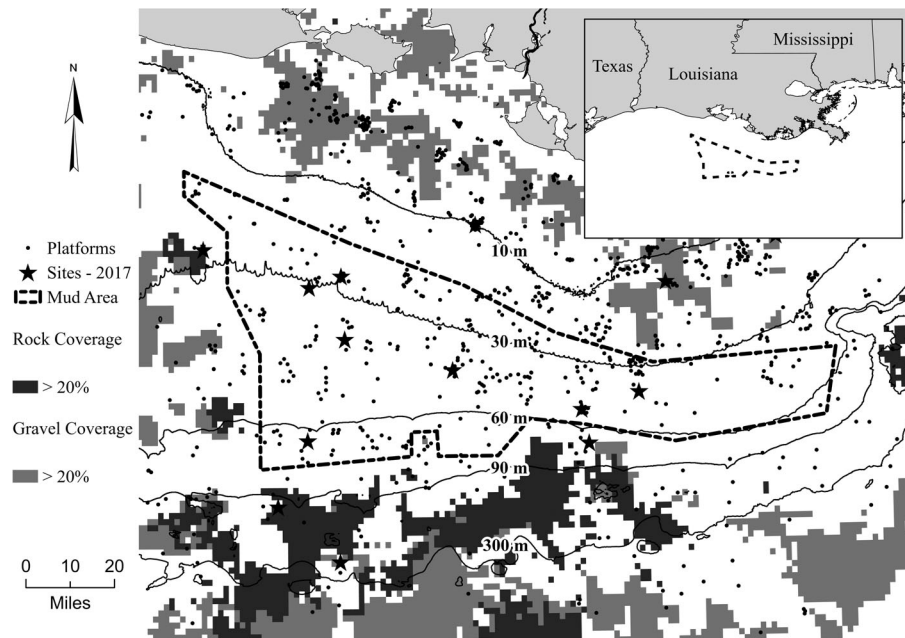


FIGURE 4. An area offshore of western Louisiana dominated by mud and sand substrates (polygon bounded by dashed line), where no rock or gravel substrates or charted natural reefs are present. However, 312 platforms were present in this area in 2017.

have been 496,675 kg (1,103,723 lbs). (A. Lasseter, Gulf of Mexico Fishery Management Council, personal communication), which is about the same as the biomass of Red Snapper within our polygon. The ultimate removal of all the platforms in this large area will have a major impact on the Red Snapper fisheries with a

disproportionately large negative effect on recreational fisheries that target platforms in western Louisiana.

Greater Amberjack

Our finding that 48% of the total Gulf of Mexico Greater Amberjack stock resided on platforms in 2018

and that 45% of the total stock was still present in 2019 following removal of 89 platforms was surprising. If true, platform removal has the potential to have dramatic impacts on the Gulf of Mexico Greater Amberjack stock. This stock is currently considered to be overfished and overfishing is occurring (SEDAR 2016). In contrast, the Atlantic stock of Greater Amberjack appears healthy and is not considered to be overfished and overfishing is not occurring. We suspect that differences in fishing effort and landings between the eastern and western Gulf of Mexico, combined with a high degree of site fidelity for this species, may help explain the differences in stock status, as outlined below. We first provide a brief life history overview for context.

Greater Amberjack are found circumglobally in subtropical and temperate waters. Greater Amberjack live a maximum of 15 years and reach a maximum weight of 81 kg. Males reach a maximum size of 1,814 mm FL and females reach a maximum size of 1,940 mm FL (SEDAR 2014). They have been documented between the surface and 360 m (Randall 1995) and captured in the Gulf of Mexico as deep as 355 m (Gulak and Carlson 2013) but are most commonly captured in depths of 80–91 m. They range from coastal pelagic environments to deep reef drop-offs, from the surface to the bottom, and often but not exclusively associated with structure. Stanley and Wilson (2003) found this species to be most abundant (1,052 fish) at a platform 200 m deep, and next most abundant (289 fish) at a platform in 60-m-deep water. In our study, we found Greater Amberjack most abundant (500 to 600 fish per platform) at platforms located between depths of 30 and 300 m.

The spawning season for Greater Amberjack extends from March to June but peaks during April and May (Cummings and McClellan 1996; Harris et al. 2007). Greater Amberjack are considered mixed spawners; i.e., some individuals migrate to participate in spawning aggregations of tens to hundreds of individuals. Other Greater Amberjack are resident spawners that spawn within their relatively small home range (Biggs et al. 2018). Young-of-the-year Greater Amberjack (3–210 mm SL) are commonly collected in May and June in association with pelagic *Sargassum* mats (Bortone et al. 1977; Wells and Rooker 2004). Late juvenile Greater Amberjack transition from pelagic *Sargassum* mats to demersal, hard structures (e.g., reefs, wrecks, and rocks) at 5–6 months of age (200–300 mm TL; Wells and Rooker 2004; Pollack and Ingram 2013) in the Gulf of Mexico. Greater Amberjack begin to associate with structure as subadults and adults at sizes >400 mm SL (Manooch and Potts 1997).

The Southeast Data Assessment and Review (SEDAR 2014) summarized much of the mark-recapture data for Greater Amberjack and concluded, based mainly on McClellan and Cummings (1997), that there was little

exchange between Atlantic and Gulf of Mexico stocks (0.94% to 1.5%), the majority of the recaptures were within 25 nm of the release site, and 48% of the recaptures showed no net movement. Murie et al. (2011) observed that Greater Amberjack tagged in coastal waters from western Florida to Louisiana traveled an average distance of about 70 km from their tagging site, and the median distance traveled was only 8.0 km. However, two of the tagged fish were recaptured over 1,000 km from their tagging site. Hargrove et al. (2018) provided a perspective, noting that

Combined, tagging study results suggest most individuals exhibit site fidelity (i.e., nearly resident) while select individuals wander widely. The observation of limited large-scale movements by Greater Amberjack appears to corroborate our genetic results; modest gene flow (i.e., handfuls of individuals per generation) between populations is realistic, and these movements may explain the low levels of genetic differentiation detected among populations (Waples 1998).

There are several possible explanations for our finding that total Greater Amberjack abundance on platforms in the western Gulf was over 45% of the total estimated Gulf of Mexico stock. The stock size estimates reported in SEDAR (2016) were driven in large part by fishery effort and landings data. Yet estimates based on the directed fleets were “problematic, with contributing factors including very low sample sizes, truncated distributions, and the appearance of many small fish in some years” (SEDAR 2014:36). Commercial, recreational and headboat landings and effort are far higher from the west coast of Florida than areas west of the mouth of the Mississippi River (Murie and Parkyn, 2013; SEDAR 2014, Figure 3.4). Increasing directed fishery-independent sampling effort designed to capture larger fish (in deeper waters, in the western Gulf of Mexico, and at spawning aggregations) would likely reduce uncertainty in the upcoming Greater Amberjack stock assessment and thus help contextualize the numbers on platforms reported herein.

Assessing the Potential for Bias

We first discuss several sources of potential bias that should be considered when interpreting the results of this study. First, we were unable to count fish under the platform per se and other fish behaviors (such as attraction/avoidance) might have resulted in bias, such as multiple counting of fish that moved from one depth layer to another or not counting fish that were present but under the platform. While these may have had some level of impact on our results, similar issues are present in essentially every survey using similar methods, and we do not believe that the potential bias resulting from those were substantial. An issue of perhaps greater importance in terms of introducing bias was that our random selection procedure did not yield any sites from the cluster of platforms located west and southwest of Matagorda Bay, Texas (e.g., south Texas platforms; compare Figures 1

and 2). Thus, there may be concern that the fish communities associated with these regions were not accounted for and thus our results are biased. However, a recent survey of artificial reef fish communities in this region shows similar results to ours. Ajemian et al. (2015) surveyed 3 standing platforms and 12 artificial reef sites located within a depth gradient of 30 to 84 m. Fish were counted using remotely operated vehicles and opportunistically sampled using vertical longlines. Ajemian et al. (2015) observed that the Gallaway and Lewbel (1982) fish community characterization across the shelf was supported by their results for the southern Texas platforms they investigated. As we obtained similar results to Gallaway and Lewbel (1982) based on sampling more northerly and easterly platforms, we conclude that the omission of more southerly platforms from our study did not result in a major source of bias.

Ajemian et al. (2015), like this study, used the MaxN count metric to characterize catches. Of interest, their MaxN counts for Greater Amberjack (15), Gray Triggerfish (4), and Cobia (0) were similar to what we observed at more northern and eastern platform sites (MaxN counts of 12, 6, and 2, for Greater Amberjack, Gray Triggerfish, and Cobia, respectively). While Ajemian et al.'s (2015) Red Snapper (46) and Vermilion Snapper (28) MaxN counts were the highest they observed for any federally managed species, these were lower than the MaxN counts we observed on platforms at similar depths further north (143 for Red Snapper and 285 for Vermilion Snapper). Of interest, the Ajemian et al. (2015) study area is subject to intense illegal snapper fishing by Mexico-based *lanchas*, which might contribute to somewhat lower abundance (Coast Guard News 2017).

To further address the effects from all sources of bias on our abundance estimates made using the hydroacoustic/SRV approach, we conducted mark-recapture studies of Red Snapper at 10 platforms in the 18–30-m depth zone and compared the results to results obtained using hydroacoustic/SRV methods (Gallaway et al. 2020). In summary, the median value of the 10 mark-recapture estimates was 1,166 Red Snapper, which was remarkably similar to the median hydroacoustic/SRV estimate of 1,015 Red Snapper for the same platforms. All things considered, we recognize the potential for bias in our estimate but do not believe that it was a major problem.

CONCLUSION

As of 2018, there were 1,171 offshore petroleum platforms in the Gulf of Mexico, with 75% of these located in the Louisiana Red Snapper state management zone. On a Gulf-wide basis, these platforms were estimated to harbor 1.8 million Red Snapper (4.9% of the total stock), with 1.4 million of these fish on platforms offshore of western Louisiana. Given the paucity of natural habitat in the

Louisiana Red Snapper state management zone, the ultimate removal of these platforms will greatly impact the regional fishery for Red Snapper. Moreover, platform removals from the Louisiana (and Mississippi) Red Snapper management areas will not only impact the Red Snapper fishery, but all of the other federally managed reef fish fisheries as well. These areas are largely devoid of any reef habitat other than offshore platforms. Serious consideration should be given to mitigating lost fishing opportunity by reefing platforms in this area.

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Appendix: Comparison of Species Assemblage Structure Estimates Based on MaxN to Known Assemblage Structures via Hypothetical Simulations

The accuracy and precision of MaxN versus Mean-Count in the context of estimating true abundance (TA) for a single species has been studied by Schobernd et al. (2014) and Campbell et al. (2015). The former advocates for the use of the MeanCount method, while the latter recommends MaxN. Both acknowledge that MaxN from a single frame of a one-directional video seems to exhibit a nonlinear power relationship with TA. Causation was assigned to “screen saturation”; that is, only so many individuals can be seen in a single frame. Therefore, the proportion of individuals counted by MaxN declines exponentially as TA increases. Based on simulations, Campbell et al. (2015) showed the MaxN versus TA relationship to deviate from linear and become asymptotic beyond a TA of 200 (TA range = 2–300). Using Pinfish *Lagodon rhomboides* in a laboratory experiment, Schobernd et al. (2014) found nonlinearity beyond a TA of 20 (TA range = 1–60). Using data points inferred from graphs in both publications, we estimated parameters for this power relationship: $\text{MaxN} = 0.91\text{TA}^{0.80}$ (Figure A.1).

Both studies use the term “relative abundance” when referring to how MaxN or MeanCount compare relative to TA for a single species. Perhaps in this context, “abundance index” should be used henceforth to avoid ambiguity. In ecological studies, the term relative abundance for a single species (or density if applicable) typically refers to its proportion of the TA of individuals summed across all species from a given sample or site; all relative abundances taken together, which sum to one, then define the species assemblage’s structure (Smith and Smith 2001). In the current study, the response of interest was assemblage structure based on data from the SRV surveys in that it was used to apportion the hydroacoustic estimates of total fish abundance (TFA) across species. We found no study in the literature that quantified how assemblage structure based on MaxN could be biased due to its nonlinear relationship with TA for each species. For example, a structure with a highly abundant species may be more undercounted by MaxN than lesser abundant species causing its proportion (relative abundance) to be biased low and the other species to be biased high. While the direction of this bias seems logical, the potential magnitude was unknown.

To gain some insight as to how the current study could have misallocated TFA estimates from the hydroacoustic surveys across species due to such bias, we generated hypothetical species assemblage structures based on “known” TAs for each species. We then produced MaxN values given the estimated power relationship above. In the current study, three site-depth layer combinations had observed MaxN values close to 1,000 (909, 997, and 1,064), averaging about nine taxa across the three

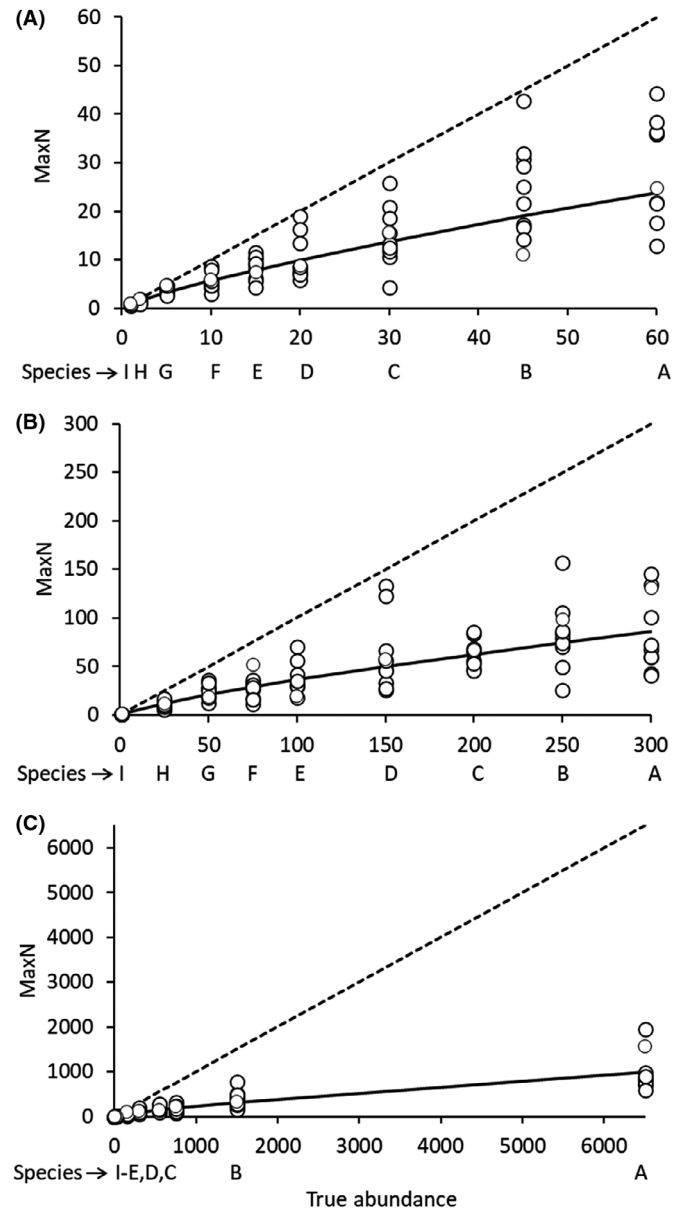


FIGURE A.1. A single iteration of randomized MaxN values (circles) across 10 revolutions for species A–I from a simulated power relationship between MaxN and true abundance, TA ($\text{MaxN} = 0.91\text{TA}^{0.80}$). For each revolution and species, MaxN was allowed to vary around the regression line (black solid line), assuming lognormal error structure with a geometric coefficient of variation (CV) equal to 50%. Species assemblage structure for this iteration can be estimated as the max of the 10 MaxN values for each species integrated to one across all species. Alternatively, a measure of central tendency across the 10 values, such as the delta-lognormal mean, could be used (see Figure A.2 and Figure A.3 for comparisons). The dashed line represents equality. (A) represents abundance scenarios across species presented in Schobernd et al. (2014), (B) represents abundance scenarios from Campbell et al. (2015), and (C) is the worst-case scenario in the current study.

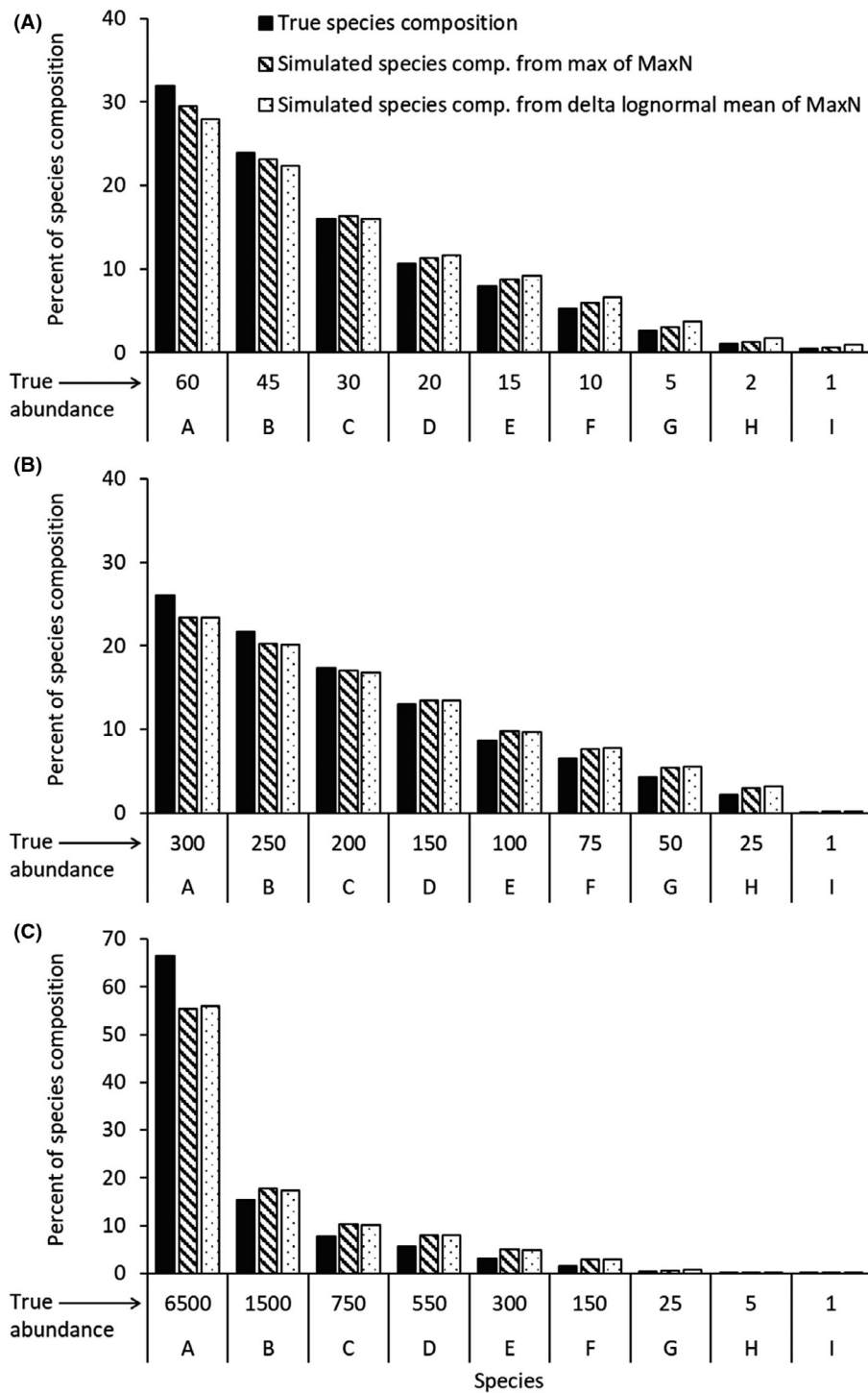


FIGURE A.2. Species assemblage structures for species A–I. True structures (black bars) are compared to the biased estimated structures occurring from the simulated power relationship between MaxN and true abundance (TA) as depicted in Figure A.1. Structures for the maximum of MaxN (dashed bars) and delta-lognormal mean of MaxN (dotted bars) represent these respective metrics taken across 10 revolutions, which were each simulated 1,000 times (Figure A.1 illustrates a single iteration). (A) represents abundance scenarios across species presented in Schobernd et al. (2014), (B) represents abundance scenarios from Campbell et al. (2015), and (C) shows the worst-case scenario in the current study.

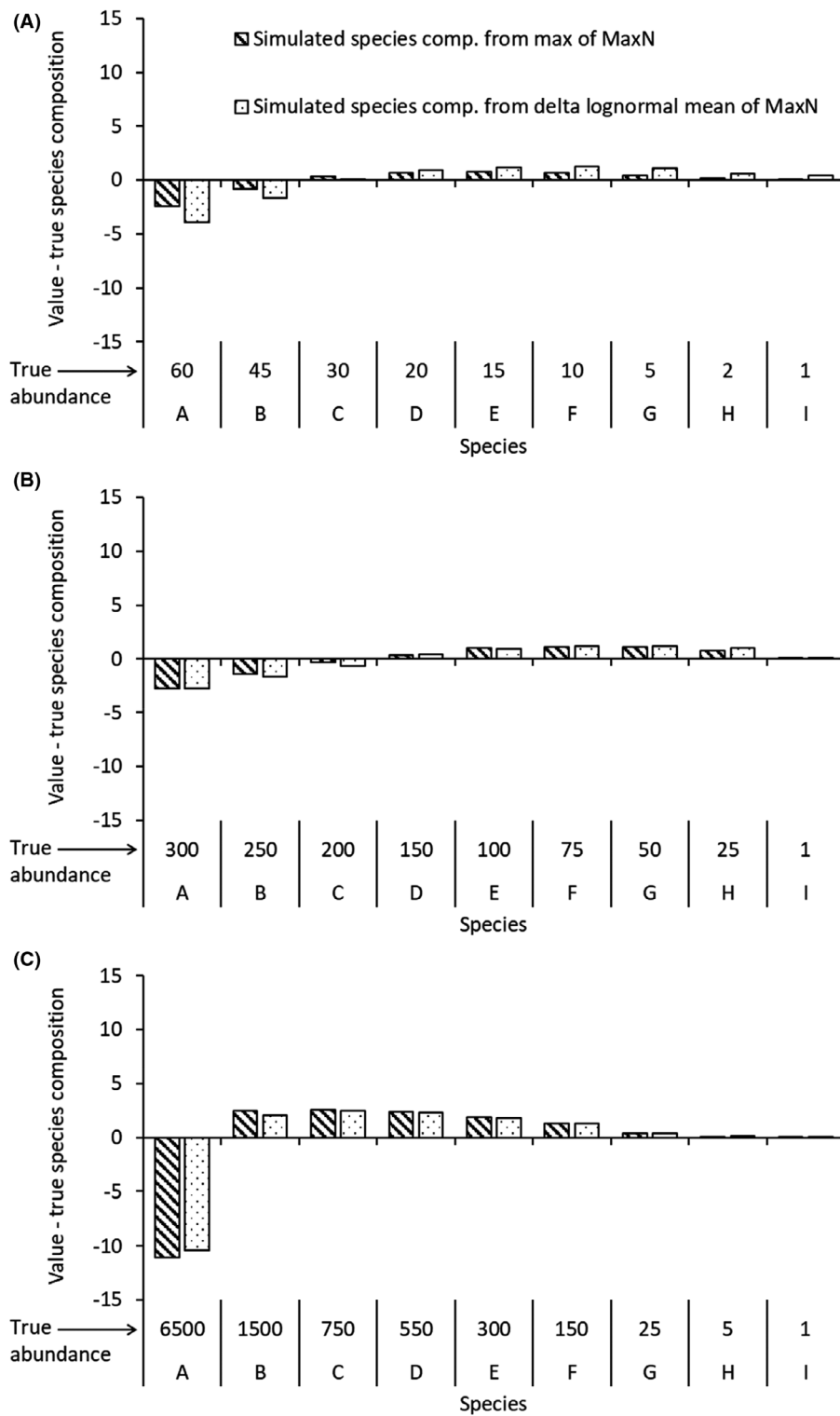


FIGURE A.3. Difference between each species' true percent representation in the assemblage structure and the average of 1,000 simulated proportions for species A–I. **(A)** represents abundance scenarios across species presented in Schobernd et al. (2014), **(B)** represents abundance scenarios from Campbell et al. (2015), and **(C)** shows the worst-case scenario in the current study.

combinations (9, 11, and 8, respectively). These samples represent the worst-case scenarios with respect to the potential for screen saturation to bias assemblage structure. Thus, we chose a hypothetical structure with nine species (A–I) for which $\text{MaxN}=1,000$ for the most numerous species. Solving for TA in the equation above, a $\text{MaxN}=1,000$ corresponds to a $\text{TA}=6,500$. Two other species structures were assessed, with the most numerous species having TAs of 60 and 300 equivalent to the range of values investigated by Schobernd et al. (2014) and Campbell et al. (2015), respectively.

Variability in MaxN for each species across the 10 revolutions by the SRV at each depth layer was simulated as follows. For each of 1,000 randomized iterations, 10 MaxN values for each species were allowed to vary around the predicted MaxN from the power relationship, assuming log-normal error structure with a geometric coefficient of variation (CV) equal to 50%. An example of a single randomized iteration for the three species structures is shown in

Figure A.1. Both the maximum of the 10 MaxN values and the delta-lognormal mean were recorded for all species and averaged across the 1,000 iterations.

The simulated effect of screen saturation biased species structures as expected; however, the magnitude of this bias was less so. Given the worst-case scenario mimicked for this study, species proportions (reported as percentages) were close to the true values (Figure A.2). Species A, the most numerous, was underestimated by 11 percentage points (Figure A.3). While this may seem sizeable, in our data set, this species would represent a schooling baitfish such as Atlantic Bumper or Gulf Menhaden, which were not the focus of our study. All other species discrepancies for this structure scenario were less than three percentage points. Furthermore, species structures based on the maximum of MaxN and the delta-lognormal mean of MaxN yielded almost the same estimates. Differences were even less for the other two hypothetical structures with lower abundances.