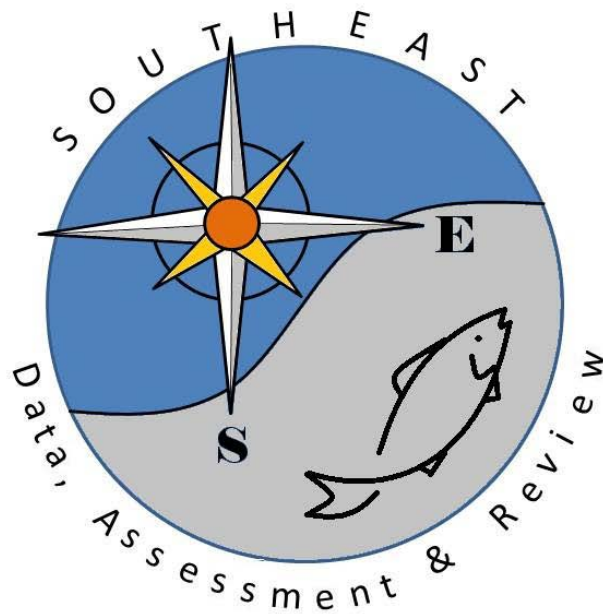


Examination of Red Snapper Fisheries Ecology on the Northwest Florida Shelf (FWC-08304): Final Report

William F. Patterson III, Joseph H. Tarnecki, and Joshua T. Neese

SEDAR31-RD27

14 August 2012



**Examination of Red Snapper Fisheries Ecology on the Northwest
Florida Shelf (FWC-08304):
Final Report**

William F. Patterson III, Joseph H. Tarnecki, and Joshua T. Neese

Department of Biology, University of West Florida
11000 University Parkway, Pensacola, Florida 32514

October 15, 2010



Introduction

Reef fishes are both ecologically important members of shelf communities and economically important to the fishing economy of Florida's Panhandle region. Among the fishes targeted in this region, none is more economically significant than red snapper, *Lutjanus campechanus*, which is targeted at both natural and artificial reefs throughout the region. Red snapper are long-lived fish that occur across the shelf of the northern Gulf of Mexico (Gulf) from the mouths of bays to the shelf break. Recent work has suggested that red snapper associate with habitats that provide small scale (cm) vertical relief and complexity, such as worm tubes or shell rubble, soon after settling out of the plankton (Patterson et al. 2005; Wells et al. 2008), but relatively little is known about their ontogenetic movement to more complex habitats, or whether fish are spatially segregated by size class across the shelf. These are important questions not only for understanding red snapper ecology, but they also have important fishery implications. If small fish are predominantly found closer to shore, then protecting inshore nursery habitats would be key to rebuilding this severely overfished stock. Alternatively, if large, older fish are predominantly found farther out in deeper waters, then protecting those areas may protect spawning stock biomass. If no size segregation with depth is apparent, then perhaps altering gear selectivity would be a means to protect undersized fish from being captured, regardless of depth.

Red snapper fishermen tend to focus on artificial reef sites in the Panhandle when fishing within 20 miles of the coast. Artificial reefs have been deployed on the northeastern Gulf shelf since just after World War II with the goals of enhancing reef fish populations as well as providing fishing opportunities close to shore. While resource managers often cite more than one goal for a given artificial reef program, recreational and commercial fishers generally are among the most vocal proponents of artificial reefs because increased catch rates often follow reef creation (Bohnsack 1989; Lindberg 1997; Grossman et al. 1997; Bortone 1998). This increase in catch rates is the subject of an ongoing debate among fishery biologists and managers as to whether artificial reefs function more as enhancers of reef fish production, or are more likely to simply increase catchability due to attracting fishes from surrounding areas (Bohnsack 1989; Lindberg 1997; Pickering and Whitmarsh 1997). This issue is especially important in the northern Gulf of Mexico (Gulf) where many large reef fishes (e.g., snappers and groupers) targeted at artificial reefs are estimated to be fully exploited or overfished (NOAA 2007; Patterson and Cowan 2003). Therefore, concern exists that creation of artificial reefs actually may exacerbate unsustainable levels of fishing mortality if artificial reefs function more as reef fish attractants than as production enhancers (Polovina and Sakai 1989; Polovina 1991; Grossman et al. 1997; Pitcher and Seaman 2000).

Currently, insufficient data exist in many artificial reef systems to evaluate the ecological versus fishery role of reefs. However, several scientists working in the state of Florida and off Alabama have been leaders in trying to tease apart these aspects of artificial reef function. Bohnsack and Sutherland (1985) were among the first scientists to question whether artificial reefs generally increased fish production or merely aggregated fishes from surrounding natural hardbottom habitats. They suggested a greater understanding was needed of how artificial reefs effect fish populations and marine ecosystems prior to the mass deployment of reefs. Bohnsack (1989) developed a conceptual model, based on his empirical studies, as to what conditions may favor enhanced productivity versus enhanced catchability of reef fishes following artificial reef creation. While holistic, Bohnsack's (1989) model did not explicitly include reef density as a factor that might predict artificial reef function, but later Ingram (2001) and Strelcheck et al.

(2005) showed that density of artificial reefs, as well as proximity to natural hardbottom areas, could affect fish growth and mortality due to density-dependent effects. Lindberg et al. (2006) also demonstrated that artificial reefs might negatively affect gag, *Mycteroperca microlepis*, population dynamics on the west Florida shelf, as fish selected artificial reef habitat even when sub-optimal spacing lead to depressed growth due to density effects. Together, these studies indicate reef spacing and surrounding habitat types have important implications for artificial reef function.

Since 2004, we have been studying the ecological function of a subset (n = 27; Fig. 1) of the so-called refugia (i.e., unreported) reefs that were built by the state of Florida in the Escambia East Large Area Artificial Reef Site (EE-LAARS) off the Panhandle in 2003 (Patterson et al. 2009a, 2010). Patterson et al. (2009a) reported that artificial reefs had a lower biomass of fishery important species and an elevated biomass of planktivores after their coordinates were reported to the public. They linked these differences to an increase in disappearance rates of fishery species that they inferred resulted from fishing mortality at reported sites. However, high disappearance rates for red snapper (but not other species) even at unreported reefs indicates they were either leaving unfished reefs and were targeted by fishermen at other reefs in the region, or that fish recruited to unsampled, and presumably deeper, reefs as they grew larger. These issues could not be resolved, however, because the spatial distribution of red snapper size classes across the shelf is not known. Furthermore, little is known about differences in fish communities or ecological function between natural and artificial reefs, which is especially important in this case due to the fact that artificial reefs have mostly been deployed in waters <30 m deep and within 20 miles of the coast, while high relief (>1 m) natural hardbottom habitats are most common in waters >60 m deep out to the shelf edge.

The primary goal of the current study was to examine aspects of red snapper fisheries biology and ecology at artificial and natural reefs in the northeastern Gulf. Secondary objectives were to compare community and trophic structure of the entire reef fish community between natural and artificial reefs. Lastly, because sampling of northeastern Gulf reef sites began in spring 2009, a dataset of reef community and trophic structure estimates existed prior to the Deepwater Horizon (DWH) oil spill. Sampling in the current study was ongoing from May to August 2010, thus any acute effects of the DWH spill on reef communities and trophic structure could be assessed.

Methods

Video Sampling and Analysis:

Video sampling of reef fish communities on the northeastern Gulf of Mexico continental shelf occurred on 24 research cruises conducted between June 11, 2009 and August 23, 2010. Eighty video samples were recorded at natural (n = 23) and artificial (n = 26) reefs that ranged in depth between 18 and 72 m (Fig. 1). Sampling was conducted with either a VideoRay Pro3 (dimensions: 30 cm long, 24 cm tall, 22 cm wide; mass = 3.8 kg) or Pro4 micro remotely operated vehicle (ROV; dimensions: 36 cm long, 28 cm tall, 22 cm wide; mass = 4.8 kg). Both ROVs have a depth rating of 170 m, a wide angle (105° or 116°, respectively) lens on a 570-line forward-looking color camera, and can be equipped with a red laser scale (10 cm between lasers) to estimate fish size. The ROVs were tethered to the surface where they were controlled by a

pilot via an integrated control box that contains a 38-cm video monitor to observe video captured by the ROV's camera during sampling.

Video sampling was conducted at study reefs with either a point-count or transect method, depending on habitat type and dimensions (Fig. 2). The point-count method, which is described in Patterson et al. (2009b), was used to sample a 15-m cylinder around isolated reef habitat, such as single artificial reef modules (Fig. 2C,D). In that method, the ROV was positioned 1 m above the seafloor and approximately 5.5 m away from a given reef. The ROV slowly was pivoted 360° and then moved to the opposite side of the reef. Once there, it was positioned 1 m above the seafloor and approximately 5.5 m away from the reef and pivoted 360°. The ROV then was flown to 1 m directly above the reef and pivoted 360° to video fishes in the water column above the reef. Next, the ROV was flown to ~10 m above the reef and pivoted 360°. Once all sample segments were completed, the ROV was flown back down to the reef and positioned such that fishes inside the reef structure were captured on video.

A transect sampling method was utilized for reef habitat that was more broadly distributed, such as was characteristic of natural reef habitat examined in this study (Fig. 2A,B). The goal of that method is to video sample a 10-m wide transect as the ROV moved forward along a 25-m long transect. Given known viewing angles for the forward cameras of Pro3 (105°) and Pro4 (116°) ROVs, the ratio of the height of an ROV off the seafloor to the width of a video transect (i.e., distance across field of view) can be controlled by changing the camera's tilt (Fig. 3). This can be accomplished prior to deployment for a Pro3 ROV, but a Pro4 ROV's operating system has the capability of controlling the camera's tilt within the software. Either way, simple trigonometry allowed for the field of view of a transect to be estimated, thus the total area video sampled to be computed. Typically, 3 to 4 transects were sampled at a given reef site, with transects being offset from adjacent transects by headings of 120° or 90°, respectively.

Analysis of video samples was performed in the Fisheries Laboratory at UWF with a Sony DVCAM DSR-11 digital VCR and a Sony LMD-170 high resolution LCD monitor. When the point-count method was employed, fish counts were summed among all sampling segments and then divided by the sampling cylinder's area (176.7 m²) to estimate fish density. Fish density for transect samples was computed by summing taxa-specific fish counts and then dividing by the total area estimated to have been sampled among transects.

Fork length (FL) was estimated for fishes struck by the laser scale during video sampling at study reefs. This was accomplished by multiplying the length of a given fish measured in a video frame by the known distance between lasers (100 mm), and then dividing that product by the distance measured between lasers in the frame. For example, if a red snapper measured 38 mm in a video frame and the distance between the laser points measured 12 mm, the fish would be estimated to be 317 mm $\{[(38 \text{ mm} * 100 \text{ mm}) / 12 \text{ mm}] = 317 \text{ mm}\}$. Fork length was converted to total length (TL) with regression equations developed from fish captured with hook and line.

Community Structure Analysis:

Differences in reef fish community structure were tested between habitat types (natural versus artificial), among three depth strata (<30 m, 30-45m, and >45 m), and between two time stanzas (before May 2010 and between May and August 2010) with single-factor analysis of similarity (ANOSIM) models in the Primer software package (Clark 1993; Clark and Warwick 2001), with taxa-specific fish density (fish 10³ m⁻²) as the dependent variables. Fish density was square-root transformed and standardized. Then, a Bray-Curtis similarity matrix was computed, which consisted of all of the individual similarity coefficients computed among sites. Individual

ANOSIM models then were computed for habitat type, depth stratum, and time stanzas. The experiment-wise error rate was set *a priori* to 0.05 for all ANOSIM models. However, since three separate analyses were conducted, α was split three ways such that the resultant critical value was 0.0167 for each model. An analysis of similarity percentages (SIMPER) was also computed in Primer for significant ANOSIM models to determine which taxa contributed most to Bray-Curtis dissimilarity between factor levels.

Fishing Experiments:

Following video sampling, fish were captured with hook and line for 30 minutes by between 6 and 8 fishermen. Two-hook bottom rigs were deployed on each fishing rod and consisted of a 1.5-m leader constructed of 60-lb monofilament which had two shorter leaders extending ~0.5 m horizontally from the main leader. Terminal tackle on the ends of the horizontal leaders was either 9/0, 12/0, or 15/0 Mustad circle hooks. Hooks were fished with either cut squid or mackerel scad as bait. At a given site, half the fishermen fished with one size of circle hooks and the other half fished with another size. Fish were randomly sampled for biological samples and retained, otherwise they were returned to the water following measurement of their fork length (FL) and total length (TL). Retained fish had coded cable ties attached to them that identified individual fish, and then were placed on ice.

Fish were weighed to the nearest 0.01 kg once back on shore and several biological samples were extracted from each fish, including both sagittal otoliths, stomachs, and ~100 g of lateral muscle. Otoliths were rinsed of adhering tissue and placed in plastic cell wells. Stomach samples were wrapped in cheesecloth and placed in plastic bags, fixed in 10% neutral buffered formalin for at least 48 hours, and then transferred to plastic bottles and stored in 70% isopropyl alcohol. Muscle tissue samples were placed in plastic bags and frozen. Frozen muscle tissue samples were stored in an ultralow freezer at between -70 and -80 °C.

Red Snapper Age and Growth:

Red snapper sagittae were embedded in epoxy and sectioned through their core with an Isomet low-speed saw. Otolith sections were ~500 μm thick and were glued to microscope slides with Cytoseal adhesive. Sections that were judged to be too thick after observing with transmitted light under a dissecting microscope were sanded with 3500 grit polishing cloth and then polished with 0.3 μm alumina suspension on a felt pad. Cytoseal then was applied to the surface of all sections.

Fish were aged by counting opaque zones in otolith sections. The algorithm of Patterson et al. (2001) was used to assign fractional age based on number of opaque zones observed, marginal condition (opaque or translucent), and date of sampling. Size at age was plotted separately for red snapper captured at natural versus artificial reefs. A linear regression was fit to each plots, as well as to the combined data, and a likelihood ratio test was computed in Excel to test if slopes, hence growth rates, were significantly different between habitat types. Lastly, catch curve analysis was performed by fitting linear regressions to descending limbs of plots of the natural log of numbers of fish versus integer age. Regressions were fit to data from natural and artificial reefs separately.

Diet Analysis:

Gut contents were identified to the lowest taxonomic level possible with the aid of a dissecting microscope. Prey were separated by taxa, dried in an oven at 60 °C for at least 24

hours, and weighed. The percent frequency of occurrence was calculated for abundant fish taxa as (Bowen 1996):

$$\%FO = \frac{\text{Number of stomachs containing a prey category}}{\text{Number of stomachs with any prey category}}$$

An index of relative importance (IRI) also was computed as (Hacunda 1981):

$$IRI = (\%N + \%M) \times \%FO$$

where:

%N = % by total number of prey

%M = % by total weight of prey

%FO = frequency of occurrence.

Percent IRI (%IRI) was computed as:

$$\%IRI = \left(\frac{\text{IRI for each prey category}}{\text{Sum of the IRI values among categories}} \right) \times 100.$$

Qualitative differences in diet were assessed by inspection of %IRI results among fish taxa and habitat types.

Stable Isotope Analysis:

Fish muscle samples were removed from the ultralow freezer placed in a -20 °C freezer and then a refrigerator at 40 °C to thaw. Once thawed, any associated bone and scales were removed and samples were rinsed with double-distilled 18 MΩ cm⁻¹ polished water. Tissue samples then were placed in aluminum weighing boats and placed in a drying oven at 60 °C for 24-48 hours. Dried samples were mechanically ground with an electric tissue grinder and then further pulverized with acid-leached glass mortar and pestles. Pulverized samples were stored in plastic microcentrifuge tubes and approximately 10 g of each sample was sent to Iso-Analytical, a contract analytical chemistry laboratory in Cheshire, England, for analysis of stable isotopes of C, N, and S.

Stable isotope analysis was performed with a Europa Scientific GSL/Geo 20-20 isotope ratio mass spectrometer. Analytes included δ¹³C_{V-PBD} (δ¹³C), δ¹⁵N_{Air} (δ¹⁵N), and δ³⁴S_{V-CDT} (δ³⁴S). International Atomic Energy Agency (IAEA) standard reference materials (SRMs) were run periodically to assess machine performance, while analytical precision was estimated from duplicate analysis of randomly selected samples. Results from IR-MS analysis of C, N, and S stable isotopes are reported in the standard delta notation. Delta values are deviations in parts per mil (‰) from a standard reference material. Values were computed as:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$$

where:

$$X = {}^{13}\text{C}, {}^{15}\text{N}, \text{ or } {}^{34}\text{S}$$

$$R = {}^{13}\text{C}/{}^{12}\text{C}, {}^{15}\text{N}/{}^{14}\text{N}, \text{ or } {}^{34}\text{S}/{}^{32}\text{S}.$$

Standards were Pee Dee Belemnite for C, air for N, and Canyon Diablo Triolite for S.

Results of stable isotope analysis were used to infer source of production and trophic position of fish and invertebrate samples. Typical northern Gulf of Mexico phytoplankton ranges of -20 to -18‰ for $\delta^{13}\text{C}$, 8 to 9‰ for $\delta^{15}\text{N}$, and 18 to 20‰ for $\delta^{34}\text{S}$ (Fry 1988). Trophic fractionation (enrichment of the heavier isotope) from prey to consumer was assumed to average 1‰ for $\delta^{13}\text{C}$ and 3‰ for $\delta^{15}\text{N}$ (Fry et al. 1984; Fry 2006); trophic fractionation is known not to occur for $\delta^{34}\text{S}$ (Connolly et al. 2004; Fry 2006). Thus, trophic level was inferred from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Values of $\delta^{34}\text{S}$ were used to estimate if the predominant prey source(s) of fish samples was pelagic or benthic. Benthic S processes impart a $\delta^{34}\text{S}$ signature of ~15‰ in benthic prey species, while pelagic phytoplankton has a $\delta^{34}\text{S}$ signature approximately 19 to 20‰ (Connolly et al. 2004). Lastly, $\delta^{13}\text{C}$ values of fishes collected between May and August 2010 were examined to assess whether there was any evidence that organic carbon from the DWH oil spill had entered the foodweb and been transferred to fishes (MacAvoy et al. 2002), which would be evidenced by extremely low fish muscle $\delta^{13}\text{C}$ values (i.e., -25 to -30‰).

Results and Discussion

Eighty-one fish taxa were observed at study reefs during 2009-10, with 88% of taxa being identified to the level of species (Table 1). There was a significant difference in fish community structure between natural and artificial reefs (ANOSIM; $p = 0.004$), but no difference was detected among depth strata (ANOSIM; $p = 0.121$) or between the two time stanzas of sampling (ANOSIM; $p = 0.623$). Differences in fish communities between habitat types were driven by relatively large reef fishes, such as lutjanids, haemulids, and balistids having much higher densities on artificial reefs than on natural reef habitat (Tables 2&3). Artificial reefs also had much higher numbers of unidentified small fishes observed. That may have resulted from there being high densities of gobioid fishes present that were observed within the invertebrate fowling community on artificial reefs, but their small size and cryptic nature left them unidentifiable. Alternatively, many more small, cryptic fishes could have occurred on natural reefs but went undetected due to the higher rugosity and structural complexity of those habitats (Fig. 2). Of the gobioid fishes that were identified, gobies, blennies, and jawfishes had much higher densities on natural reefs (Table 2).

Another key difference in fish communities between natural and artificial reefs was that small planktivores or invertivores had higher densities at natural than artificial reefs (Table 2, Fig. 4). Pomacentrids (damselfishes) had the third highest density on natural reefs among all families, and had the second highest number of species observed ($n = 10$), yet were rarely observed on artificial reefs. Other small, obligate reef fishes, such as apogonids, chaetodontids, labrids, priacanthids, pomacanthids, and tetraodontids had much higher densities on natural than artificial reefs. These trends become even more apparent in the SIMPER results examining habitat differences (Table 3), as grunts, snappers, and damselfishes dominant the cumulative Bray-Curtis dissimilarity in fish communities between natural and artificial reefs.

One interesting result was that small transient planktivores or invertivores, such as mackerel scad, sardines, or pinfish, were not observed on any of the reef sites. Patterson et al. (2009a) reported that those fishes combined made up approximately 25% of the total numbers of fishes observed at 27 artificial reef sites off Pensacola, Florida that were sampled quarterly from 2004-2008. However, they also reported that those species were highly abundant (100s to 1000s of individuals) when present, but their frequency of occurrence was <10%. Therefore, it is likely

that schooling, transient fishes did visit study reef sites but were not observed on days when sampling occurred. This issue deserves greater scrutiny moving forward as small planktivorous fishes would be most likely to suffer food web effects if DWH oil or dispersants negatively impacted plankton communities in the ecosystem.

Another point to make when examining differences in fish communities at natural versus artificial reefs is that while large invertivorous or piscivorous reef fishes were more dense at artificial reefs, the footprint of artificial reefs also was much smaller. Many artificial reefs in the northern Gulf occur on spatial scales of a 100 m² or smaller, while much of the natural reef habitat occurs on spatial scales of km². The artificial reefs examined in this study also typically had vertical relief between 2 and 5 m, while natural reef habitats typically had vertical relief <2 m, and often <1 m. Therefore, tall artificial reefs may have attracted larger reef fishes, which in turn occurred at higher densities than the same species on natural reefs, but those high densities occurred over spatial scales that were several orders of magnitude smaller than spatial scales typical of natural reefs.

Species-specific fish size ranges, as scaled by lasers attached to the ROV, were similar between natural and artificial habitats for all species except greater amberjack, which were nearly 20% larger on artificial reefs (Fig. 5). Among all reef fishes, there was no apparent trend in fish size range with increasing depth (Fig. 6A), although most fish >800 mm TL were observed in water depths >50 m. In the case of red snapper, there was substantial overlap in the range of fish observed among depths sampled, but few fish <250 mm TL, and all fish scaled to be >650 mm TL, were observed at reef sites >50 m deep (Fig. 6B). There was also a clear trend of red snapper TL increasing with depth (Fig. 6C), but the mean size of fish scaled even in the deepest stratum (>45 m) was <380 mm for a fish that can reach lengths of 1 m. Therefore, while there was some increase in TL with depth for red snapper, small young fish were observed across the shelf and few fish >600 mm TL were observed regardless of depth.

Fishing Experiments:

A total of 1,605 fish from 31 species was captured during hook and line sampling, with red snapper dominating the catch (66.4% of individuals caught). Size distributions of fishes present on reef sites versus those captured with hook and line demonstrates that larger circle hooks selected for larger fish (Fig. 7). That trend was even more prominent for red snapper than it was for all fishes in general (Figs. 8&9). Interestingly, the catch rates of other reef fishes declined precipitously with increasing hook size, but red snapper catch rate remained fairly constant (Fig. 10). Therefore, the percentage of the catch that was red snapper increased from 46% for 9/0 hooks to 76% for 12/0 hooks to 86% for 15/0 hooks.

Currently, maximum sustainable yield (MSY) for Gulf red snapper is estimated as the yield at F_{26%SPR}. For a fish with red snapper's life history, biomass at MSY (B_{MSY}) or a B_{MSY} proxy would be higher than 26%SPR were it not for fish being fully selected by the predominant fishing gears at relatively small sizes and ages. For example, Porch (2007) estimated that fish were fully vulnerable to recreational fishing gear by age 1 when fish are still much smaller than the legal size limit of 408 mm (16 inches) TL. The size limit itself would be set much higher to maximize yield per recruit were it not for discarding issues that also result from small fish being fully selected by the fishing gear. Discard mortality, especially in the recreational fishery, is not only a significant issue for red snapper fisheries management, but it also is critical to the assessment and management of other large reef fishes like gag or greater amberjack.

The hook selectivity work presented here is an important first step in beginning to examine what the likely effects on the recreational reef fish fishery in the northeastern Gulf would be if hook size were regulated. While the results presented herein are only semi-quantitative and no attempt was made to estimate selectivity directly, results clearly indicate that altering hook size would have important implications for the fishery. Sub-legal red snapper catch rates dropped when larger hook sizes were used, but not nearly as sharply as did catch rates for other species. Therefore, regulating hook size to facilitate red snapper stock recovery likely would have direct effects on fisherman attempting to target other reef fishes as well.

Lastly, minimum size limits in heavily prosecuted fisheries have been shown potentially to have unintended negative effects on population genetics in that the fastest growing fish reach the size limit first, thus fast growing genes are disproportionately removed from the population (Conover and Munch 2002). It is possible that altering hook size such that only larger fish are fully selected to the gear could elicit similar effects, not to mention that selecting large females might have unintended negative implications for spawning stock biomass. Simulation analysis to explore these likely population-level effects should be part of the selectivity work in the future.

Red Snapper Age and Growth:

Sample sizes for red snapper age and growth analysis were 182 fish for natural reefs and 286 for artificial reefs (Fig. 11A). Fish size ranged from 238 to 762 mm TL, and age ranged from 1 to 9 years. Linear regressions fit separately to natural and artificial reef red snapper size at age data did not significantly improve the fit over the regression fit to the combined data (Likelihood Ratio Test; $p = 0.624$). Therefore, no significant difference in red snapper growth rate was detected between habitat types.

One thing that is apparent in the linear regression of red snapper size versus age is the considerable variability in size at age among the samples (Fig. 11A). To evaluate that issue further, the distribution of residuals of the red snapper von Bertalanffy growth function (VBGF) reported by Patterson et al. (2001) were compared to residuals of observed size at age from the current study minus predicted size at age that resulted from applying the Patterson et al. (2001) VBGF. The residual distributions are nearly identical (Fig. 11B), thus indicating that growth has not changed in the 10 years since the Patterson et al. (2001) data were collected and that variability in red snapper size at age is similar today to what it was estimated to be historically.

Catch curve analysis resulted in slopes of -1.31 and -1.24 for natural and artificial reefs, which translate to instantaneous disappearance rates (D) of 1.31 and 1.24 y^{-1} , respectively (Fig. 12). To put that in perspective, Gulf red snapper is estimated to have an instantaneous rate of natural mortality (M) of 0.1 y^{-1} for fish 2+ years old (Porch 2007), and that is not accounting for the likely decrease in M with age. Therefore, the ratio of $D:M$ for samples collected in this study was 13.1 for natural reefs and 12.4 for artificial reefs. However, selectivity could affect estimates of numbers at age if selectivity declined with fish size, therefore age. A comparison of red snapper FL distributions from laser data versus the catch reveals that the catch actually had a higher percentage of larger fish than did the overall population of red snapper on study sites (Fig. 13). One caveat to that interpretation would be that if larger fish avoided the ROV and fishing gear, then they would appear in neither data set. From observing fish behavior in video samples, that scenario seems unlikely.

The components of D are M plus instantaneous fishing mortality (F) plus net instantaneous emigration (E'). If M is basically equal between natural and artificial reefs, and there is no bias in estimates of D due to selectivity issues, then the enormous difference between

D and M must be due to F and/or E'. Patterson et al. (2009a) reported that D for unreported (i.e., unfished) artificial reef sites off Pensacola was 0.93 y^{-1} and 1.16 y^{-1} for reported sites. They concluded that the difference in D between fished and unfished reefs was clearly due to F. However, that did not explain a D:M ratio of 9.3 for unfished sites. That high D must have been due to fish being targeted by fishermen at unreported reefs (there was no evidence of that and gray triggerfish did not show this pattern), high regional F affecting the age composition of the red snapper population in the entire region, or net movement of fish to other habitats, presumably offshore.

In the current study, F was known to occur at all study sites, so a reef being unreported or reported to the public is not an issue. In the most recent red snapper stock assessment, mean F in the eastern Gulf in 2008 was estimated to be 0.77 y^{-1} among age classes observed in the current study. Therefore, either mortality has increased despite more restrictive fishing regulations, or a large percentage of fish emigrated away from study reefs with increasing size and age. Interestingly, when catch curves were recomputed with data collected prior to May 2010 versus between May and August 2010, estimated D was 1.28 and 1.32 y^{-1} , respectively. Therefore, no acute mortality effects on red snapper appear to have occurred during the time period when significant amounts of DWH oil were present in surface waters over the shelf.

The issue of high D for red snapper in this study, as well as in the study reported by Patterson et al. (2009a), clearly warrants further investigation. Sample reefs in the Patterson et al. (2009a) study were mostly <35 m deep, with the deepest site being 41 m. In the current study, both natural and artificial reefs were examined, with several study sites being 60 to 72 m deep, yet few fish older than 5 years were observed (15% of samples) for a species that can live to be 60 years old. The question remains, where are the older fish? Are they dead, do they avoid both the ROV and hook and line gear, or have they recruited to unsampled habitat?

Mitchell et al.'s (2004) longline study of the size and age distribution of red snapper along shelf-edge banks in the northeastern and northwestern Gulf provides some insight into this latter possibility. The terminal tackle on longlines they deployed was 15-0 circle hooks, for which Porch (2007) reported that 3 year-old red snapper had a vulnerability of less than 10% and that vulnerability increased almost linearly from age 3 until age 8, when it was nearly 100%. Adjusting the age distribution reported by Mitchell et al. (2004) in the northeastern Gulf for this change in vulnerability with age, and then computing a linear regression on the $\ln(\text{catch})$ at age, yields a positive slope of 0.08 y^{-1} , which would correspond to the instantaneous rate of immigration to offshore reefs, or the converse of instantaneous net emigration (E'). If 0.08 y^{-1} were subtracted from the Ds computed here, we would still be unable to account for much of the decline in numbers of red snapper at age.

Diet and Trophic Analyses:

The diet of 854 fish representing 27 species was analyzed via examination of stomach contents, with red snapper constituting 58% of the samples. Among all samples, 77% had identifiable prey items present in their stomachs and 99 different prey items were identified. Prey items were placed into 9 categories, which included fish, Decapoda, Stomatopoda, Cephalopoda, Gastropoda, Amphipoda, other invertebrates, zooplankton, and macroalgae to examine diet differences among species and habitats. It should be noted that most (>90%) of the amphipods identified in stomach samples were pelagic hyperiid amphipods, thus zooplankton themselves.

There were 18 reef fish species for which there were multiple stomach samples that contained prey items (Fig. 14), although not all were collected in both natural and artificial

habitats. Sampled gag, lane snapper, greater amberjack, scamp, and whitespotted soapfish were principally if not exclusively piscivores. Among the invertivores, several ate fish as well. After fish, decapods (principally crabs and shrimps) were the next most important prey type, especially with respect to %IRI (Fig. 14C). Vermilion snapper diet had the highest percentage of zooplankton, with over 50% of their diet consisting of amphipods and other zooplankton, which was true regardless of habitat type.

Small sample sizes for many reef fishes makes it difficult to infer predominant diet or trophic position from stomach content analysis. Sufficient samples sizes existed for red snapper, however, to examine habitat and ontogenetic effects on diet (Fig. 15). Overall, red snapper were fairly omnivorous regardless of size category or habitat type. All fish tended to have a high percentage (20-60%) of their diet being fish, with decapods also being important. Fish sampled in natural reef environments tended to have higher percentages of cephalopods by mass than fish captured at artificial reef sites. McCawley and Cowan (2007) indicated that zooplankton appearing in the diet of adult red snapper off Alabama likely indicated that high densities of artificial reefs resulted in too many fish grazing down the forage base, thus causing red snapper to switch to a sub-optimal food source. However, in the current study about a third of red snapper diet consisted of pelagic amphipods and other zooplankton regardless of habitat or fish size (Fig. 15).

Analysis of fish muscle stable isotope ratios allows inference to be drawn about a species' trophic position without the need for large ($n > 50$) sample sizes. Also, stable isotope signatures are integrated over weeks to months as muscle tissue turnover rates are much longer than digestion rates for stomach contents (Fry 2006). Among the samples analyzed in this study, the one gray snapper sampled from natural habitat had the highest $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, thus fed at the highest trophic level, while vermilion snapper, gray triggerfish, and bank seabass all fed at about a trophic level below gray snapper and other reef fishes like greater amberjack, lane snapper, and gag (Fig. 16A). The omnivorous red snapper and tomtate, along with the invertivore red grouper, all clustered together in the middle of the range of $\delta^{15}\text{N}$ values.

Most of the fishes analyzed tended to have pelagic $\delta^{34}\text{S}$ signatures, with mean values mostly ranging between 17.5 and 19‰. Tomtate and gag had the lowest $\delta^{34}\text{S}$ values, indicating they mostly ate benthic prey. Those two species also displayed a trend that was common among several fishes in that their $\delta^{34}\text{S}$ values from natural reefs had a more benthic signature than samples from artificial reefs did. High densities of reef fishes can deplete benthic prey in soft or sandy bottom foraging halos around reef structure (Frazer et al. 1991; Galvan et al. 2008). That might explain the more pelagic versus benthic $\delta^{34}\text{S}$ signatures for fish sampled in artificial versus natural habitats if high fish densities on artificial reefs grazed down benthic prey, thus fish had to switch to pelagic prey resources.

Larger red snapper sample size ($n = 90$) permits a more comprehensive assessment of their trophic position based on stable isotope values. The range in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values indicates that among fish sampled there was a full trophic level range in their feeding (Fig. 17A). However, there was no relationship between trophic position and fish size (Fig. 17C,D), and there was no difference in mean trophic level between fish sampled in natural versus artificial reefs (Fig. 17F). Plotting $\delta^{34}\text{S}$ versus $\delta^{13}\text{C}$ values indicates that fish that fed at higher trophic levels tended to consume benthic versus pelagic prey (Fig. 17B), but no relationship in $\delta^{34}\text{S}$ with fish size was apparent and there was no difference in $\delta^{34}\text{S}$ between natural and artificial reefs (Fig. 17E,F). With increased sample sizes it may be possible to examine the effect of fish density

on trophic position and $\delta^{34}\text{S}$ values, as well as to relate red snapper trophic ecology to mean size at age.

Lastly, the timing of muscle tissue sampling, before and after May 2010, permits the examination of whether differences in trophic ecology occurred among sampled reef fishes before versus after the DWH oil spill. Few differences exist between the two time periods among all the fish sampled (Fig. 18), any differences that do exist are minor, and no general trend in higher versus lower trophic position or a general switch between pelagic and benthic prey is apparent. Plots of mean stable isotope values among all fishes sampled also confirms that no general difference existed between reef fish trophic ecology before May 2010 versus between May and August 2010 (Fig. 19). A slight increase in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in samples collected after May 2010 is apparent in the data (Fig. 19A), but it is important to note that mean $\delta^{15}\text{N}$ was only approximately 0.15‰ higher and $\delta^{13}\text{C}$ was only approximately 0.2‰ higher after May 2010. Regardless, trophic position did not decrease, and there is no evidence that oil-derived carbon, with its depleted ^{13}C signature, had reached the upper trophic levels of the ecosystem by late August 2010. These data do provide an excellent baseline to examine that issue in the future, and this study in general provides several sources of data that will allow us to test for potential chronic effects of the DWH spill on reef fish community structure, size at age, and trophic ecology in the northeastern Gulf of Mexico

Acknowledgements

We thank Luiz Barbieri and Bob McMichael at the Florida Fish and Wildlife Research Institute for facilitating this study. We thank Captains Seth Wilson, Johnny Greene, Sean Kelley, and Gary Jarvis for providing us access to their boats and for all their help in sampling reefs. Lastly, we thank the many volunteers that helped us in sampling fish in the field, as well as processing fish samples back in the laboratory. In particular, we thank Rachel Scharer, Heather Moncrief, Stephanie Peakman, and Joe Flynn for countless hours contributed to this study.

References

- Bohnsack, J.A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bulletin of Marine Science* 44:631-644.
- Bohnsack, J.A. and S.P. Sutherland. 1985. Artificial reef research: a review with recommendations for future priorities. *Bulletin of Marine Science*. 37:11-39.
- Bortone, S.A. 1998. Resolving the attraction-production dilemma in artificial reef research: Some yeas and nays. *Fisheries*. 23:6-10.
- Clarke, K. R. 1993. Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* 18:117-143
- Clarke, K.R. and R.M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. Primer E, Plymouth.
- Connolly, R. M., M. B. Guest, A. J. Melville, and J. M. Oakes. 2004. Sulfur stable isotopes separate producers in marine food-web analysis. *Oecologia* 138:161-167.
- Conover, D.O. and S.B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297: 94-96.

- Frazer, T., Lindberg, W., Stanton, G., 1991. Predation on sand dollars by triggerfish, *Balistes capriscus*, in the northeastern Gulf of Mexico. *Bulletin of Marine Science* 48:159-164.
- Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography* 33:1182-1190.
- Fry, B. 2006. *Stable Isotope Ecology*. Springer. New York, NY. 308 pp.
- Fry, B., R. K. Anderson, L. Entzeroth, J. L. Bird, and P. L. Parker. 1984. ¹³C enrichment and oceanic food web structure in the northwestern Gulf of Mexico. *Contributions in Marine Science* 27:49-63.
- Galvan, D.E., A.M. Parma, and O.O. Iribarne. 2008. Influence of predatory reef fishes on the spatial distribution of *Munida gregaria* (= *M. subrugosa*) (Crustacea; Galatheidæ) in shallow Patagonian soft bottoms. *Journal of Experimental Marine Biology and Ecology* 354:93-100.
- Goodyear, C.P. 1995. Red snapper in U.S. waters of the Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Science Center, Miami Laboratory, Miami MIA-95/96-05.
- Grossman, G.D., G.P. Jones, and W.J. Seaman, Jr. 1997. Do artificial reefs increase regional fish production? A review of existing data. *Fisheries* 22:17-23.
- Ingram, G.W., Jr. 2001. Stock structure of gray triggerfish in the northern Gulf of Mexico. Ph.D. 228 pp.
- Lindberg, W.J. 1997. Can science solve the attraction versus production debate? *Fisheries* 22:10-13.
- Lindberg, W.J., T.K. Frazer, K.M. Portier, F. Vose, J. Loftin, D. Murie, D.M. Mason, B. Nagy, and M.K. Hart. 2006. Density-dependent habitat selection and performance by a large mobile reef fish. *Ecological Applications* 16:731-746.
- McCawley, J.R and J.H. Cowan, Jr. 2007. Seasonal and size specific diet and prey demand of red snapper on Alabama artificial reefs. Pages 277-104 in W.F. Patterson, III, J.H. Cowan, Jr., D.A. Nieland, and G.R. Gitzhugh, editors. *Population Ecology and Fisheries of U.S. Gulf of Mexico Red Snapper*. American Fisheries Society. Bethesda, Maryland.
- MacAvoy, S. E., R. S. Carney, C. R. Fisher, and S. A. Macko. 2002. Use of chemosynthetic biomass by large, mobile, benthic predators in the Gulf of Mexico. *Marine Ecology Progress Series* 225:65-78.
- National Oceanographic and Atmospheric Administration (NOAA). 2009. The Status of US Fisheries:NOAA Fisheries 2008 Report to Congress. 28 pp.
- Patterson, W.F., III and J.H. Cowan, Jr. 2003. Site fidelity and dispersion of tagged red snapper, *Lutjanus campechanus*, in the northern Gulf of Mexico. Pages 181-194 in D.R. Stanley and A. Scarborough-Bull, editors. *Fisheries, Reefs, and Offshore Development*. American Fisheries Society, Bethesda.
- Patterson, W.F., III, D.T. Addis, and M.A. Dance. 2009a. The effect of unpublished artificial reefs deployed on the northwest Florida shelf (FWC-06120): 2005-08 Modeling Report. Final Report to Florida Fish and Wildlife Conservation Commission. 51 pages.
- Patterson, W.F., III, D.T. Addis, and J.H. Tarnecki. 2010. The effect of unpublished artificial reefs deployed on the northwest Florida shelf (FWC-07019): Final Report. Final Report to Florida Fish and Wildlife Conservation Commission. 37 pages.
- Patterson, W.F., III, M.A. Dance, and D.T. Addis. 2009b. Development of a remotely operated vehicle based methodology to estimate fish community structure at artificial reef sites in

- the northern Gulf of Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute* 61:263-270.
- Patterson, W.F., III, J.H. Cowan, Jr., C.A. Wilson, and R.L. Shipp. 2001. Age and growth of red snapper from an artificial reef area in the northern Gulf of Mexico. *U.S. Fishery Bulletin*, 99:617-627.
- Patterson, W.F., III, C.A. Wilson, J.H. Cowan, Jr., S.J. Bentley, T.A. Henwood, Y.C. Allen, and T.A. Dufrene. 2005. Delineating essential juvenile red snapper habitat in the north central Gulf of Mexico. Pages 277-288 in P.W. Barnes and J.P. Thomas, editors. *Effects of Fishing on Benthic Habitats*. American Fisheries Society, Bethesda.
- Pickering, H. and D. Whitmarsh. 1996. Artificial reefs and fisheries exploitation: A review of the “attraction versus production” debate, the influence of design and its significance for policy. *CEMARE Research Papers Number 107*. 28 p.
- Pitcher, T.J., and W. Seaman. 2000. Petrarch’s principle: how protected human-made reefs can help the reconstruction of fisheries and marine ecosystems. *Fish and Fisheries* 1:73-81.
- Polovina, J.J. 1991. Fisheries application and biological impacts of artificial habitats. in W. Seaman, Jr. and L.M. Sprague, editors. *Artificial habitats for marine and freshwater fisheries*. Academic Press, New York
- Polovina, J.J., and I. Sakai. 1989. Impacts of artificial reefs on fishery production in Shimarmaki, Japanese. *Bulletin of Marine Science* 44:997-1,003.
- Porch, C.E. 2007. An assessment of the red snapper fishery in the U.S. Gulf of Mexico using a spatially-explicit age-structured model. Pages 325-351 in W.F. Patterson, III, J.H. Cowan, Jr., D.A. Nieland, and G.R. Gitzhugh, editors. *Population Ecology and Fisheries of U.S. Gulf of Mexico Red Snapper*. American Fisheries Society. Bethesda, Maryland.
- SEDAR. 2009. Stock assessment of red snapper in the Gulf of Mexico, Report of the Update Assessment Workshop. August 24-28, 2009, Miami, Florida. 224 pp.
- Strelcheck, A.J, J.H. Cowan, Jr. and W.F. Patterson, III. 2007. Site fidelity, movement, and growth of red snapper, *Lutjanus campechanus*: Implications for artificial reef management. Pages 135-148 in W.F. Patterson, III, J.H. Cowan, Jr., D.A. Nieland, and G.R. Gitzhugh, editors. *Population Ecology and Fisheries of U.S. Gulf of Mexico Red Snapper*. American Fisheries Society. Bethesda, Maryland.
- Wells, R.J.D., J.H. Cowan, Jr., W.F. Patterson, III, and C.J. Walters. 2008. Trawling effects and habitat selection on life history parameters of Gulf of Mexico red snapper. *Canadian Journal of Fisheries and Aquatic Sciences* 65:2399-2411.

Tables and Figures

Table 1. Reef fish taxa observed at natural (NR) and artificial (AR) reef sites during 2009-2010. Residency: R = reef resident, RA = seasonally reef-associated neritic pelagic species, S = demersal or benthic shelf species, and T = transient. Trophic position: H = herbivore, P = planktivore, I = invertivore, F = piscivore. Life stage: J = juvenile and A = adult. Reef limited: O = obligate reef resident likely to demonstrate habitat-limited populations and G = fishes for which reefs may function to increase growth or decrease natural mortality. Multiple letters for trophic position indicate feeding on more than one trophic level. Multiple letters for life stage indicate more than one stage present. Mean density is the taxa-specific mean among all sampling events; density units are fish 10³ m⁻².

Family	Scientific Name	Common	Residency	Trophic Position	Life Stage	Reef Limited	Mean Density on NR	Mean Density on AR	Overall Mean Density
Acanthuridae	<i>Acanthurus chirurgus</i>	doctorfish	R	H	A	G	0.14	0.00	0.06
Apogonidae	<i>Apogon pseudomaculatus</i>	twospot cardinalfish	R	P	J,A	O	0.42	0.21	0.30
Ballistidae	<i>Ballistes capriscus</i>	gray triggerfish	R	I	A	G	1.05	14.72	8.95
Batrachoididae	<i>Opsanus pardus</i>	leopard toadfish	R	I	A	G	0.00	0.05	0.03
Blenniidae	Blenniidae	blenny	R	PI	J,A	O	6.32	0.00	2.67
Blenniidae	<i>Parablennius marmoratus</i>	seaweed blenny	R	I	A	O	1.61	2.39	2.06
Bothidae	<i>Paralichthys albigutta</i>	gulf flounder	S	IF	A	G	0.00	0.15	0.09
Bothidae	<i>Paralichthys lethostigma</i>	southern flounder	S	IF	A	G	0.00	0.92	0.53
Carangidae	Carangidae	jack	T	PIF	A	G	0.42	0.00	0.18
Carangidae	<i>Caranx crysos</i>	blue runner	T	PI	A	G	0.42	0.00	0.18
Carangidae	<i>Seriola dumerilii</i>	greater amberjack	RA	F	A	G	18.04	16.76	17.30
Carangidae	<i>Seriola rivoliana</i>	almaco jack	RA	F	A	G	1.68	0.53	1.01
Carcharhinidae	<i>Carcharhinus limbatus</i>	blacktip shark	T	F	A	G	0.21	0.00	0.09
Carcharhinidae	<i>Carcharhinus plumbeus</i>	sandbar shark	T	F	A	G	0.14	0.00	0.06
Carcharhinidae	<i>Carcharhinus</i> sp.	requiem shark	T	F	A	G	0.28	0.00	0.12
Chaetodontidae	<i>Chaetodon aya</i>	bank butterflyfish	R	PI	A	O	1.96	0.00	0.83
Chaetodontidae	<i>Chaetodon ocellatus</i>	spottfin butterflyfish	R	PI	A	O	0.84	2.34	1.71
Chaetodontidae	<i>Chaetodon sedentarius</i>	reef butterflyfish	R	PI	A	O	1.12	0.00	0.47
Dasyatidae	<i>Dasyatis americana</i>	southern stingray	S	IF	A	G	0.14	0.10	0.12
Ephippidae	<i>Chaetodipterus faber</i>	Atlantic spadefish	R	I	A	G	0.00	51.99	30.04
Gobiidae	Gobiidae	goby	R	PI	J,A	O	0.42	0.00	0.18

Table 1. continued.

Family	Scientific Name	Common	Residency	Trophic Position	Life Stage	Reef Limited	Mean Density on NR	Mean Density on AR	Overall Mean Density
Haemulidae	<i>Haemulon aurolineatum</i>	tomtate	R	I	A	G	133.61	865.00	556.19
Haemulidae	<i>Orthopristis chrysoptera</i>	pigfish	R	I	A	G	0.98	0.00	0.41
Holocentridae	<i>Holocentrus poco</i>	saddle squirrelfish	R	PI	A	O	6.46	0.00	2.73
Holocentridae	<i>Holocentrus sp.</i>	squirrelfish	R	PI	A	O	0.14	0.00	0.06
Holocentridae	<i>Myripristis jacobus</i>	blackbar soldierfish	R	PI	A	O	0.21	0.00	0.09
Labridae	<i>Bodianus pulchellus</i>	spotfin hogfish	R	I	A	O	1.26	0.00	0.53
Labridae	<i>Bodianus rufus</i>	Spanish hogfish	R	I	A	O	0.00	0.63	0.36
Labridae	<i>Halichoeres bivittatus</i>	slippery dick	R	I	A	O	16.35	2.68	8.45
Labridae	Labridae	wrasse	R	I	J,A	O	0.28	0.00	0.12
Lutjanidae	<i>Lutjanus campechanus</i>	red snapper	R	IF	A	G	55.65	378.44	242.15
Lutjanidae	<i>Lutjanus griseus</i>	gray snapper	R	IF	A	G	28.49	36.11	32.89
Lutjanidae	<i>Lutjanus synagris</i>	lane snapper	R	IF	A	G	2.39	15.08	9.72
Lutjanidae	<i>Rhomboplites aurorubens</i>	vermillion snapper	R	PI	J,A	G	147.65	15.28	71.17
Monocanthidae	<i>Aluterus monoceros</i>	unicorn filefish	R	I	A	G	0.00	0.64	0.37
Monocanthidae	<i>Aluterus schoepfii</i>	orange filefish	R	I	A	G	0.14	0.87	0.56
Monocanthidae	<i>Aluterus scriptus</i>	scrawled filefish	R	I	A	G	0.28	0.00	0.12
Monocanthidae	<i>Monacanthus setifer</i>	pygmy filefish	R	PI	A	G	0.00	0.44	0.25
Opistognathidae	<i>Opistognathus sp.</i>	jawfish	R	P	J,A	O	0.84	0.00	0.36
Ostraciidae	<i>Lactophrys quadricornis</i>	scrawled cowfish	R	I	A	G	0.00	0.00	0.00
Pomacanthidae	<i>Holacanthus bermudensis</i>	blue angelfish	R	I	A	G	2.18	1.17	1.59
Pomacanthidae	<i>Holacanthus ciliaris</i>	queen angelfish	R	I	A	G	0.28	0.21	0.24
Pomacanthidae	<i>Pomacanthus paru</i>	French angelfish	R	I	A	G	0.14	0.00	0.06
Pomacentridae	<i>Chromis cyanea</i>	blue chromis	R	P	J,A	O	17.12	0.00	7.23
Pomacentridae	<i>Chromis enchrysur</i>	yellowtail reeffish	R	P	J,A	O	13.82	0.00	5.84
Pomacentridae	<i>Chromis scotti</i>	purple reef fish	R	P	J,A	O	48.56	0.00	20.50
Pomacentridae	<i>Chromis sp.</i>	damselfish	R	P	J,A	O	0.28	0.00	0.12

Table 1. continued.

Family	Scientific Name	Common	Residency	Trophic Position	Life Stage	Reef Limited	Mean Density on NR	Mean Density on AR	Overall Mean Density
Pomacentridae	<i>Microspathodon chrysurus</i>	yellowtail damselfish	R	P	J,A	O	0.14	0.00	0.06
Pomacentridae	<i>Stegastes fuscus</i>	dusky damselfish	R	P	J,A	O	2.95	0.00	1.24
Pomacentridae	<i>Stegastes leucostictus</i>	beaugregory	R	P	J,A	O	0.42	0.21	0.30
Pomacentridae	<i>Stegastes partitus</i>	bicolor damselfish	R	P	J,A	O	1.96	0.00	0.83
Pomacentridae	<i>Stegastes sp.</i>	damselfish	R	P	J,A	O	0.42	0.00	0.18
Pomacentridae	<i>Stegastes variabilis</i>	cocoa damselfish	R	P	J,A	O	2.81	0.96	1.74
Priacanthidae	<i>Priacanthus arenatus</i>	Atlantic bigeye	R	PI	A	O	2.81	0.00	1.19
Priacanthidae	<i>Pristigynys alta</i>	short bigeye	R	PI	A	O	1.54	0.00	0.65
Sciaenidae	<i>Equetus acuminatus</i>	high-hat	R	I	A	O	0.42	0.00	0.18
Sciaenidae	<i>Equetus iwamotoi</i>	blackbar drum	R	I	A	G	0.28	0.00	0.12
Sciaenidae	<i>Equetus lanceolatus</i>	jackknife fish	R	I	A	O	0.49	4.79	2.97
Sciaenidae	<i>Equetus sp.</i>	reef drum	R	I	A	R	0.56	0.00	0.24
Sciaenidae	<i>Paraques umbrosus</i>	cubbyu	R	I	A	O	5.05	2.82	3.76
Scorpaenidae	<i>Scorpaena brasiliensis</i>	barbfish	S	IF	A	G	0.00	0.22	0.13
Serranidae	<i>Centropomus ocyurus</i>	bank seabass	S	I	A	G	1.82	1.52	1.65
Serranidae	<i>Dipllectrum formosum</i>	sandperch	S	IF	A	G	0.14	0.00	0.06
Serranidae	<i>Epinephelus adscensionis</i>	rock hind	R	IF	A	G	0.14	0.00	0.06
Serranidae	<i>Epinephelus cruentatus</i>	graysby	R	IF	A	G	0.84	0.00	0.36
Serranidae	<i>Epinephelus morio</i>	red grouper	R	IF	A	G	1.05	0.42	0.69
Serranidae	<i>Holanthias martinicensis</i>	rougtongue bass	R	P	J,A	O	0.56	0.00	0.24
Serranidae	<i>Liopropoma eukrines</i>	wrasse bass	R	PI	A	O	0.42	0.00	0.18
Serranidae	<i>Mycteroperca microlepis</i>	gag	R	F	A	G	0.84	0.91	0.88
Serranidae	<i>Mycteroperca phenax</i>	scamp	R	F	A	G	7.37	6.53	6.89
Serranidae	<i>Rypticus maculatus</i>	whitespotted soapfish	R	I	A	G	0.14	8.79	5.14
Serranidae	Serranidae	grouper	RA	IF	A	G	0.14	0.00	0.06
Serranidae	<i>Serranus phoebe</i>	tattler	R	I	A	O	2.53	0.00	1.07

Table 1. continued.

Family	Scientific Name	Common	Residency	Trophic Position	Life Stage	Reef Limited	Mean Density on NR	Mean Density on AR	Overall Mean Density
Serranidae	<i>Serranus subligarius</i>	belted sandfish	S	I	A	G	1.12	0.21	0.59
Sparidae	<i>Archosargus probatocephalus</i>	sheepshead	R	I	A	G	0.00	0.94	0.54
Sparidae	<i>Calamus leucosteus</i>	whitebone porgy	S	I	A	G	0.14	0.10	0.12
Sparidae	<i>Calamus penna</i>	sheepshead porgy	T	I	A	G	0.00	0.10	0.06
Sparidae	<i>Pagrus pagrus</i>	red porgy	R	I	A	G	15.30	1.93	7.58
Sphyraenidae	<i>Sphyraena barracuda</i>	greater barracuda	RA	F	A	G	0.00	2.36	1.36
Tetraodontidae	<i>Canthigaster rostrata</i>	Caribbean sharpnose puffer	R	I	A	G	1.12	0.22	0.60
	Unidentified small fish						3.79	130.26	76.86

Table 2. Estimated density (fish 10^3 m^{-2}) of reef fish families observed at natural and artificial reefs in the northeastern Gulf of Mexico in 2009-2010.

Family	Species	Mean Density on Natural Reefs	Mean Density on Artificial Reefs	% Difference Between Natural and Artificial	Mean Overall Density
Lutjanidae	4	234.18	444.91	-90	355.94
Haemulidae	2	134.60	865.00	-543	556.61
Pomacentridae	10	91.09	2.54	97	39.92
Carangidae	4	20.56	17.28	16	18.67
Labridae	4	17.89	3.31	82	9.47
Serranidae	13	17.12	18.38	-7	17.85
Sparidae	4	15.44	3.07	80	8.30
Blenniidae	2	7.93	2.39	70	4.73
Holocentridae	3	6.81	0.00		2.87
Sciaenidae	5	6.81	7.61	-12	7.27
Priacanthidae	2	4.35	0.00		1.84
Chaetodontidae	3	3.93	2.34	40	3.01
UID smal fish	1	3.79	130.26	-3,337	76.86
Pomacanthidae	3	2.60	1.37	47	1.89
Tetraodontidae	1	1.12	0.22	81	0.60
Balistidae	1	1.05	14.72	-1,298	8.95
Opistognathidae	1	0.84	0.00		0.36
Carcharhinidae	3	0.63	0.00		0.27
Apogonidae	1	0.42	0.21	51	0.30
Gobiidae	1	0.42	0.00		0.18
Monacanthidae	4	0.42	1.95	-362	1.30
Acanthuridae	1	0.14	0.00		0.06
Dasyatidae	1	0.14	0.10	27	0.12
Batrachoididae	1	0.00	0.05		0.03
Ephippidae	1	0.00	51.99		30.04
Ostraciidae	1	0.00	0.00		0.00
Scorpaenidae	1	0.00	0.22		0.13

Table 3. Results from SIMPER analysis examining differences in fish community structure between natural and artificial reefs that were video sampled with a micro remotely operated vehicle in the northeastern Gulf of Mexico during 2009-10. Dissimilarity between habitat types is indicated for the twenty species that displayed the greatest Bray-Curtis dissimilarity between habitats. Units for fish density are fish per 10^3 m^2 .

Species	Habitat Type		Mean Bray-Curtis Dissimilarity (SD)	% Total Dissimilarity	Cumulative % Dissimilarity
	Natural	Artificial			
<i>Haemulon aurolineatum</i>	865.0	133.6	8.92 (1.14)	12.17	12.2
<i>Lutjanus campechanus</i>	378.4	55.7	8.72 (1.41)	11.90	24.1
<i>Rhomboplites aurorubens</i>	15.3	147.7	7.05 (9.16)	9.63	33.7
<i>Lutjanus griseus</i>	36.1	28.5	4.57 (0.92)	6.23	39.9
<i>Chromis scotti</i>	0.0	48.6	2.36 (0.56)	3.23	43.2
<i>Halichoeres bivittatus</i>	2.7	16.4	2.28 (0.72)	3.11	46.3
<i>Balistes capriscus</i>	14.7	1.1	2.23 (1.07)	3.04	49.3
<i>Pagrus pagrus</i>	1.9	15.3	2.16 (0.69)	2.94	52.3
<i>Chromis enchrysur</i>	0.0	13.8	2.08 (0.69)	2.84	55.1
<i>Chaetodipterus faber</i>	52.0	0.0	2.00 (0.46)	2.73	57.8
<i>Seriola dumerili</i>	16.8	18.0	1.85 (0.74)	2.53	60.4
<i>Mycteroperca phenax</i>	6.5	7.4	1.85 (1.15)	2.52	62.9
Unidentified Small Fish	130.3	3.8	1.58 (0.36)	2.16	65.0
<i>Paraques umbrosus</i>	2.8	5.1	1.52 (0.65)	2.08	67.1
<i>Rypticus maculatus</i>	8.8	0.1	1.45 (0.92)	1.98	69.1
<i>Lutjanus synagris</i>	15.1	2.4	1.37 (0.54)	1.87	71.0
<i>Priacanthus arenatus</i>	0.0	2.8	1.31 (0.68)	1.79	72.8
<i>Holacanthus bermudensis</i>	1.2	2.2	1.16 (0.96)	1.58	74.3
<i>Parablennius marmoratus</i>	2.4	1.6	1.07 (0.47)	1.46	75.8
<i>Stegastes variabilis</i>	1.0	2.8	1.02 (0.70)	1.40	77.2

Figure 1. Geographic distribution of study reefs along the northeastern Gulf of Mexico Continental Shelf. Green circles indicate natural reefs that were sampled during 2009-10, while yellow circles indicated artificial reefs. Pink stars demarcate the corners of the Escambia East Large Area Artificial Reef Site. The red star indicates the location of Pensacola, Florida. Bay abbreviations: MB = Mobile Bay, PB = Pensacola Bay, CB = Choctawhatchee Bay, and SAB = St Andrews Bay.

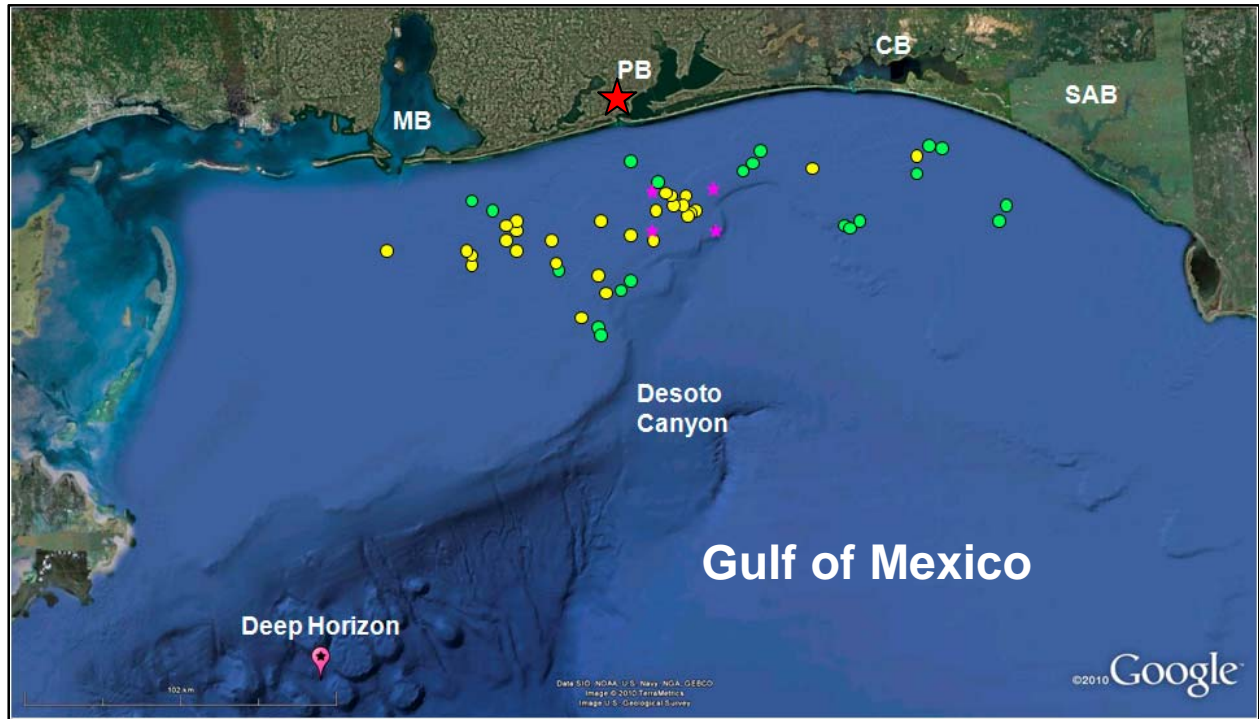


Figure 2. Digital images of A&B) natural and C&D) artificial reef habitats video sampled with a micro remotely operated vehicle during this study.

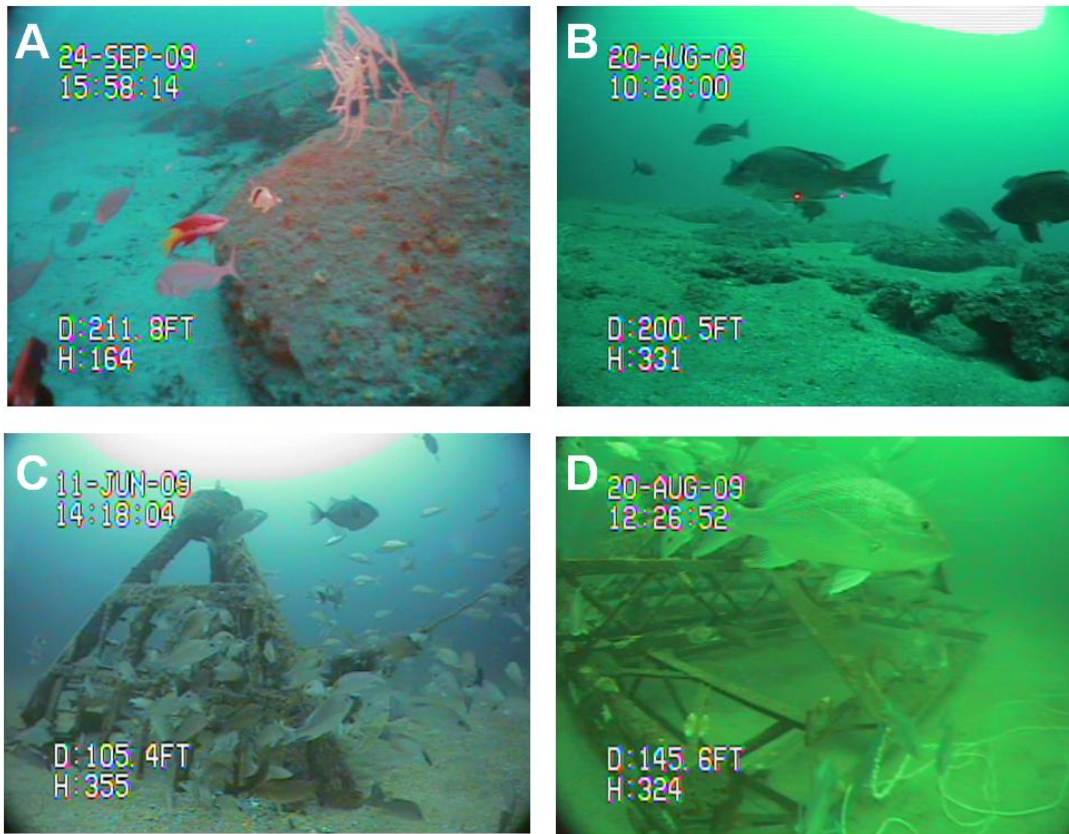


Figure 3. Trigonometry of estimating the width of a video transect given the height a remotely operated vehicle (ROV) is above the seafloor, the angle of its camera's tilt (θ_1), and the angle of the camera's view. The view angle ($2\cdot\theta_2$) is 105° for a VideoRay Pro3 ROV and 116° for a Pro4 ROV; therefore, θ_2 would be 52.5° and 58° , respectively, for the ROVs. If the camera's tilt angle (θ_1) was set to 45° , then the ratio of transect width (w) to ROV height (h) would be 3.69 for a Pro3 ROV and 4.53 for a Pro4. The same ratios would be 5.21 and 6.40 for Pro3 and Pro4 ROVs, respectively, if θ_1 was set to 60° .

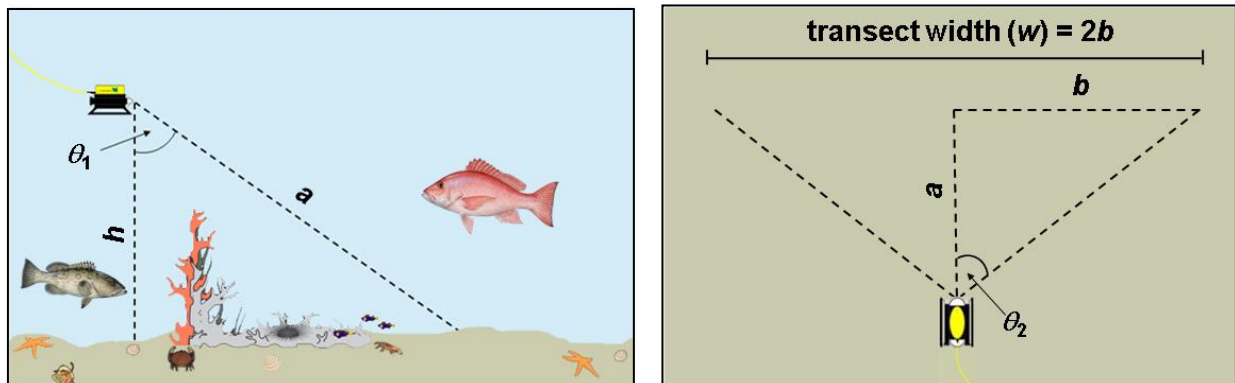


Figure 4. Mean (\pm SE) trophic level-specific fish density A) between natural and artificial reefs and B) among depth strata by trophic level for fishes video sampled with a micro remotely operated vehicle at reef sites in the northeastern Gulf of Mexico during 2009-2010.

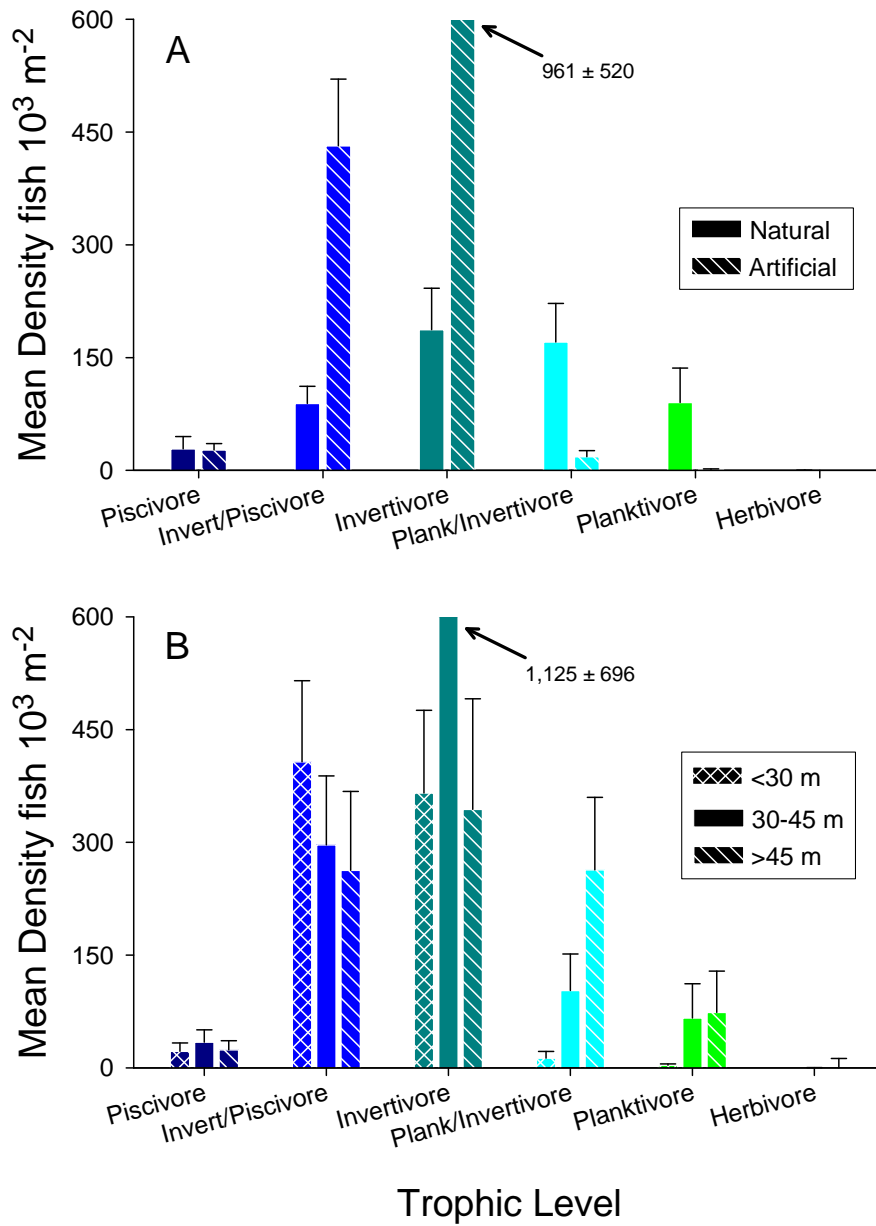


Figure 5. A) Mean (\pm SE) FL of predominant reef fish taxa estimated from laser scale data at study reef sites at natural and artificial reef sites in the northeastern Gulf of Mexico. B) Box plots of fork length (FL) distributions of predominant reef fish species scaled with lasers. Horizontal bars in the center of boxes indicate median FL. Upper and lower extended bars indicate 10th and 90th percentiles of FL, while symbols indicate individual fish whose FL was outside those percentiles for natural (circles) or artificial (triangles) reefs.

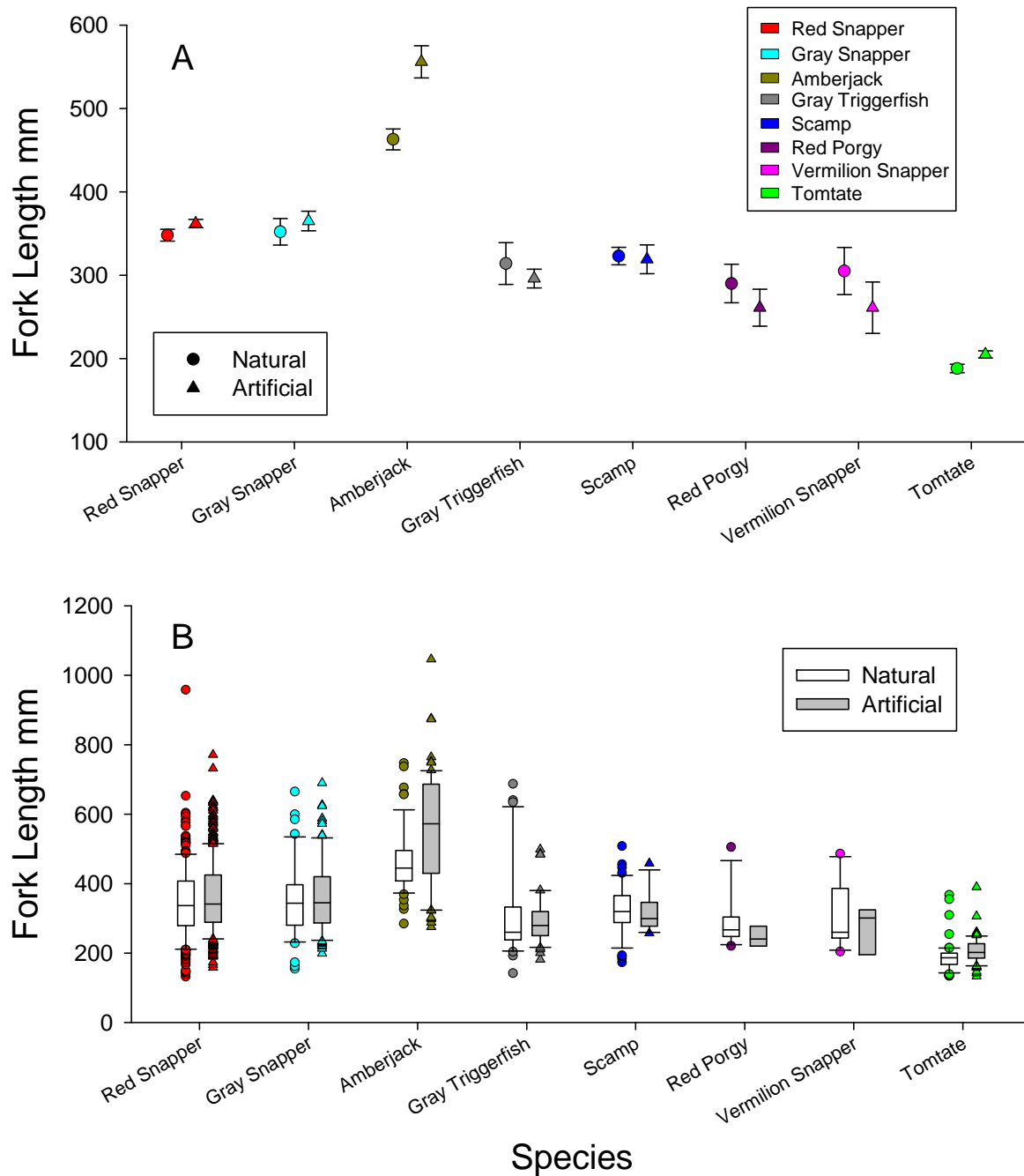


Figure 6. Distribution of fork length for A) all fishes observed and B) red snapper that were estimated with a laser scale attached to a micro remotely operated vehicle while video sampling at study reefs in the northeastern Gulf of Mexico during 2009-10. Panel C indicates mean fork length of all fishes and red snapper from the three depth strata sampled.

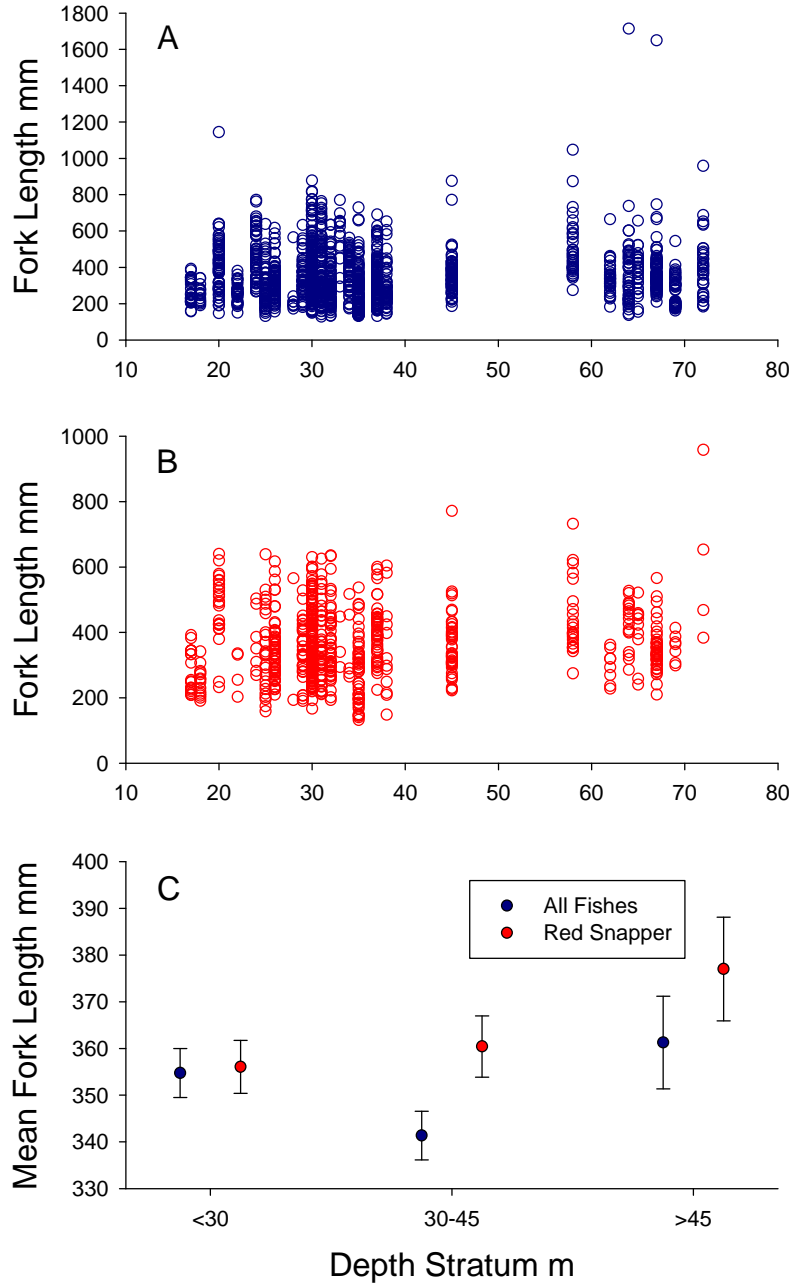


Figure 7. Total length (TL) frequency distributions of all fish scaled with lasers at natural and artificial reef study sites in the northeastern Gulf of Mexico plotted next to TL distributions of all fish captured at study sites with 9/0, 12/0, and 15/0 Mustad circle hooks.

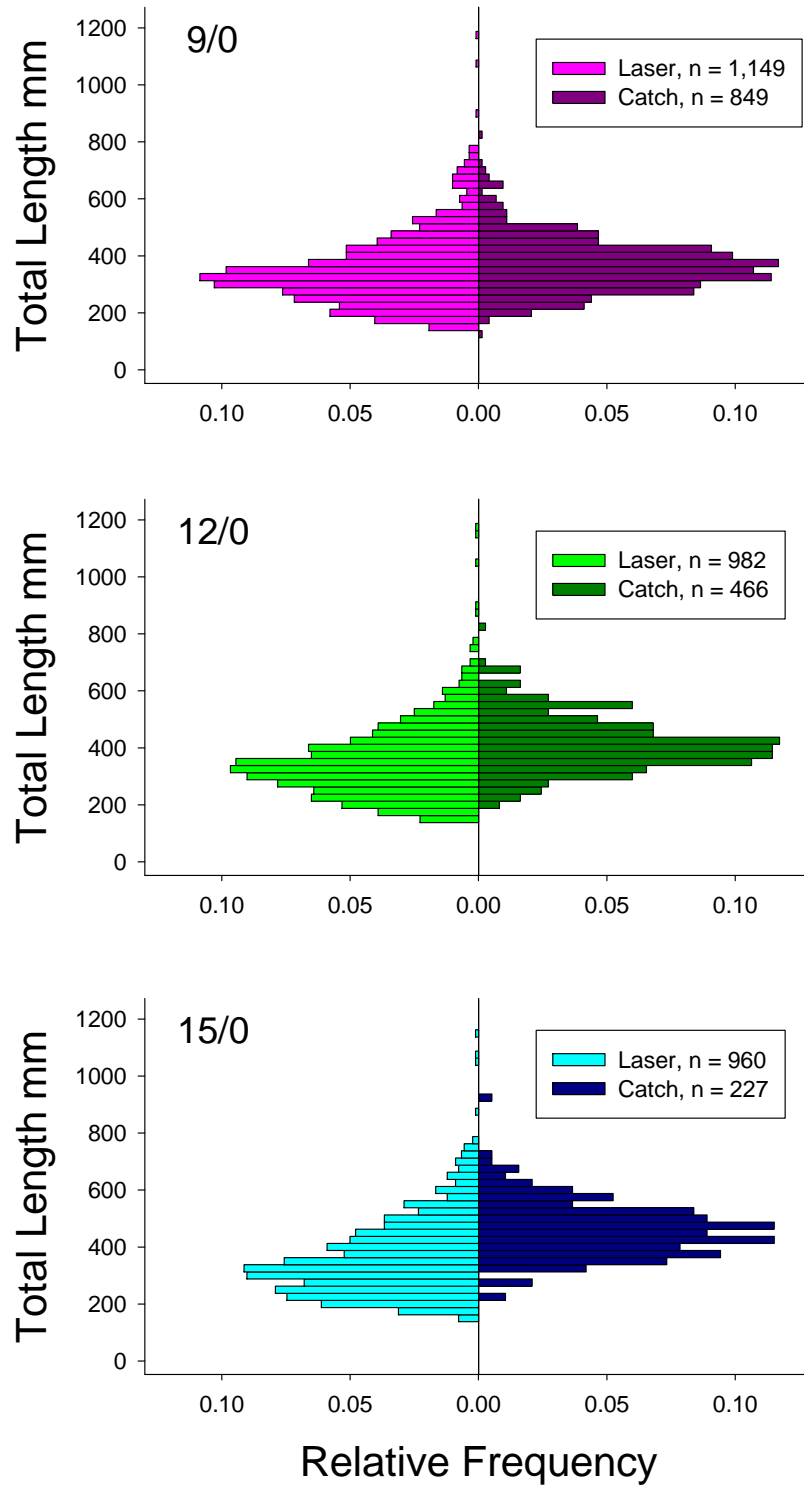


Figure 8. Frequency distributions of red snapper total length (TL) scaled with lasers at natural and artificial reef study sites in the northeastern Gulf of Mexico plotted next to TL distributions of red snapper captured at study sites with 9/0, 12/0, and 15/0 Mustad circle hooks.

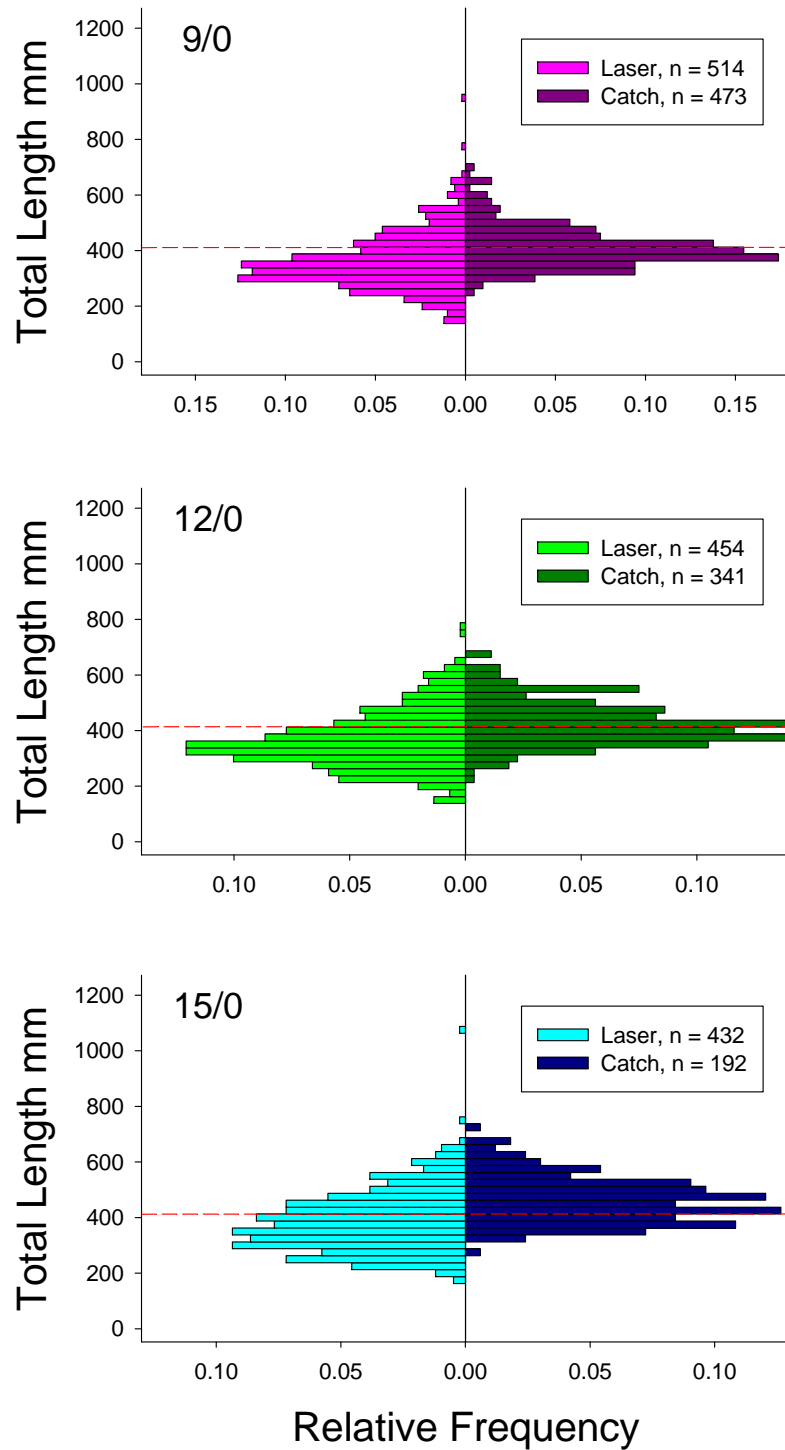


Figure 9. Mean total length (\pm) of A) all fish and B) red snapper scaled with a laser scale attached to a micro remotely operated vehicle or captured with Mustad circle hooks at natural and artificial reef study sites in the northeastern Gulf of Mexico during 2009-10. The horizontal dashed line on panel B indicates the minimum size (408 mm) for retention of red snapper in the recreational fishery.

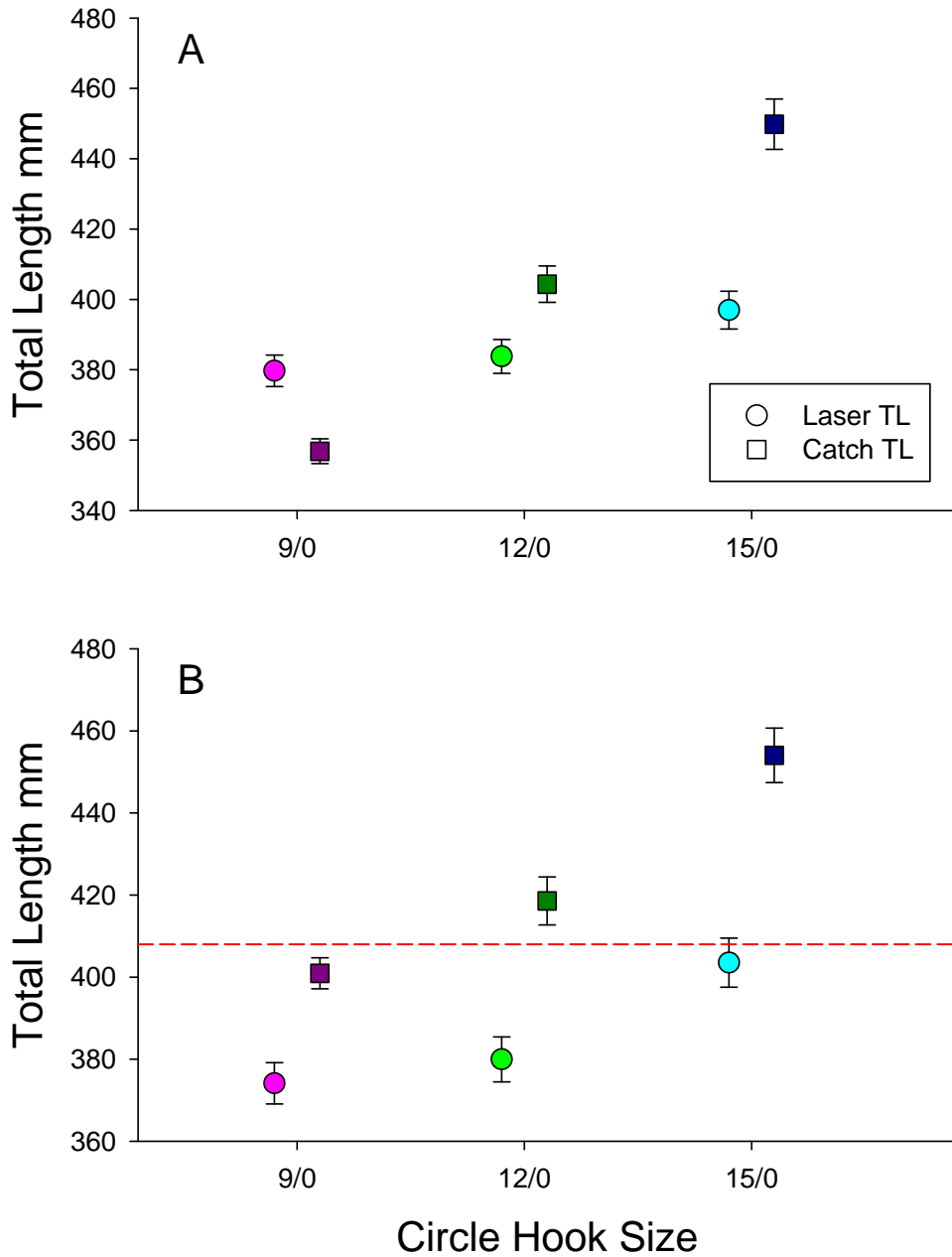


Figure 10. Overall catch per unit of effort for sampling conducted during 2009-10 with three different sized circle hooks at natural and artificial reef sites in the northern Gulf of Mexico.

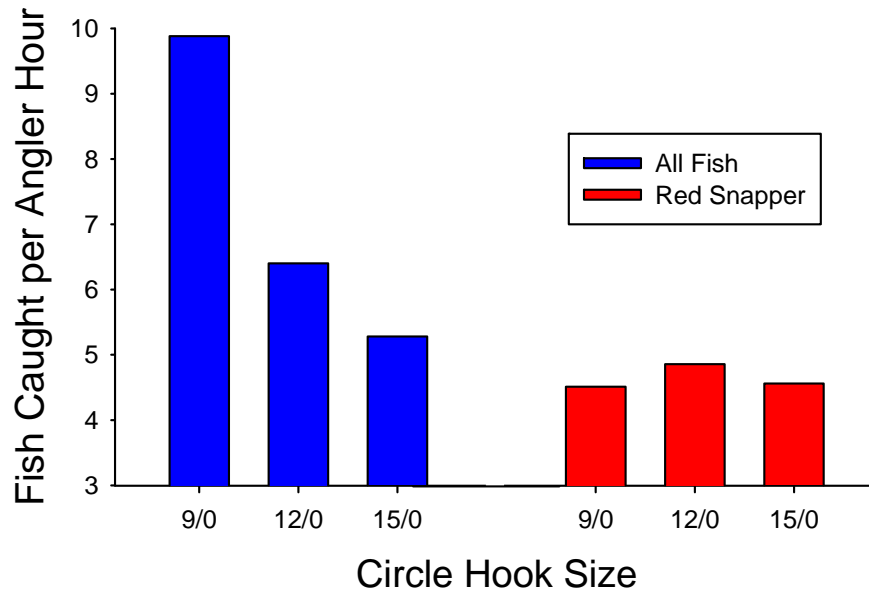


Figure 11. A) Size at age for red snapper sampled at natural (n = 182 fish) and artificial (n = 286 fish) reefs in the northeastern Gulf of Mexico, with fractional ages determined from counts of opaque zones in thin sections of sagittal otoliths, edge condition of otolith sections, and date of sampling. The plotted linear regression was fitted to the combined data. B) Residual distributions of observed minus size at age predicted from the Patterson et al. (2001) red snapper von Bertalanffy growth function (VBGF) for the original data to which the VBGF was fit, as well as for the fish aged in the current study.

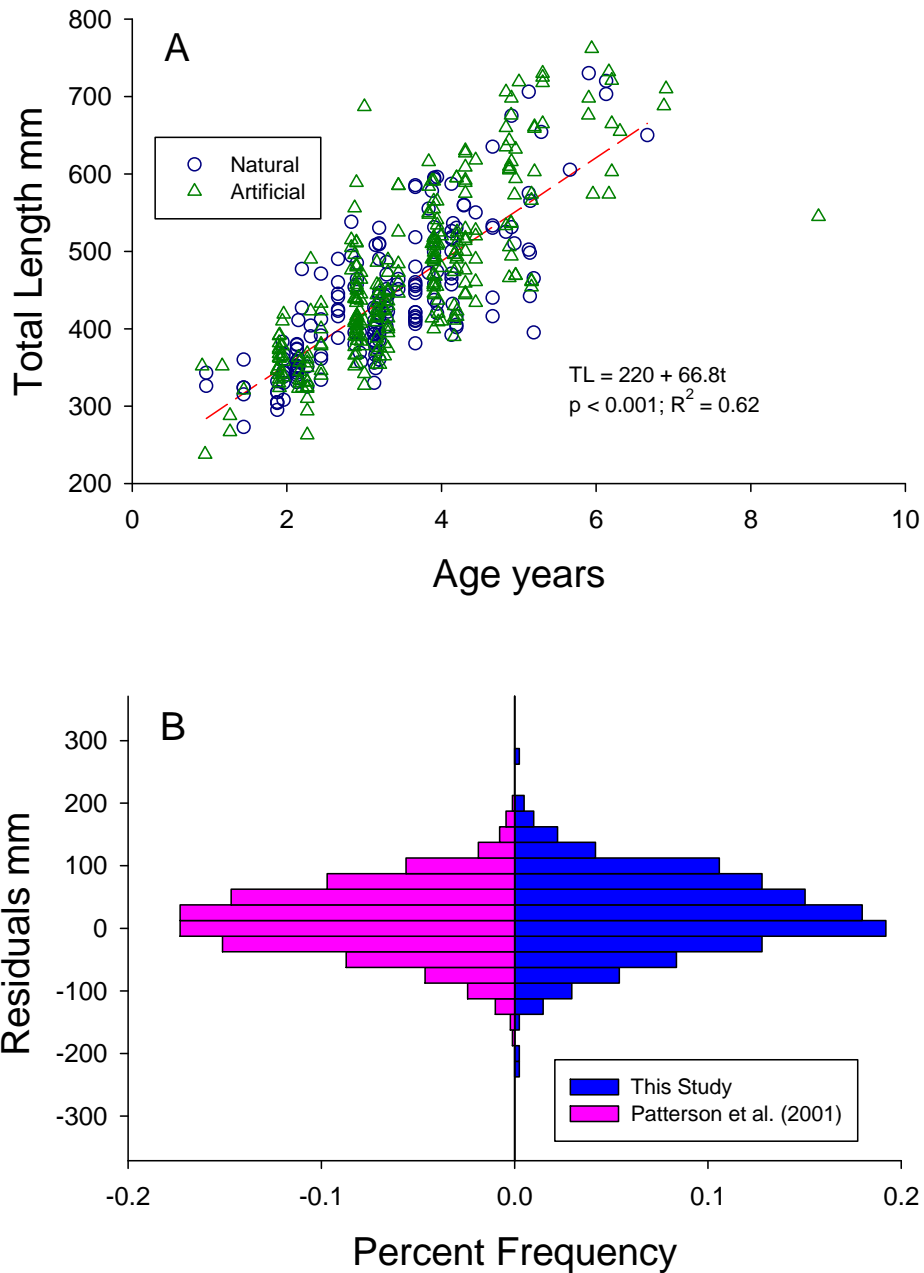


Figure 12. Catch curves fit to the $\ln(\text{numbers at age})$ data for red snapper captured with hook and line at natural and artificial reef sites in the northeastern Gulf of Mexico. Total sample sizes were 182 for fish captured at natural reefs and 286 for artificial reefs. Curves were fit only to data shown with filled symbols. Instantaneous rates of disappearance with age (y^{-1}) are shown for each curve; both regressions were highly significant ($p < 0.001$) with R^2 values > 0.98 .

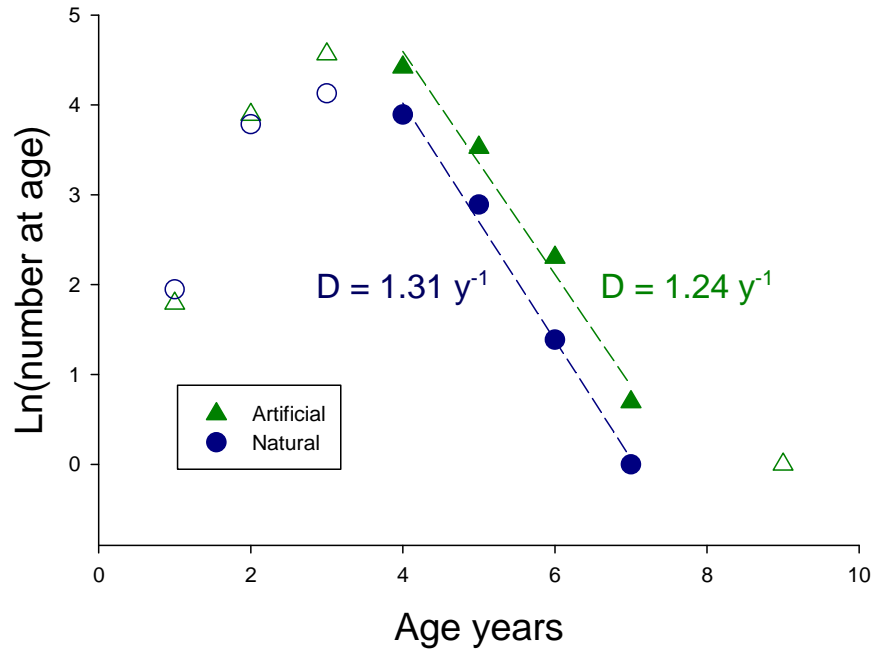


Figure 13. Distribution of red snapper total lengths either estimated with a laser scale attached to a micro remotely operated vehicle while video sampling at study reefs in the northeastern Gulf of Mexico during 2009-10, or measured directly for fish captured with hook and line gear while collecting biological samples at study reefs.

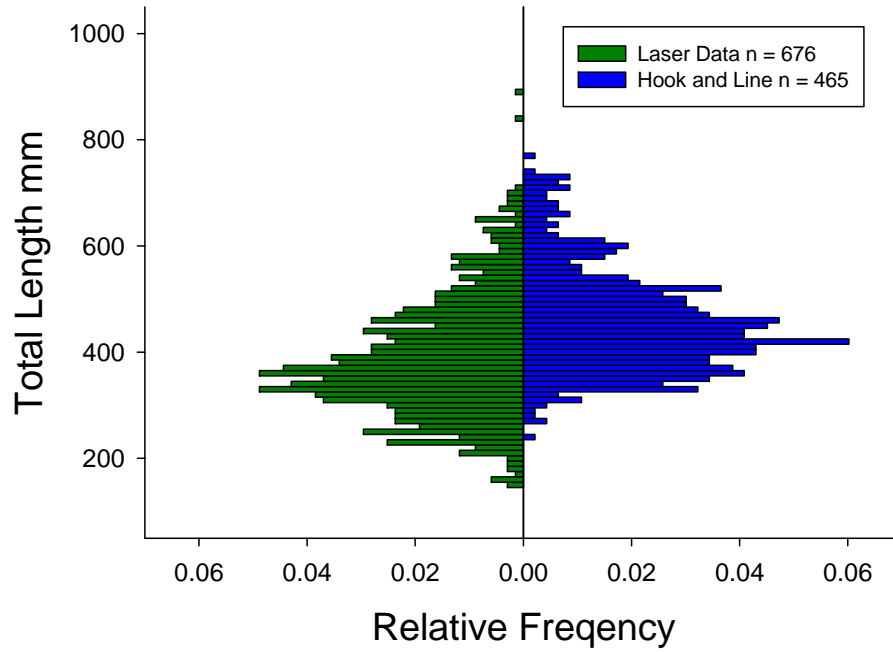


Figure 14. Species- and habitat-specific diet of predominant reef fishes sampled in the northeastern Gulf of Mexico based on gut content analysis. Plots indicate diet differences based on A) percent number of prey items observed, B) percent mass of total prey mass, and C) percent index of relative importance. Plain bars indicate samples from natural reefs and hatched bars indicate samples from artificial reefs. Species abbreviations: LS = lane snapper, AJ = greater amberjack, Soap = whitespotted soapfish, TT = tomtate, BR = blue runner, BRf = banded rudderfish, BSB = bank seabass, GT = gray triggerfish, Tat = tattler, RG = red grouper, RP = red porgy, GS = gray snapper, VS = vermilion snapper, AJJ = almaco jack, HH = highhat, and BIA = blue angelfish.

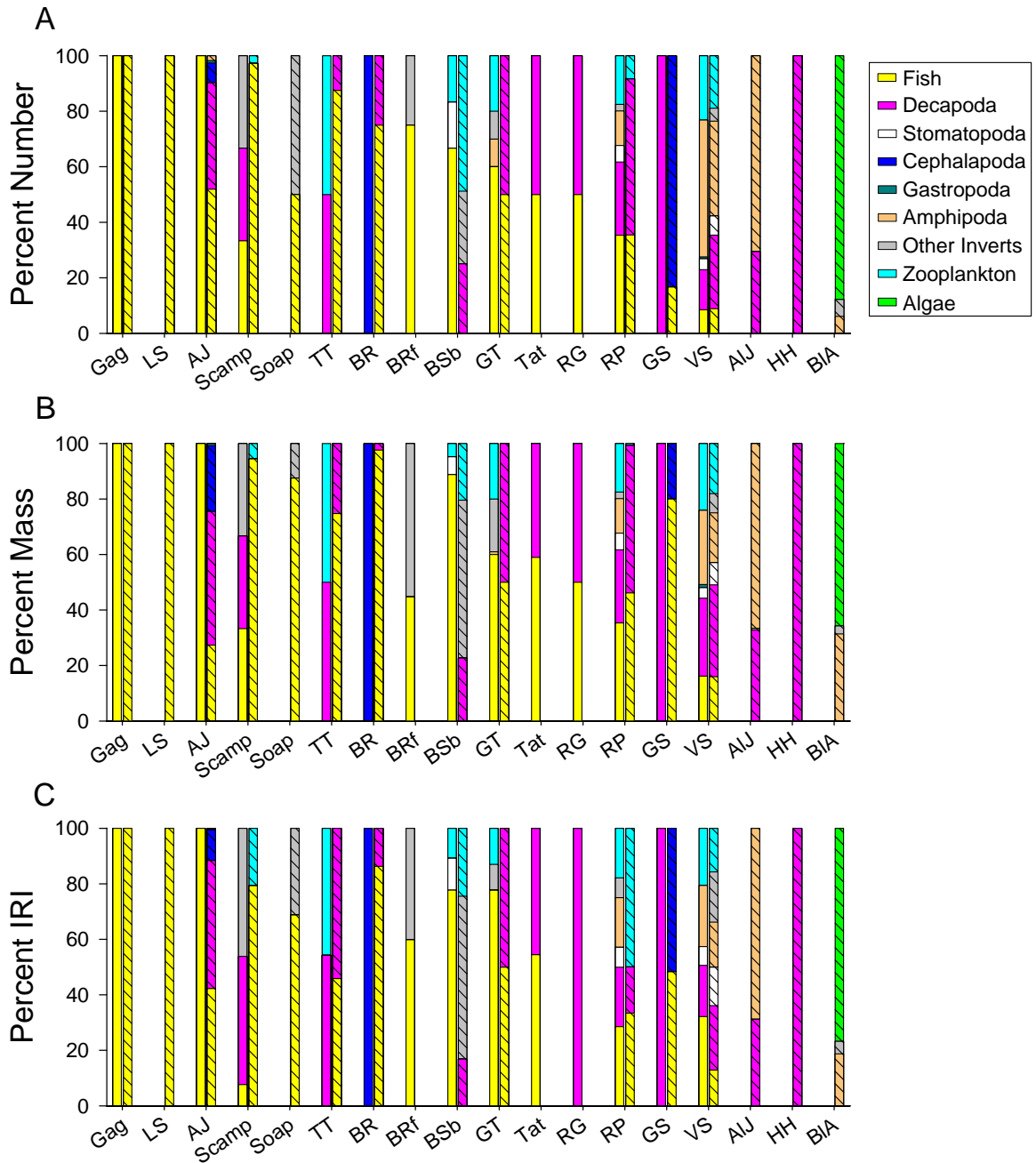


Figure 15. Percentage of red snapper diet derived from different prey categories estimated from gut content analysis of fish from three different size ranges samples on natural and artificial reefs in the northeastern Gulf of Mexico. The prey category-specific percentage of diet is presented based on A) percent number of prey items observed, B) percent mass of total prey mass, and C) percent index of relative importance. Plain bars indicate samples from natural reefs and hatched bars indicate samples from artificial reefs.

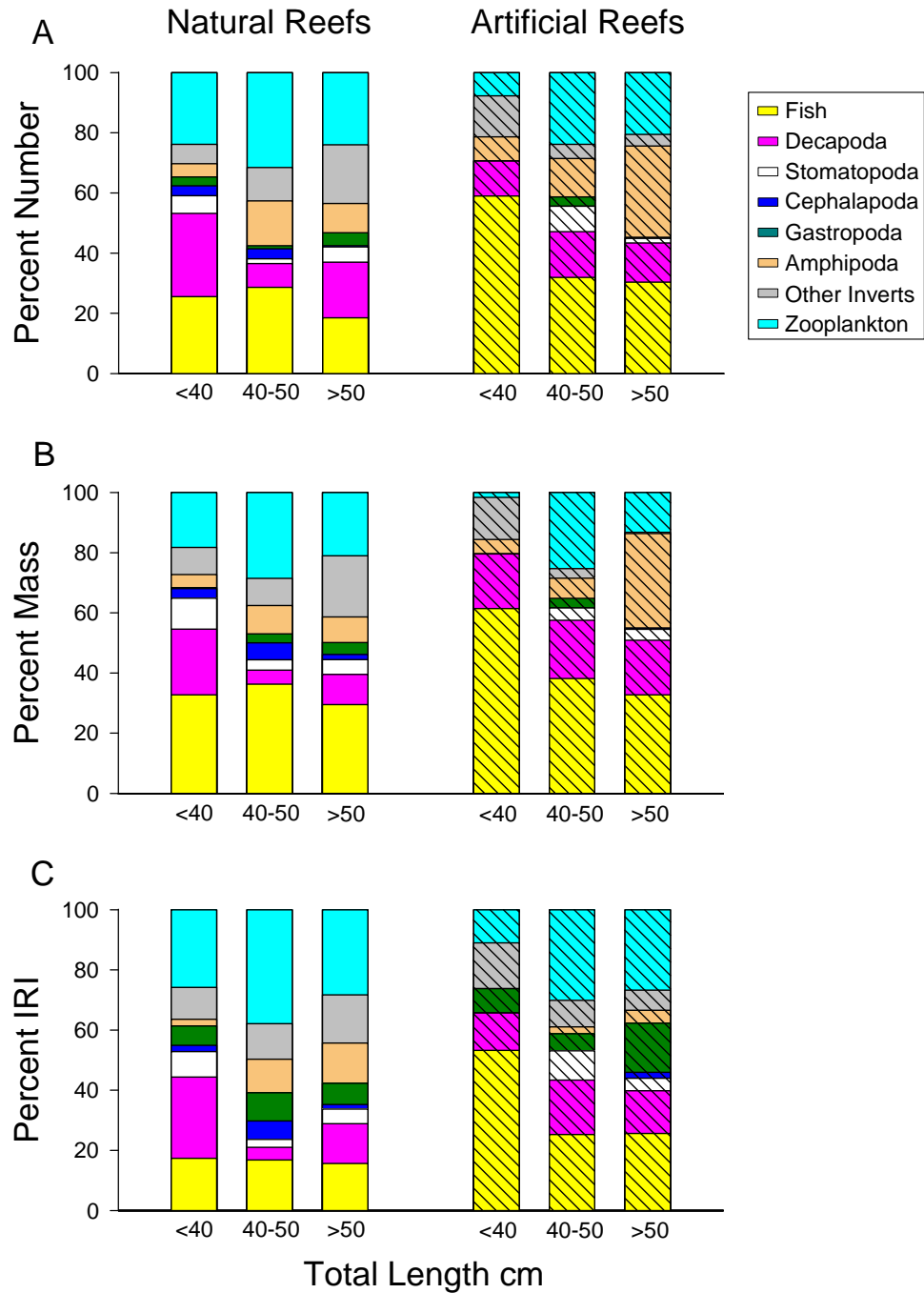


Figure 16. Plots of mean (\pm SE) stable isotope ratios for fish sampled at natural and artificial reef sites in the northeastern Gulf of Mexico during 2009-10.

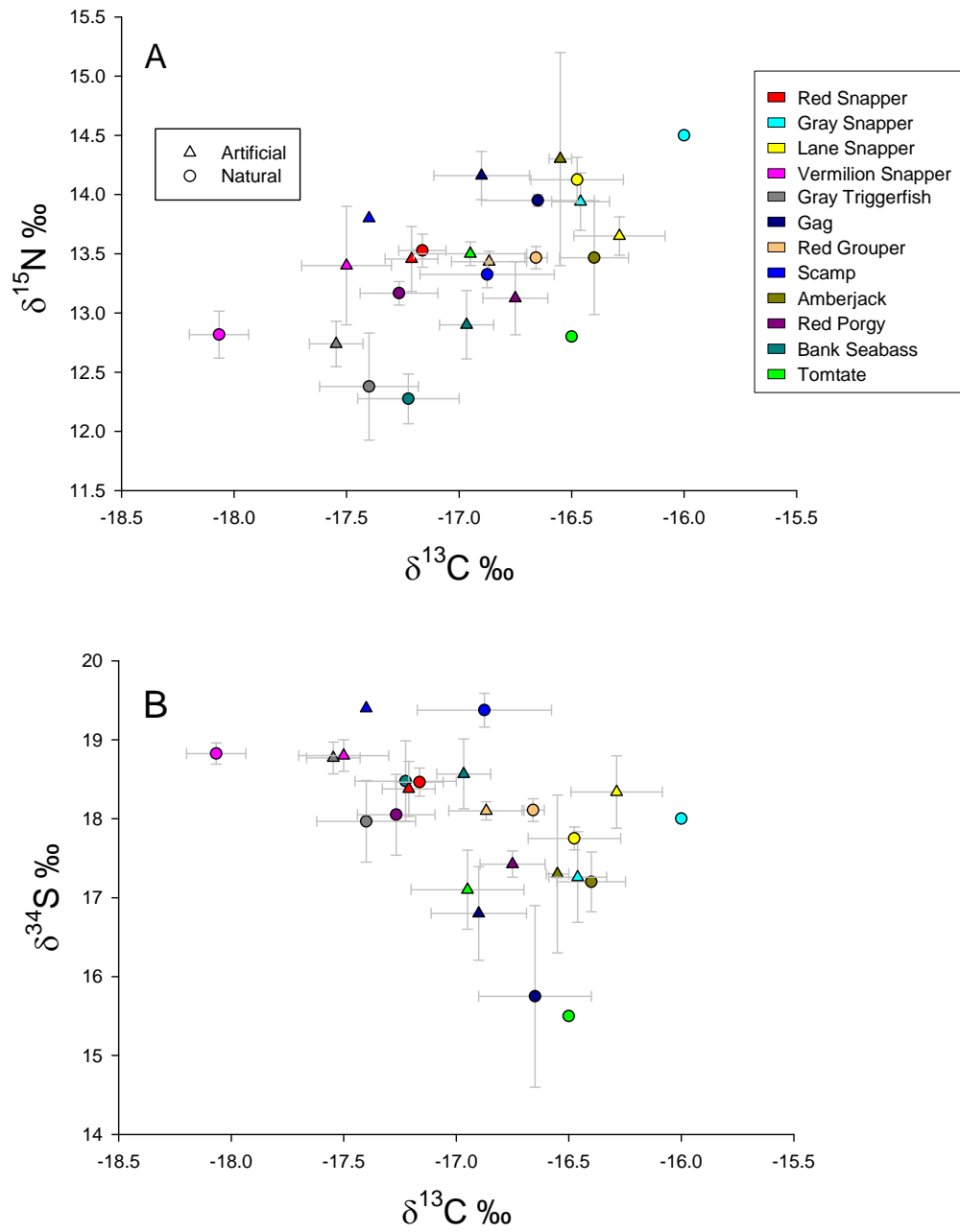


Figure 17. Plots of red snapper A) $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$, B) $\delta^{34}\text{S}$ versus $\delta^{13}\text{C}$, C) $\delta^{15}\text{N}$ versus total length, D) $\delta^{13}\text{C}$ versus total length, E) $\delta^{34}\text{S}$ versus total length, and F) mean ($\pm\text{SE}$) standardized $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and $\delta^{34}\text{S}$ values for fish sampled at natural (circles; $n = 56$) and artificial (triangles; $n = 34$) reef sites in the northeastern Gulf of Mexico during 2009-10.

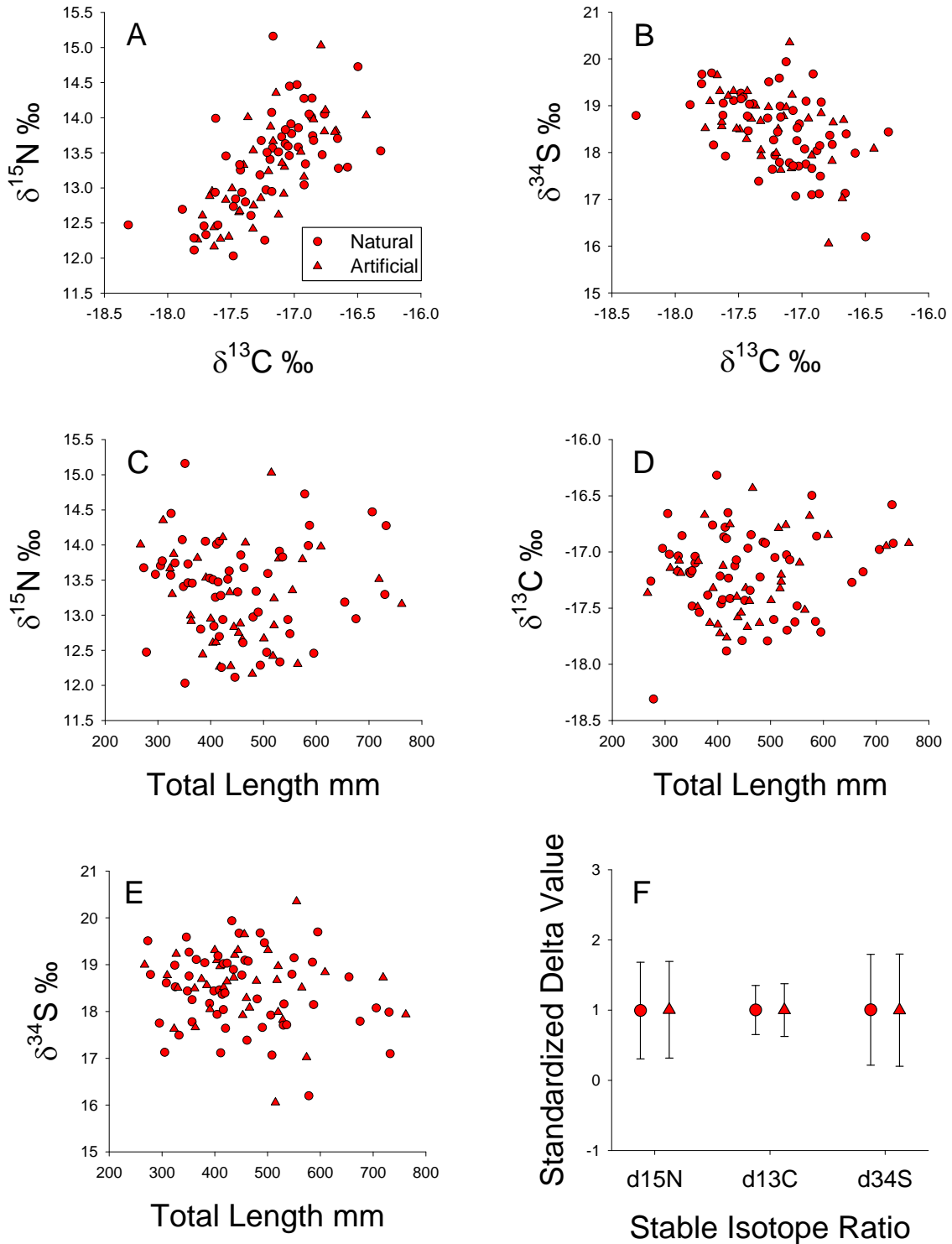


Figure 18. Species-specific stable isotope plots for fish sampled at natural and artificial reef sites in the northeastern Gulf of Mexico from September 2009 to May 2010 (n = 84 fish; pre DWH) and between May and August 2010 (n = 67 fish; post DWH), when oil from Deepwater Horizon was over the shelf. Error bars in each plot are standard error of the mean.

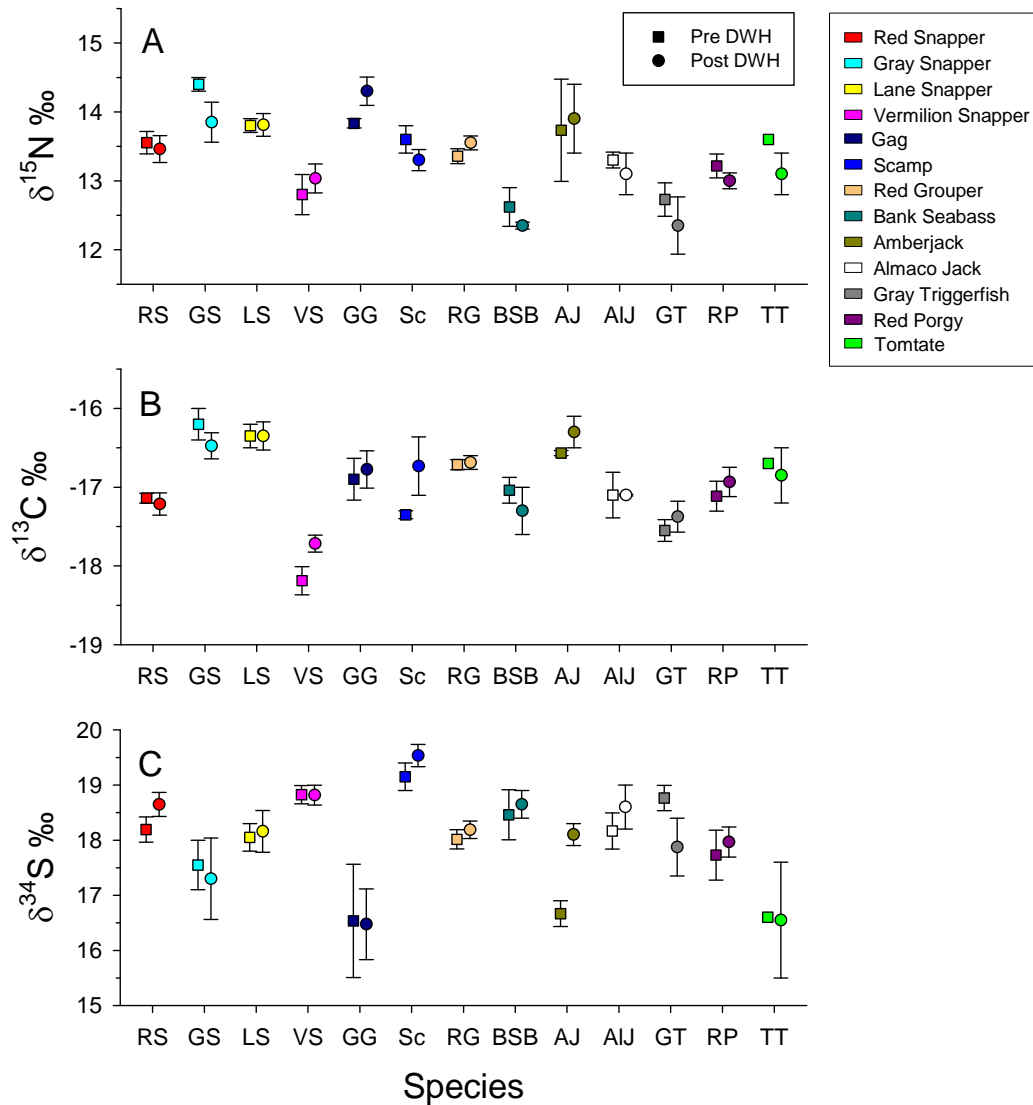


Figure 19. Plots of mean (\pm SE) stable isotope ratios for fish sampled at natural and artificial reef sites in the northeastern Gulf of Mexico from September 2009 to May 2010 (n = 76 fish; pre DWH) and between May and August 2010 (n = 75 fish; post DWH), when significant amounts of oil from the Deepwater Horizon (DWH) spill existed over the shelf.

