

ARTICLE

Integrating assemblage structure and habitat mapping data into the design of a multispecies reef fish survey

Theodore S. Switzer¹ | Sean F. Keenan¹ | Kevin A. Thompson¹ | Colin P. Shea¹ | Anthony R. Knapp² | Matthew D. Campbell³ | Brandi Noble³ | Chris Gardner⁴ | Mary C. Christman⁵

¹Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg, Florida, USA

²Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Senator George Kirkpatrick Field Laboratory, Cedar Key, Florida, USA

³National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Mississippi Laboratories, Pascagoula, Mississippi, USA

⁴National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory, Panama City, Florida, USA

⁵MCC Statistical Consulting LLC, Gainesville, Florida, USA

Correspondence

Theodore S. Switzer

Email: ted.switzer@myfwc.com

Present address

Kevin A. Thompson, Southeast Fisheries Science Center, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Miami, Florida, USA

Funding information

National Fish and Wildlife Foundation, Grant/Award Number: FL 40624, FL 45766, FL 50347, FL 54269 and FL 58101; National Oceanic and Atmospheric Administration, Grant/Award Number: NA11NMF4350047, NA16NMF4350165 and NA19NOS4510192; U.S. Fish and Wildlife Service, Grant/Award Number: F14AF00328, F15AF01222, F16AF00898 and F17AF00932

Abstract

Objective: Since 2010, three spatially disjunct reef fish video surveys have provided fishery-independent data critical to the assessment and management of reef fishes in the Gulf of Mexico. Although analytical approaches have recently been developed to integrate data from these surveys into a single measure of relative abundance and size composition, a more parsimonious approach would be to integrate survey efforts under a single Gulf-wide survey design. Accordingly, we conducted a retrospective analysis of historical video- and habitat-mapping data to develop a novel stratified random sampling design for conducting surveys of natural and artificial reef habitats.

Methods: We conducted a series of classification and regression tree analyses to delineate both spatial and habitat strata, and conducted simulations to assess the performance of an optimized survey design.

Result: Spatially, classification and regression tree results identified three depth strata (10–25 m, >25–50 m, >50–180 m) and three regional strata (north-central Gulf, Big Bend, southwest Florida) in the eastern Gulf. For both natural and artificial reefs, habitat strata were delineated based on a combination of relative relief (low, medium, high) and size of the individual reef feature, although reef scale differed markedly between natural (<100 m², 100–1000 m², >1000 m²) and artificial habitats (<25 m², 25–100 m², >100 m²). To optimize effort among sampling strata, effort was allocated proportionally based on a combination of habitat

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *Marine and Coastal Fisheries* published by Wiley Periodicals LLC on behalf of American Fisheries Society.

availability and managed-species richness for each stratum. Simulation results indicated that relative median biases were <10% and relative median absolute deviations <30% on estimates of abundance for most species examined on natural reefs under the optimal design, except Greater Amberjack *Seriola dumerili*. These measures of bias and imprecision were similar or higher for most species simulated using simple random and stratified random survey designs. Estimated relative median bias and relative median absolute deviations were notably higher for artificial reef surveys.

Conclusion: Based on these results, survey efforts were integrated as the Gulf Fishery Independent Survey of Habitat and Ecosystem Resources (G-FISHER) in 2020.

KEYWORDS

Gulf of Mexico, reef fish, reef habitats, survey design, video survey

INTRODUCTION

The application of advanced stock assessment models (e.g., statistical catch-at-length or catch-at-age models) requires data from statistically robust surveys from which both indices of stock size and annual estimates of size or age composition can be generated (Hilborn and Walters 1992; Siegfried et al. 2016). Early single-species stock assessments in the Gulf of Mexico relied heavily on harvest data collected from the fishery (i.e., fishery-dependent data) to make determinations of stock status in relation to key management reference points. However, increasingly restrictive and complex management measures have altered fishing behavior and eroded the utility of fishery-dependent data for quantifying population trends for most species (Bryan and McCarthy 2015; Smith et al. 2015; SouthEast Data, Assessment, and Review [SEDAR] 2018a).

As a result, data from fishery-independent surveys are critical for meeting stock assessment and management needs. To be most useful, these scientific surveys should strive to provide statistically robust data for multiple species that encompass the full geographic extent of the stocks being managed (Bryan et al. 2016). Survey efforts should also be designed to provide data on environmental conditions along with habitat quality and availability that are critical to model-based approaches used to generate indices of relative abundance. Ultimately, statistically robust survey data, along with relevant environmental data, can be incorporated into analyses that account for the influence of various factors that, combined with the effects of fishing and associated regulatory changes, may alter mortality, stock productivity, and abundance (Harford et al. 2018).

Impact statement

Data from reef fish video surveys were analyzed to develop a new survey design in the Gulf of Mexico. The new design provides better estimates of reef fish abundance from natural and artificial reef habitats and will improve the assessment and management of multiple reef fishes.

In the U.S. Gulf of Mexico (Figure 1), some of the greatest assessment and management challenges involve reef-associated fishes that support valuable commercial and recreational fisheries. From 2010 to 2020, several reef fish stocks (e.g., Gag *Mycteroperca microlepis*, Gray Triggerfish *Balistes capriscus*, Greater Amberjack *Seriola dumerili*, Red Snapper *Lutjanus campechanus*) in the Gulf have been variously assessed as overfished or subject to overfishing (SEDAR 2014a, 2014b, 2015, 2016a, 2016b, 2018b). Several existing surveys provide fishery-independent data for specific taxa or their life history stages, including estuarine seine and trawl surveys (Flaherty-Walia et al. 2015; Switzer et al. 2015), offshore trawl surveys (Matheson et al. 2017), vertical and bottom longline surveys (Campbell et al. 2014; Karnauskas et al. 2017; Powers et al. 2018), and ROV surveys (Powers et al. 2018). However, three collaborative video surveys (the Southeast Area Monitoring and Assessment Program survey, the Panama City survey, and the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute survey) provide the most comprehensive multispecies characterization of abundance and size composition of reef-associated fishes in the Gulf (Gardner et al. 2017; Thompson et al. 2017; Campbell et al. 2019). All three surveys are conducted

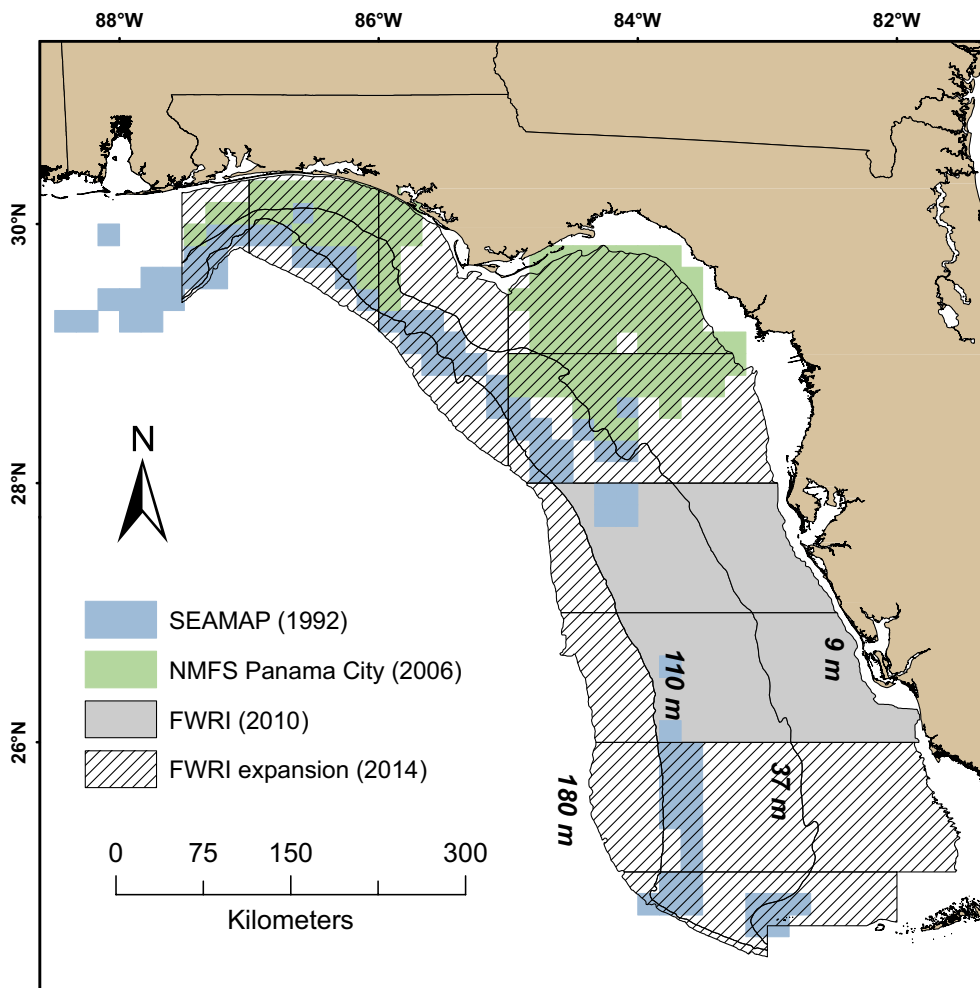


FIGURE 1 Area covered by earlier reef fish video surveys conducted by the Southeast Area Monitoring and Assessment Program (SEAMAP), National Marine Fisheries Service (NMFS) Panama City, and the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWRI) in the eastern Gulf of Mexico. In the legend, the years in parentheses represent the year in which each survey began. Contour lines are isobaths.

using identical stereo-baited remote underwater video (S-BRUV) arrays that are capable of effectively sampling a wider range of species and sizes of reef fish than do traditional capture gear (Cappo et al. 2007; Christiansen et al. 2020, 2022). Because of differences in spatial coverage and statistical design among these three surveys, novel analytical approaches have recently been developed to combine data from all three surveys (Thompson et al. 2022). These methods first involve classification and regression tree analyses to generate a common habitat classification system among all three surveys; combined data are then analyzed within a generalized linear modeling framework that weights resultant indices by estimates of survey-specific habitat availability. Indices of relative abundance and size composition from these surveys have a long track record of use in stock assessments of Gulf reef fishes (SEDAR 2014a, 2014b, 2015, 2016a, 2016b, 2018a, 2018b). The utility of S-BRUV survey data in the Gulf, however, could be improved upon by addressing concerns

regarding insufficient sampling intensity, limited spatial extent of the surveys, and differences in statistical design among the surveys, especially in terms of the quality and composition of reef habitats sampled by each survey.

Although methods have been developed to combine data from all three surveys, it would be more parsimonious and powerful to integrate survey efforts under a new, unified sampling design. Other surveys of reef fishes have benefited from the implementation of spatial and habitat stratification that subdivides the survey domain into homogeneous strata to effectively partition population variance (Smith et al. 2011; Richards et al. 2016; Ault et al. 2018). In this paper, we conduct a retrospective analysis of data from surveys of reef fishes and associated habitats in the eastern Gulf of Mexico to accomplish three primary goals: (1) delineate biologically relevant spatial and habitat strata, (2) define optimal allocation of sampling effort based on a combination of habitat availability and species richness for managed species, and (3) assess and compare the relative performance of

the final optimized survey design to the performance of simple random and spatially stratified designs for several key reef fish taxa. Such a design should ultimately improve our ability to accurately assess trends for use in single-species stock assessment, provide robust data for ecosystem-based models, and facilitate empirical analyses to characterize multispecies responses to environmental drivers at varied temporal and spatial scales.

METHODS

The primary objective of all three reef fish video surveys conducted in the Gulf of Mexico is to provide data on fishes associated with reef habitats from which indices of relative abundance and size composition can be generated in support of stock assessments. In addition to relative abundance data, these surveys also provide associated habitat and water quality data that are critical to model-based approaches to index development (Thompson et al. 2022). Specific details of each respective survey follow below (see Table 1 for a review of key similarities and differences between these surveys).

Southeast Area Monitoring and Assessment Program reef fish video survey

The Southeast Area Monitoring and Assessment Program reef fish video (SRFV) survey is conducted primarily

along the shelf break (70–100-m water depth) and in areas of extensive high-relief reef habitat (e.g., Florida Middle Grounds, Pulley Ridge) throughout the U.S. Gulf of Mexico (Figure 1). This survey was conducted during 1992–1997 and 2001–2002 and has been conducted annually since 2004, with sampling generally done during April–August. This survey follows a two-stage stratified random sampling design. First, survey blocks (measuring 10' latitude × 10' longitude) are randomly selected with proportional allocation from seven strata: south Florida (small [$<20\text{ km}^2$] and large [$>20\text{ km}^2$] reef blocks), northeast Gulf (small and large reef blocks), Louisiana–Texas shelf (small and large reef blocks), and south Texas (small reef block only). The second stage of the design uses a random uniform selection process to select specific sampling units (measuring 0.1 nm × 0.1 nm) containing reef habitat (generated from previously mapped topographic features) from an overlaid set of grid cells separated by approximately 200 m × 200 m over the mapped reef area.

National Marine Fisheries Service Panama City survey

The National Marine Fisheries Service (NMFS) Panama City survey is conducted along nearshore shelf waters (10–57 m) in the northeastern Gulf of Mexico (Figure 1). This survey has been conducted since 2005, with sampling conducted during May–November. The Panama City survey

TABLE 1 A summary of key similarities and differences among historical Southeast Area Monitoring and Assessment Program (SEAMAP), Panama City, and Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWRI) reef fish surveys. Abbreviations: H = horizontal pixels, HFV = horizontal field of view, V = vertical pixels, and VFV = vertical field of view.

Survey characteristic	SEAMAP	Panama City	FWRI
Depth	Shelf break	Inner shelf	Shelf and shelf break
Spatial extent	Gulf wide	Northeastern Gulf	Eastern Gulf
Habitat mapping	Multibeam sonar	Side scan sonar	Side scan sonar
	Targeted	Targeted or random	Random
Habitat	Natural	Natural	Natural and artificial
Spatial strata	Four regions	Two regions, three depths	Nine regions, three depths
Habitat strata	Small and large reef	Three reef-quality strata	Artificial and natural reef
Allocation	Proportional to reef	Unequal probability	Proportional to area
Design	2-stage design	2-stage design	2-stage design
Sampling gear	Cameras with resolution of 1920 H × 1200 V with 86.3° HFV and 60.7° VFV	Cameras with resolution of 1920 H × 1200 V with 86.3° HFV and 60.7° VFV	Cameras with resolution of 1920 H × 1200 V with 86.3° HFV and 60.7° VFV
Bait	Squid	Atlantic Mackerel	Atlantic Mackerel
Abundance metric	MaxN	MaxN	MaxN
Taxa enumerated	Managed fishes	All fishes	All fishes

uses a two-stage unequal-probability sampling design to ensure uniform geographic and bathymetric coverage. In the first stage, survey blocks (measuring 5' latitude \times 5' longitude) are randomly selected, with allocation proportional to their frequency by region (east and west of Cape San Blas) and depth stratum (10–20 m, 20.1–30 m, >30 m). In the second stage, two individual reef features are randomly selected, at least 250 m apart, from selected blocks. Known reef features were located via side-scan sonar mapping, and habitats classified later following the Coastal and Marine Ecological Classification Standard (Federal Geographic Data Committee 2012). For each reef feature, a scaled, composite score of habitat quality is calculated based on physical attributes of the reef (using relief, reef area, and rugosity), and the range of values is parsed into quantiles. Sites are finally selected using unequal-probability sampling, in which the second and third quantiles are three times as likely to be selected as the first quantile, and the fourth quantile is five times as likely to be selected as the first quantile.

Fish and Wildlife Research Institute natural reef survey

The Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWRI) initiated an annual survey of natural reef habitats on the central West Florida Shelf in 2010 (Figure 1). Sampling for this survey was done from May through October. The FWRI survey followed a two-stage stratified random design in which annual sampling effort is allocated between two latitudinal strata (26°N–27°N and >27°N–28°N) and two depth strata (nearshore = 9–37 m; offshore = >37–110 m). Effort was allocated equally between latitudinal strata, while within each latitudinal stratum, effort was allocated proportionally based on total area in each depth stratum. Within each stratum, sampling units measuring 0.54 km north–south by 0.18 km east–west were randomly selected to sample each year. Data on the distribution of natural reef habitats in the eastern Gulf of Mexico are of insufficient spatial resolution to direct sampling efforts. Accordingly, standardized habitat mapping surveys were first conducted at randomly selected sites (mapping surveys include each randomly selected sampling unit as well as 20 additional surrounding units for a total mapped area of 2.1 km²) using an L3-Klein 3900 side-scan sonar operating at 445 kHz. Habitat mapping data were analyzed to manually digitize polygon boundaries of individual reef features (i.e., those >2 m across) that were classified using a derivative of the geoform and surface geological components of the Coastal and Marine Ecological Classification Standard (Table 2; Federal Geographic

TABLE 2 Natural and artificial reef habitat types (geoforms) identifiable via interpretation of side-scan sonar backscatter data. Geoforms are ordered by increasing relief. Values are provided for relief rank for those geoforms for which reef fish assemblage data were available. Habitat strata indicates whether each habitat was classified as low relief, moderate relief, or high relief in the resultant habitat stratification scheme. See Keenan et al. (2022) for a full description of habitat types.

Relief rank	Geoform	Habitat strata
Natural reef habitats		
	Seagrass	Low relief
1	Flat hard bottom	Low relief
2	Pavement	Low relief
3	Mixed hard bottom	Low relief
4	Potholes	Moderate relief
5	Rubble field	Moderate relief
6	Fracture	Moderate relief
7	Reef rubble	High relief
8	Fragmented hard bottom	High relief
	Individual patch reef	High relief
	Aggregate patch reef	High relief
9	Aggregate coral reef	High relief
10	Ledge	High relief
11	Boulder	High relief
12	Spur and groove	High relief
13	Spring or sink	High relief
14	Pinnacle	High relief
15	Escarpment	High relief
Artificial reef habitats		
	Cable	Low relief
	Dredge deposit	Low relief
1	Tires	Low relief
	Dredged channel	Low relief
2	Rock piles	Low relief
3	Pipelines	Low relief
4	Construction materials	Moderate relief
5	Reef modules	Moderate relief
6	Chicken coops	High relief
7	Marine wreckage	High relief
8	Other vehicles	High relief
9	Small vessels	High relief
10	Military tanks	High relief
11	Oil-platform materials	High relief
	Aircraft	High relief
12	Large vessels	High relief

Data Committee 2012). Additional details of natural reef habitat mapping and classification protocols can be found in Keenan et al. (2018, 2022). During second-stage site

selection, a sampling unit containing natural reef habitat was randomly selected, and one or two individual reef features, at least 100 m apart, were selected for sampling.

The FWRI natural reef survey was expanded in 2014 to incorporate the Florida Panhandle and in 2016 to incorporate remaining waters off the Florida Gulf Coast, including a “deep” depth stratum (110–180 m). Sampling allocation and site selection protocols for these expanded natural reef survey efforts were identical to those from the original survey implemented in 2010.

Fish and Wildlife Research Institute artificial reef survey

Along with a spatial expansion of the FWRI natural reef survey, FWRI initiated a complementary survey of artificial reef habitats in 2014 so that indices of relative abundance and size composition of populations specifically associated with artificial reef habitats, which receive disproportionately high fishing effort in comparison to natural reef habitats, could be generated. The FWRI artificial reef survey utilized the same sampling frame as the FWRI natural reef survey. However, since all legally deployed artificial reefs must be reported to the state of Florida, this survey was conducted under the assumption that the artificial reef sampling universe was fully described. Point locations of all known shipwrecks and artificial reefs were intersected with the sampling frame to identify sampling units that contained artificial reef habitats. Annual sampling effort was then allocated proportionally among spatial strata based on the number of primary sampling units known to contain artificial reefs. Standardized habitat mapping surveys were conducted and data processed following identical protocols to those from the natural reef survey, with a primary objective of delineating and classifying the spatial extent of each artificial reef feature (Table 2). During second-stage site selection, one individual artificial reef feature was selected for sampling. Additional details of artificial reef habitat mapping and classification protocols can be found in Keenan et al. (2018, 2022).

Sampling methods: stereo-baited remote underwater video arrays

Sampling was conducted during daytime hours (between 1 h after sunrise and 1 h before sunset) using S-BRUV arrays; array-mounted or independently deployed water quality instruments were used to characterize water quality at each sampling site (e.g., temperature, salinity,

dissolved oxygen). Each S-BRUV array consisted of either four stereo video units facing 90° from each other (SRFV and NMFS Panama City surveys) or two stereo video units facing 180° apart (FWRI survey) to maximize the field of view. All stereo video units consisted of a pair of stereo cameras (Point Gray Blackfly cameras; model BFLY-U3-23S6M-C) equipped with Kowa lenses (model LM6HC), which recorded imagery at a resolution of 1920 horizontal pixels × 1200 vertical pixels with a horizontal field of view of 86.3° and a vertical field of view of 60.7°, a CPU, and a hard drive housed in an aluminum casing, mounted 30–50 cm above the bottom of an aluminum frame. Before each camera deployment, an S-BRUV array was freshly baited with 0.45 kg of squid (SRFV) or 0.45 kg of previously frozen cut Atlantic Mackerel *Scomber scombrus* (FWRI and NMFS Panama City) and deployed for approximately 30 min to allow the sediment plume to dissipate before video read time (Gledhill and David 2004). We have not empirically tested whether bait type influences the abundance of fishes observed during S-BRUV surveys. However, Driggers et al. (2017) did not detect any significant difference in the catch rates of reef fishes between hooks baited with squid and those baited with Atlantic Mackerel, so we operate under the assumption that the effect of bait is minimal. From each S-BRUV deployment, video from a single stereo video unit (among those verified to have a clear view of reef habitat) was randomly selected and annotated, although videos with low visibility, large obstructions, or camera malfunctions were not processed. Twenty minutes of video were annotated, beginning when the cloud of sediment raised by the array landing had dissipated. All managed reef fishes (Table 3) were identified to the lowest possible taxon, and abundance was estimated as MaxN (the maximum number of a given species observed in the field of view at any time during the 20 min analyzed; Ellis and DeMartini 1995), which is the standard metric of abundance used for most video surveys worldwide (Langlois et al. 2020). When possible, lengths of managed fishes were estimated (fork length in millimeters) at either the time of MaxN or the time when most measurements were possible using SeaGIS software; reef fishes observed on video range from approximately 50–1500 mm FL, although approximately 95% of all reef fish observed range from approximately 100–700 mm FL. Annotation of videos included an analysis of microhabitat characteristics of the observed habitats that are important covariates for model-based index development protocols (e.g., substrate type and composition, type and composition of attached biota, relief), although some minor habitat coding discrepancies are evident among the

TABLE 3 Species included in statistical analyses, listed by family. All species are managed under the Gulf of Mexico Fishery Management Council Reef Fish Management Plan.

Family	Species name
Lutjanidae	Queen Snapper <i>Etelis oculatus</i>
	Mutton Snapper <i>Lutjanus analis</i>
	Blackfin Snapper <i>Lutjanus buccanella</i>
	Red Snapper <i>Lutjanus campechanus</i>
	Cubera Snapper <i>Lutjanus cyanopterus</i>
	Gray Snapper <i>Lutjanus griseus</i>
	Lane Snapper <i>Lutjanus synagris</i>
	Silk Snapper <i>Lutjanus vivanus</i>
	Yellowtail Snapper <i>Ocyurus chrysurus</i>
	Wenchman <i>Pristipomoides aquilonaris</i>
Vermilion Snapper <i>Rhomboplites aurorubens</i>	
Serranidae	Speckled Hind <i>Epinephelus drummondhayi</i>
	Atlantic Goliath Grouper <i>Epinephelus itajara</i>
	Red Grouper <i>Epinephelus morio</i>
	Yellowedge Grouper <i>Hyporthodus flavolimbatus</i>
	Warsaw Grouper <i>Hyporthodus nigritus</i>
	Snowy Grouper <i>Hyporthodus niveatus</i>
	Black Grouper <i>Mycteroperca bonaci</i>
	Yellowmouth Grouper <i>Mycteroperca interstitialis</i>
	Gag <i>Mycteroperca microlepis</i>
	Scamp <i>Mycteroperca phenax</i>
Yellowfin Grouper <i>Mycteroperca venenosa</i>	
Malacanthidae	Goldface Tilefish <i>Caulolatilus chrypsops</i>
	Blueline Tilefish <i>Caulolatilus microps</i>
	Tilefish <i>Lopholatilus chamaeleonticeps</i>
Carangidae	Greater Amberjack <i>Seriola dumerili</i>
	Lesser Amberjack <i>Seriola fasciata</i>
	Almaco Jack <i>Seriola rivoliana</i>
	Banded Rudderfish <i>Seriola zonata</i>
Balistidae	Gray Triggerfish <i>Balistes capriscus</i>
Labridae	Hogfish <i>Lachnolaimus maximus</i>

three surveys (Campbell et al. 2017; Gardner et al. 2017; Thompson et al. 2017).

Analytical methods: defining sampling strata

To determine the stratification scheme for the reef fish survey, three independent series of classification and regression tree (CART) analyses were conducted to delineate (1) spatial strata, (2) natural reef habitat strata, and

(3) artificial reef habitat strata. All CART analyses were restricted to data collected during 2014–2017 and only included explanatory variables that could be identified a priori. Analyses to delineate spatial strata ($N=3487$) included data from all three surveys and were restricted to data from natural reefs only; for these analyses, latitude, longitude, and depth were included as potential explanatory variables. Analyses to delineate natural ($N=2005$) and artificial reef habitat strata ($N=260$) were restricted to data from the FWRI survey only because data were considered to be representative of the full diversity of habitats available due to the random habitat mapping approach used in this survey; for these analyses, both a measure of relative relief for each geoform type (Table 2) and the areal extent of each reef feature were included as potential explanatory variables.

For each analysis, a site-by-abundance (MaxN) matrix was first constructed that included all reef-associated taxa for which fishery management plans exist for Gulf populations (Table 3). Abundance data were fourth-root transformed to reduce the influence of highly abundant taxa (Clarke et al. 2014), and Bray–Curtis similarity matrices were estimated that included a dummy variable (value of 1 for all samples) so that sites at which no species were observed were treated as being similar (Clarke et al. 2006). Each CART analysis was conducted via the LINKTREE algorithm in PRIMER 7 (Clarke et al. 2014; Clarke and Gorley 2015). LINKTREE, which is a nonparametric analog to multivariate regression trees (De'ath 2002) with no underlying assumptions, is a constrained binary divisive clustering approach in which subdivisions of the environmental data must have some explanatory ability. To limit the number of potential strata identified, each set of analyses (analyses to delineate spatial strata, natural reef habitat strata, and artificial reef habitat strata) were constrained to minimum group sizes representing 10, 15, and 20% of available data. All permutation analyses were conducted with 9999 iterations. SIMPROF analyses (Clarke et al. 2008), which compare the true similarity profile with a series of permuted profiles generated by randomizing each species across samples, were conducted to test for statistical significance ($\alpha=0.05$) between identified groups.

Analytical methods: determining sampling allocation for natural reefs

Once natural reef sampling strata had been defined, an optimal allocation scheme was developed that incorporated measures of both habitat availability and managed-species richness for each identified natural reef habitat stratum (combination of spatial strata and habitat strata).

First, the proportional coverage of each habitat stratum (P_{NATHAB}) was calculated for each spatial stratum as

$$P_{\text{NATHAB}} = A_{\text{NATHAB}} / A_{\text{MAPPED}},$$

where A_{NATHAB} is the total area of habitat identified through side-scan sonar (calculated by summing the area of all natural reef polygons for each habitat stratum) and A_{MAPPED} is the total area mapped. This proportion was then extrapolated to estimate total natural reef habitat availability (H_{NATSTRAT}) within each spatial stratum as

$$H_{\text{NATSTRAT}} = A_{\text{SPATSTRAT}} \times P_{\text{NATHAB}},$$

where $A_{\text{SPATSTRAT}}$ is the total area of each spatial stratum. Estimates of habitat availability were calculated using FWRI natural reef habitat mapping data because they were collected following standardized, randomized mapping protocols and so were considered to be representative of unmapped areas. Next, average managed-species richness (R_{NATSTRAT}) was calculated for each natural reef sampling stratum. If managed-species richness values were unavailable for a particular stratum (e.g., if no historical S-BRUV data were available; 9% of natural reef sampling strata), a minimum managed-species richness value of 1 was assigned to ensure that sampling effort occurred within each stratum. For each stratum, the product (O_{NATALLOC}) of habitat availability and managed species richness was calculated as

$$O_{\text{NATALLOC}} = (H_{\text{NATSTRAT}})^{1/4} \times R_{\text{NATSTRAT}},$$

where extrapolated estimates of habitat availability were fourth-root transformed to downweight several highly expansive habitat strata and ensure equal contribution of habitat availability and managed species richness to final allocation. Estimated annual sampling effort ($N=1000$ S-BRUV deployments, based on estimated annual sampling effort possible given current survey funding) was then allocated proportionally among all natural reef strata based on calculated values of O_{NATALLOC} . This approach to effort optimization results in an allocation of more sampling effort among strata with a larger habitat footprint, with an adjustment to allocate more sampling effort among strata with higher managed-species richness.

Analytical methods: determining sampling allocation for artificial reefs

An optimal sampling allocation scheme was developed independently for artificial reef habitats following similar protocols to those described above for natural reefs, with two exceptions. First, due to the assumption that the

artificial reef sampling universe was fully described, there was no need to produce extrapolated estimates of total habitat availability for artificial reefs. Second, because only a subset of known artificial reefs have been mapped through prior survey efforts, we could not use the area of artificial reef polygons to calculate estimates of habitat availability. Instead, locations of all known artificial reefs were intersected with 0.18- \times 0.18-km primary sampling units (the scale of the sampling frame of the new survey which was generated by dividing each original 0.54- \times 0.18-km sampling unit into three identical grids). These intersections were conducted with replacement, meaning that each primary sampling unit could fall under multiple habitat strata (including natural reef habitats) should more than one habitat type be present. The area of all sampling units was then summed to estimate total artificial reef habitat availability for each spatial stratum (H_{ARTSTRAT}). Average managed-species richness (R_{ARTSTRAT}) was calculated for each artificial reef sampling stratum, and if no historical S-BRUV data were available, a minimum managed-species richness value of 1 was assigned to ensure that sampling effort occurred within each stratum (20% of artificial reef sampling strata). For each stratum, the product (O_{ARTALLOC}) of habitat availability and managed species richness was calculated as

$$O_{\text{ARTALLOC}} = (H_{\text{ARTSTRAT}})^{1/4} \times R_{\text{ARTSTRAT}},$$

where extrapolated estimates of habitat availability were fourth-root transformed to downweight several highly expansive habitat strata and ensure equal contribution of habitat availability and managed species richness to final allocation. Estimated annual sampling effort ($N=200$ S-BRUV deployments, based on estimated annual sampling effort possible given current survey funding) was then allocated proportionally among all artificial reef strata based on calculated values of O_{ARTALLOC} .

Analytical methods: simulations for assessing the performance of the optimal sampling design

We used generalized linear regression models combined with simulation modeling to assess the performance of three sample allocation scenarios in estimating the mean relative abundance (i.e., the expected MaxN value per S-BRUV set) of six fish species (Table 4) separately for natural and artificial reef habitats. These species, all of which are federally assessed and managed, were selected because they vary with respect to spatial distribution, habitat occupancy, and site-specific abundance patterns. Each of the three allocation scenarios reflected a different strategy for

TABLE 4 Distributions (Dist) used for regression modeling and simulations (NB = negative binomial, P = Poisson), observed means (MN), standard deviation (SD), maximum number of observed individuals (MX), and proportion of zero counts (p0) for survey data associated with each combination of species and reef type. An asterisk indicates that the model did not converge and was excluded from simulations.

Species	Artificial reefs					Natural reefs				
	Dist	MN	SD	MX	p0	Dist	MN	SD	MX	p0
Gray Triggerfish	NB	1.28	2.90	25	0.59	NB	0.48	2.90	140	0.78
Red Grouper	P	0.05	0.25	2	0.96	P	0.38	0.77	11	0.72
Red Snapper	NB	4.67	9.78	77	0.40	NB	1.33	4.19	101	0.69
Gag	NB	0.36	1.91	24	0.89	NB	0.08	0.41	6	0.95
Vermilion Snapper	NB*	14.80	46.70	299	0.67	NB	6.70	23.20	299	0.69
Greater Amberjack	NB	1.15	3.19	29	0.67	NB	0.30	2.76	127	0.91

allocating survey effort among spatial strata: an optimal allocation scenario (as developed in the present study), a spatially stratified scenario (similar to FWRI's earlier sampling design), and a simple random scenario (Tables S1 and S2 available in the Supplement separately online).

We first compiled historical (2014–2017) data for each species from camera surveys conducted on natural and artificial reefs and to each data set fitted Bayesian Poisson and negative binomial regression models (each with a natural log link function). The response variable in the regression models was MaxN, and the predictor variables included sample year and a 70-level (natural reefs; Table S1) or 44-level (artificial reefs; Table S2) categorical variable representing sampling strata, which represented a combination of spatial and habitat strata (hereafter, “SamplingStrata”). In all models, we included SamplingStrata and sample year as random effects associated with the model intercept. Under the optimal survey design, no historical data exist for multiple sampling strata; accordingly, analyses included only sampling strata for which data were available. We assessed the fit of all Poisson regression models by checking for evidence overdispersion and zero inflation using the testDispersion and testZeroInflation functions in the R package DHARMA (Hartig 2021), and, if there was evidence of either, we instead fitted a negative binomial regression model and again tested for overdispersion and zero-inflation (Table 4). All models were fitted in R version 4.0.3 using the package rstanarm (Goodrich et al. 2020), and each model run consisted of three parallel Hamiltonian Monte Carlo (HMC) chains set for 10,000 iterations, with the first 5000 iterations discarded as warm-up. For all models, we used weakly informative normal priors for SamplingStrata and sample year and exponential priors for the overdispersion parameter in negative binomial models. The models can be written as follows, where y_{ijk} represents the MaxN count during the i th camera survey collected from SamplingStrata j during year k :

Poisson and negative binomial likelihoods

$$y_{ijk} \sim \text{Poisson}(\mu_{ijk}) \text{ or } y_{ijk} \sim \text{NegativeBinomial}(\mu_{ijk}, \theta).$$

Linear predictor

$$E(y_{ijk}) = \mu_{ijk}.$$

$$\log(\mu_{ijk}) = \beta_0 \text{SamplingStrata}_j + \beta_1 \text{Year}_k.$$

Priors

$$\beta_0 \text{SamplingStrata}_j \sim \text{normal}(\text{mean} = \mu \text{SamplingStrata}, \text{standard deviation} = \sigma \text{SamplingStrata}).$$

$$\beta_1 \text{Year}_k \sim \text{normal}(\text{mean} = \mu \text{Year}, \text{standard deviation} = \sigma \text{Year}).$$

$$\mu \text{SamplingStrata} \sim \text{normal}(\text{mean} = 0, \text{standard deviation} = 2.5).$$

$$\mu \text{Year} \sim \text{normal}(\text{mean} = 0, \text{standard deviation} = 2.5).$$

$$\sigma \text{SamplingStrata} \sim \text{exponential}(\text{scale} = 1).$$

$$\sigma \text{Year} \sim \text{exponential}(\text{scale} = 1).$$

$$\theta \sim \text{exponential}(\text{scale} = 1).$$

We assessed HMC convergence for each parameter by examining trace and density plots, effective sample sizes, and Gelman–Rubin potential scale-reduction factors (Gelman and Rubin 1992), and we assessed goodness-of-fit by conducting posterior-predictive checks based on the posterior-predictive distribution of each stratum using the launch_shinystan function in the rstanarm package. Lastly, for all models we used the testResiduals function in DHARMA to construct QQ plots to assess evidence of

unexplained patterns in scaled residuals. Following model fitting, we calculated the inverse log of the posterior mean associated with each SamplingStrata. We then summarized the posterior means in two ways: (1) by calculating an area-weighted mean relative abundance by multiplying the posterior means by the percentage area occupied by each stratum and summing the resulting values and (2) by calculating an unweighted mean relative abundance by averaging the posterior means across all 70 (natural reefs) and 44 (artificial reefs) strata. Although area weighting is generally the preferred approach for generating representative indices of relative abundance (Maunder et al. 2020; Thompson et al. 2022), we included unweighted analyses to quantify potential biases should analyses not appropriately account for differences in area sampled among resultant strata. For subsequent simulations (described below), we interpreted these posterior means to be the true mean weighted and unweighted relative abundances for each stratum, averaged across years.

Using the fitted model and underlying distributional assumptions, we simulated new camera-survey data for each of the 70 (natural reefs) and 44 (artificial reefs) sampling strata by drawing random counts from stratum-specific posterior-predictive Poisson or negative binomial distributions. For each set of simulated data, we fixed the total number of samples to 1000 for natural reefs and 200 for artificial reefs, and the number of samples assigned to each stratum varied depending on the allocation scenario being used (Tables S1 and S2). Following data simulation, a Poisson or negative binomial model (depending on the species; Table 4) with the HMC settings described above was fitted to the new data, including SamplingStrata as a random effect associated with the model intercept and inverse-log-transforming the estimated stratum-specific posterior means. We again calculated unweighted and weighted mean relative abundance as described above.

Next, we calculated bias for the estimated unweighted and weighted mean MaxN for each stratum as the difference between the estimated and true mean unweighted and weighted mean relative abundances. This process was repeated 1000 times, resulting in 1000 unweighted and weighted mean relative abundance bias measures for each combination of species, reef type, and allocation scenario. Finally, we summarized the 1000 bias measures for each combination of species, reef type, and allocation scenario by calculating relative median bias as

$$\text{RBIAS} = \frac{\text{med}(\mu_{\text{Estimated}_i} - \mu_{\text{True}})}{\mu_{\text{True}}},$$

and relative median absolute deviation as

$$\text{RMAD} = \frac{\text{med}(|\mu_{\text{Estimated}_i} - \mu_{\text{True}}|)}{\mu_{\text{True}}},$$

where “med” denotes median, i denotes each of 1000 simulation replicates, RBIAS is the relative median bias across all 1000 simulation replicates, RMAD is the relative median absolute deviation across all 1000 simulation replicates, $\mu_{\text{Estimated}_i}$ is the estimated unweighted or weighted mean relative abundance for simulation replicate i , and μ_{True} is the true unweighted or weighted mean relative abundance. We summarized relative bias and imprecision using the median of bias measures instead of the mean because the former was deemed the better measure of central tendency because it was less sensitive to the skewed nature of the sampling distributions associated $\mu_{\text{Estimated}}$ for all species, as well as outliers owing to rare, unusually high or low, yet theoretically plausible, counts in a small proportion simulated data sets. For these simulations, we considered RBIAS of <15% and RMAD of <30% to be acceptable levels of bias and imprecision. These represent levels of bias and imprecision we were comfortable with, so these values may not be appropriate for all studies. However, the chosen value for RMAD corresponds to the 30% coefficient of variation threshold often used when evaluating indices for inclusion in a stock assessment, and the level of bias considered should not negatively impact estimates of relative abundance as long as bias is consistent through time.

RESULTS

Results of CART analyses indicated that, regardless of minimum group size, spatial breaks in reef fish assemblage structure were evident at ~83°W (isolating shallow assemblages off southwestern Florida) and at ~50 m (Figure 2). The CART analyses for both 10% and 20% minimum group sizes also indicated that reef fish assemblages in the Florida Panhandle were different from those on the West Florida Shelf (breaks at 84.9°W and 84.5°W, respectively), while results from both 10% and 15% minimum group sizes identified significant latitudinal breaks near the middle of the Florida peninsula. Based on these results, we developed a generalized 3 × 3 spatial stratification scheme in which the eastern Gulf of Mexico was divided into three regional strata (north-central Gulf, Big Bend, and south Florida) and three depth strata (nearshore, 10–25 m; offshore, >25–50 m; and deep, >50–180 m; Figure 3).

For natural reefs, results from CART analyses indicated that both relative relief and areal extent of individual reef features were important determinants of reef fish assemblage structure (Figure 4). Regardless of minimum group size, reef fish assemblages associated with habitats with a relief rank of ≤3 (flat hard-bottom, pavement, and mixed hard-bottom habitats; Table 2) differed from all other habitats, whereas results from analyses with a 10% minimum group size also identified significant differences in reef fish

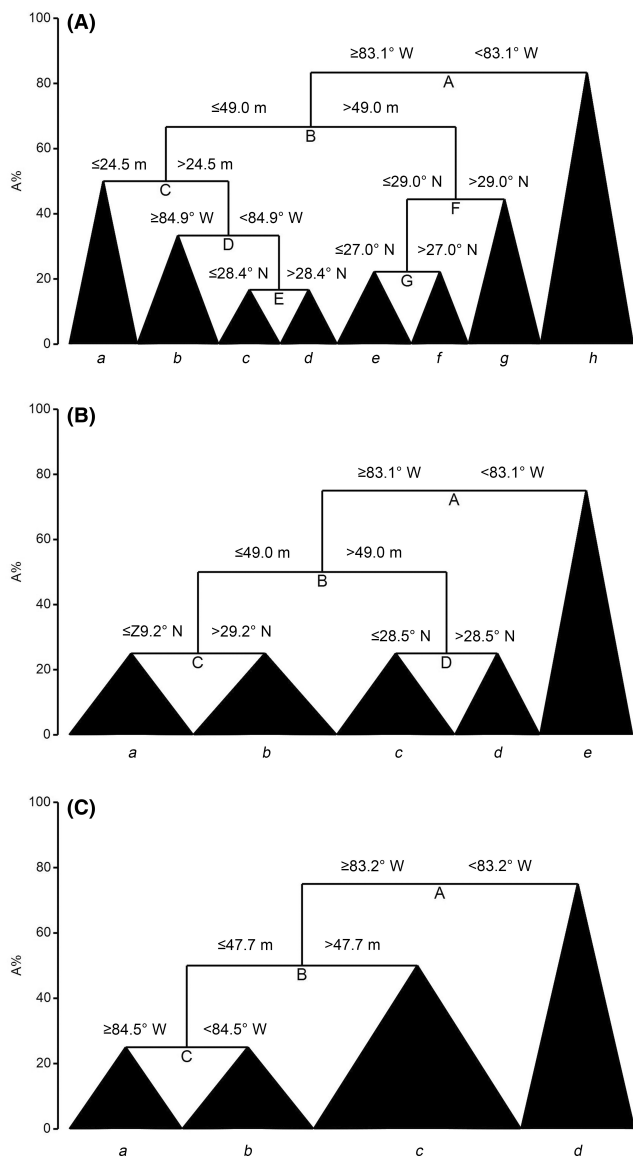


FIGURE 2 Results of classification and regression tree analyses run to identify possible predictor values for incorporation as a spatial stratification scheme for reef fish surveys in the eastern Gulf of Mexico. Analyses were conducted at minimum group sizes of (A) 10%, (B) 15%, and (C) 20% of available data. Letters on the x-axis represent final groupings, and the y-axis (A%) represents arbitrary equal spacing of the split levels to improve visualization.

assemblages on habitats with a relief rank >6 . Areal extent also was an important determinant of reef fish assemblage structure, with breaks that ranged from 60 to 12,900 m². Results from CART analyses were then generalized into a 3 × 3 stratification scheme of natural reef habitats that consisted of three relief classes (low, moderate, high; see Table 2 for all habitat types that comprised each relief class) and three size classes (small scale, <100 m²; medium scale, 100–1000 m²; large scale, >1000 m²; Figure 5), ensuring that there was an ample number of potential sampling units within each resulting stratum.

Relative relief and areal extent of individual reef features were also important determinants of reef fish assemblage structure for artificial reef habitats, although breaks identified through CART analyses were sensitive to minimum group size (Figure 6). Nevertheless, reef fish assemblages associated with low-relief artificial habitats (tires, rock piles, pipelines, and, to some extent, construction materials) were generally found to be different from those associated with habitats of higher relief. In terms of areal extent, identified breaks ranged from 21 to 1350 m². Results from CART analyses were then generalized into a 3 × 3 stratification scheme of artificial reef habitats that consisted of three relief classes (low, moderate, high; see Table 2 for all habitat types that comprised each relief class) and three size classes (small scale, <25 m²; medium scale, 25–100 m²; large scale, >100 m²; Figure 7), ensuring that there was an ample number of potential sampling units within each resulting stratum.

Extrapolated estimates of natural reef habitat indicated that low-relief, large-scale habitats and, to a lesser degree, high-relief, large-scale habitats comprised the vast majority of available natural reef habitat in all spatial strata, with especially high estimates of habitat availability in the Big Bend nearshore stratum (Figure 8). Accordingly, estimates of habitat availability were fourth-root transformed before calculations for optimal effort allocation were made to ensure a more representative distribution of sampling effort among spatial and habitat strata. Average managed-species richness also varied among sampling strata, with generally higher richness on both high-relief and low-relief habitats that were either medium scale or large scale. Proposed annual natural reef sampling effort ($N=1000$ sites annually) was then allocated optimally among strata based on the proportional product of fourth-root-transformed habitat availability and average managed-species richness, with adjustments to ensure that a minimum of two sampling sites occurred within each sampling stratum annually. This resulted in a sampling design in which effort within each spatial stratum ranged from 77 sites (south Florida deep) to 159 sites (Big Bend offshore), and the majority of effort fell within both low-relief and high-relief habitats of large scale (Figure 8); three sampling strata (out of 81) were excluded because some spatial strata lacked identified natural reef habitat strata.

Estimates of artificial reef availability indicated that most artificial reef habitats in the eastern Gulf occurred in the north-central Gulf sampling zone and, to a lesser extent, in the Big Bend nearshore sampling zone; much of these habitats were small- and medium-scale habitats of medium or high relief (Figure 9). To ensure a more uniform distribution of sampling effort among sampling strata, stratum-specific estimates of habitat availability

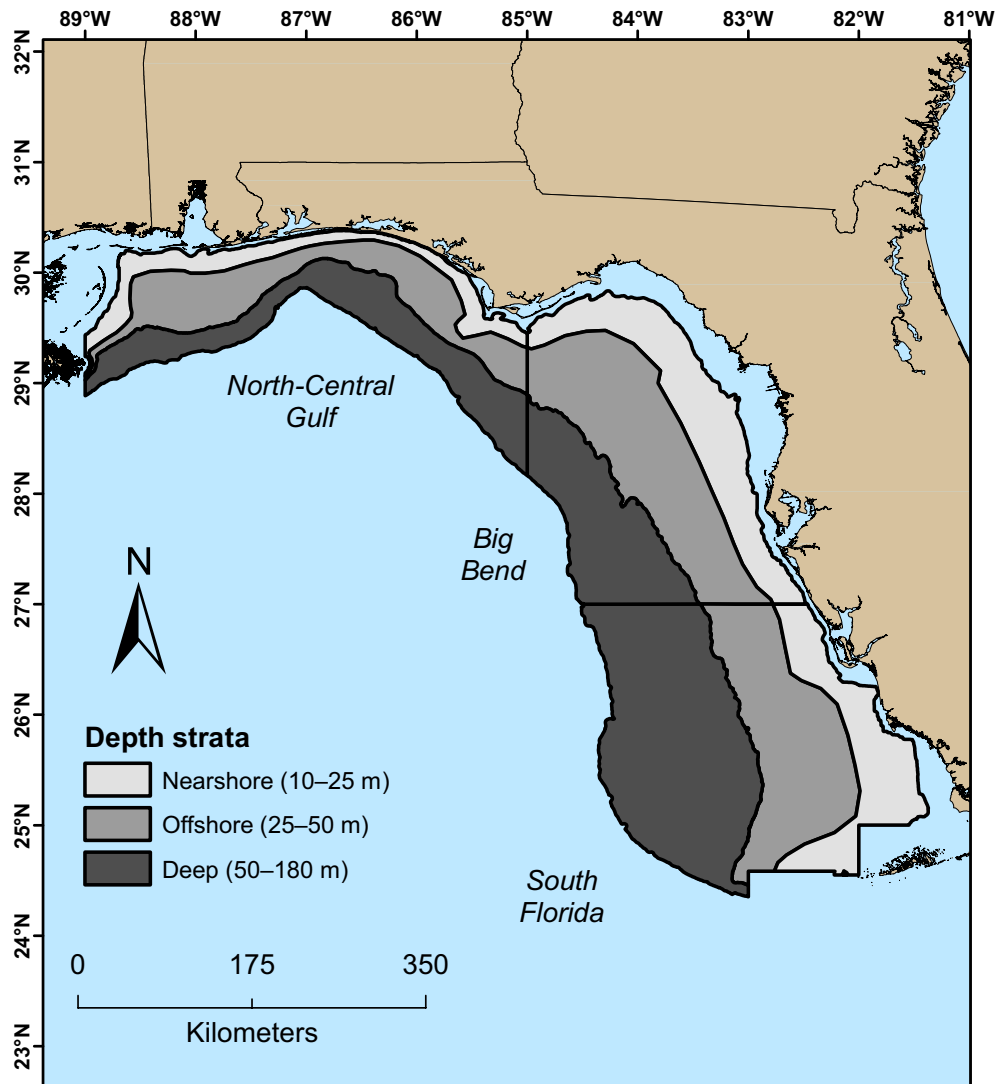


FIGURE 3 Final spatial stratification scheme developed based on interpretation of results of classification and regression tree analyses run to identify values of spatial predictor variables that differentiated reef fish assemblages in the eastern Gulf of Mexico.

were fourth-root transformed before calculations for optimal effort allocation. Average managed-species richness varied among artificial reef sampling strata, with generally higher richness on medium- and large-scale habitats of medium or high relief. Annual artificial reef sampling effort ($N=200$ sites annually) was then allocated optimally among strata based on the proportional product of fourth-root-transformed habitat availability and average managed-species richness, with adjustments to ensure that each stratum received at least two sampling sites annually. This resulted in a sampling design in which effort within each spatial stratum ranged from 10 sites (south Florida deep) to 51 sites (north-central Gulf offshore), most of the effort occurring in the north-central Gulf and Big Bend sampling zones, especially on medium- and high-relief habitats (Figure 9); 22 sampling strata (out of 66) were excluded because some spatial strata lacked identified artificial reef habitat strata.

Relative abundance for most species exhibited evidence of overdispersion for both natural and artificial reef habitats, so a negative binomial regression was used for initial model-fitting and subsequent simulations (Table 4). The sole exception was Red Grouper, for which a Poisson regression was deemed an appropriate fit to both natural and artificial reef data (Table 4). For most species and reef types, Gelman–Rubin statistics, trace plots, density plots, effective sample sizes, and posterior predictive checks indicated good mixing of HMC chains, no evidence of convergence failure, and good predictive performance. Additionally, QQ plots of scaled residuals did not reveal any unexplained patterns, again indicating that most models provided an adequate fit to the observed data. The sole exception was the negative binomial model for Vermilion Snapper in artificial reefs, which exhibited poor mixing of HMC chains and evidence of nonconvergence, even after 100,000 iterations

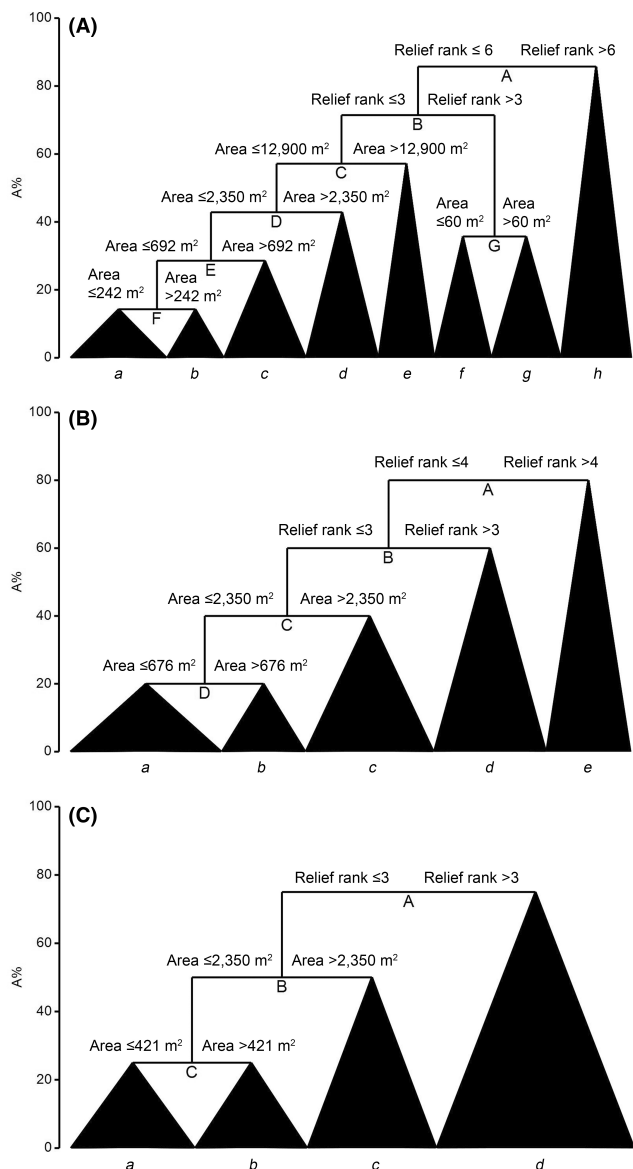


FIGURE 4 Results of classification and regression tree analyses run to identify possible predictor values for incorporation as a habitat stratification scheme for reef fish surveys of natural reef habitats in the eastern Gulf of Mexico. Analyses were conducted with minimum group sizes of (A) 10%, (B) 15%, and (C) 20% of available data. Letters on the x-axis represent final groupings, and the y-axis (A%) represents arbitrary equal spacing of the split levels to improve visualization.

with a 50,000-iteration warm-up; hence, this species was omitted from the artificial reef analysis.

The optimal survey design performed well for most species on natural reefs, with weighted RBIAS <|10%| and weighted RMAD <30% for most species (Figure 10). The one notable exception was Greater Amberjack, which exhibited the highest weighted RBIAS (+55%) and weighted RMAD (58%) of all species examined. Across species, RBIAS was most consistent and generally lowest for the simple random allocation scenario (−5% to 7%),

but, for all three scenarios, weighted RBIAS was generally similar and within 10% of the true weighted mean for Gray Triggerfish, Red Snapper, Gag, Red Grouper, and Vermilion Snapper (Figure S1 available in the Supplement separately online). Weighted RMAD in natural reefs was less than 40% for most species and, on average across species, lowest for the simple-random-allocation scenario (Figure S1). Across species, weighted RMAD was most consistent for the simple-random-allocation scenario (16% to 39%) and most highly variable for the spatially stratified (10% to 38%) and optimal allocation scenarios (15% to 58%). Interestingly, Greater Amberjack exhibited a marked increase in both weighted RBIAS and weighted RMAD with increasing stratification (i.e., from simple random to spatially stratified to optimal).

All three unweighted survey-allocation scenarios also performed reasonably well for all species in natural reefs, with unweighted RBIAS ranging from −35% to +15% (Figure S2). Among allocation scenarios, RBIAS exhibited the greatest amount of among-species variability under the simple random (−35% to +15%) and spatially stratified (−20% to +10%) allocations, whereas RBIAS was most consistent (and always positive) across species under the optimal allocation scenario (+2% to +12%). Overall, RBIAS became progressively more positive and generally less biased with increased spatial allocation, with the largest differences seen in Vermilion Snapper, Greater Amberjack, Red Snapper, and Gray Triggerfish moving from simple random to optimal allocation (Figure S2). Similarly, all three allocation scenarios exhibited similar unweighted RMAD in natural reefs, ranging from 15% to 45% across species (Figure S2). On average across species, however, the simple random allocation resulted in the highest RMAD, whereas the optimal and spatially stratified scenarios exhibited similar levels of RMAD. Most species had similar RMAD among allocation scenarios, with Vermilion Snapper showing the greatest change in RMAD moving from simple random (35%) to spatially stratified (22%) to optimal stratification (15%).

The optimal survey design did not perform as well on artificial reef habitats (Figure 10), especially for Gag and Red Grouper, which had the lowest relative abundance and highest proportion of zero observations on artificial reefs (Table 4). In contrast, Gray Triggerfish, Red Snapper, and Greater Amberjack all had weighted RBIAS <|10%|, and Gray Triggerfish and Greater Amberjack had weighted RMAD <20% under the optimal design (Figure 10). Among all scenarios and species, weighted RBIAS in artificial reefs ranged from −17% to +35% (Figure S3). Across species, weighted RBIAS was most consistent for the simple random allocation (+2% to +11%) and most variable for the spatially stratified (−17% to +37%) and optimal (−3% to +34%) allocation scenarios. With the exception

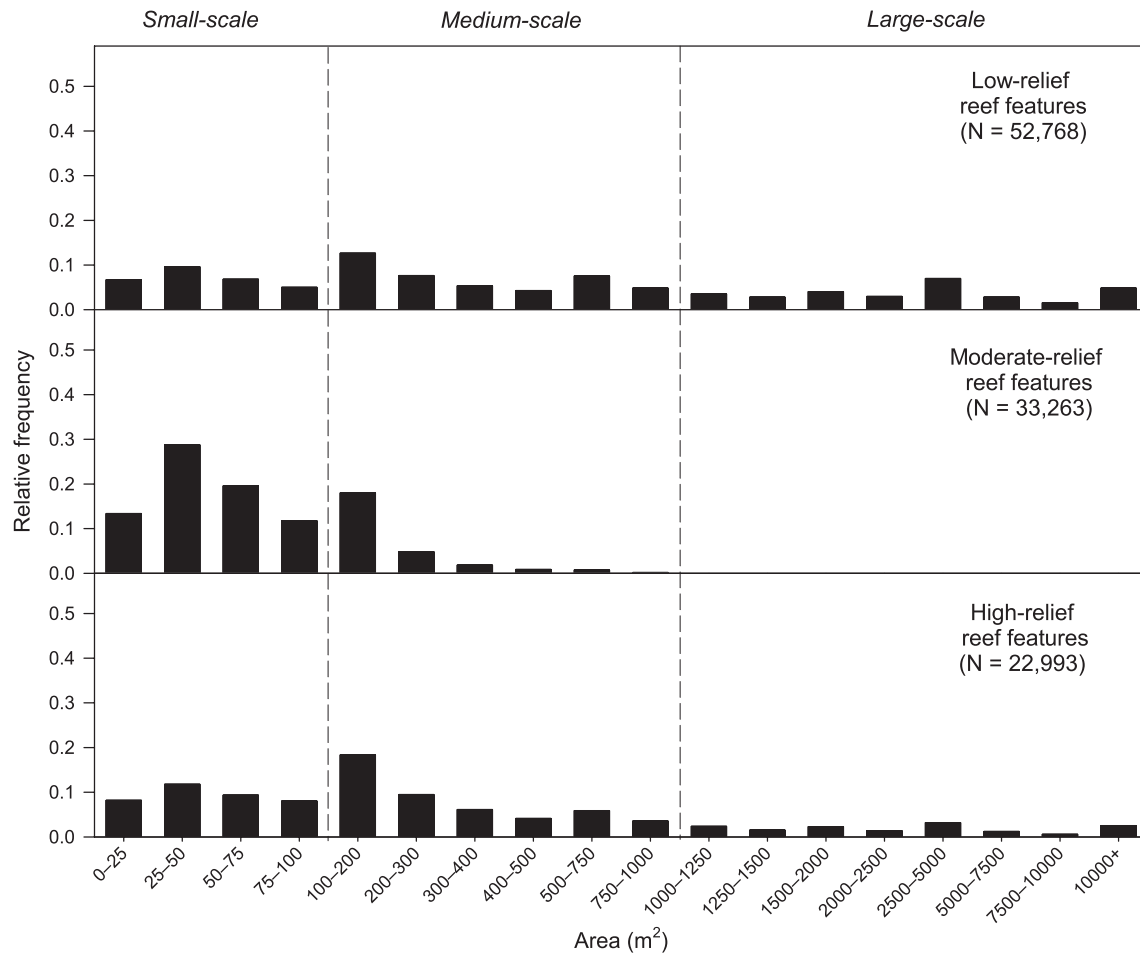


FIGURE 5 Frequency distribution of individual natural reef features identified through the classification of side-scan sonar habitat-mapping data collected by the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute. Relief (low, moderate, high) and scale categories (small, medium, large) correspond to the final natural reef habitat stratification scheme.

of Gag and Red Grouper, however, weighted RBIAS was generally similar across allocation scenarios and typically within 20% of the true weighted mean; in particular, weighted RBIAS for Greater Amberjack was consistently within 5% of the true weighted mean across all three allocation scenarios. Among allocation scenarios and species, weighted RMAD in artificial reefs ranged from 20% to 47%. Across species, weighted RMAD was lowest for Greater Amberjack and Gray Triggerfish ($\leq 25\%$ under all three scenarios) and highest for Red Snapper ($\geq 40\%$), Gag ($\geq 33\%$), and Red Grouper ($\geq 40\%$) under all three scenarios (Figure 10; Figure S3).

Among allocation scenarios, unweighted RBIAS in artificial reefs was positive for most species and ranged from -18% to $+40\%$ (Figure S4). Across species, unweighted RBIAS was most consistent for the optimal ($+3\%$ to $+30\%$) and spatially stratified (-2% to $+20\%$) scenarios and was most variable for the simple random scenario (-18% to $+40\%$). Across species and allocation scenarios, unweighted RBIAS was consistently lowest for Greater Amberjack (less than $|5\%|$ under all three scenarios) and

highest for Red Snapper under the simple random allocation scenario ($+40\%$). Among allocation scenarios and species, unweighted RMAD in artificial reefs ranged from 20% to 53%. Across species, unweighted RMAD was lowest for Greater Amberjack (20% under all three scenarios) and consistently highest for Red Snapper ($\geq 40\%$), Gag ($\geq 30\%$), and Red Grouper ($\geq 35\%$) under all three scenarios (Figure S4).

DISCUSSION

In this study, data from earlier video- and habitat-mapping surveys were integrated to develop a novel, unified design for reef fish surveys in the Gulf of Mexico. We approached survey design from a multispecies perspective, using multivariate classification and regression trees to aid in the delineation of spatial and habitat strata that were important determinants of overall assemblage structure for managed reef fishes. Allocation of sampling effort for natural and artificial reef habitats, respectively, was optimized based

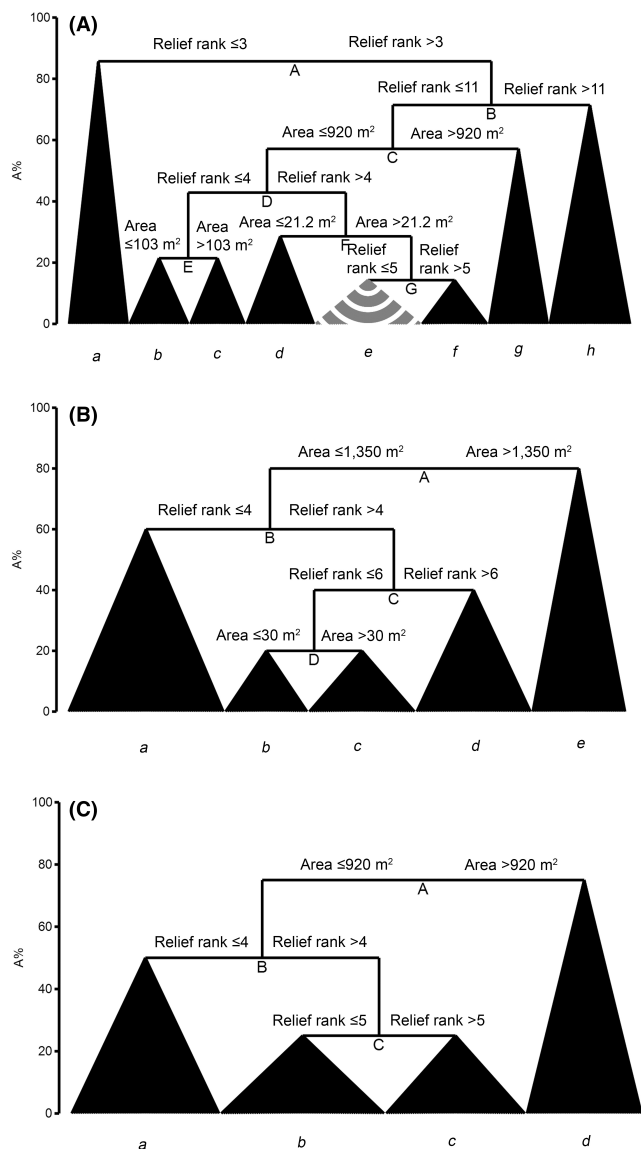


FIGURE 6 Results of classification and regression tree analyses run to identify possible predictor values for incorporation as a habitat stratification scheme for reef fish surveys of artificial reef habitats in the eastern Gulf of Mexico. Analyses were conducted with minimum group sizes of (A) 10%, (B) 15%, and (C) 20% of available data. Note that terminal nodes (G) in analyses with a minimum group size of (a) 10% were not statistically significant.

on a combination of overall habitat availability and strata-specific managed-species richness. The resultant optimal design generally performed as well as or better than other designs explored (simple random, spatially stratified) for most species tested, with the exception of Greater Amberjack on natural reefs. Notably, the optimal design performed exceptionally well for Red Snapper, with relative median bias <5%. Overall, the transition to a survey stratified by space and habitat should not only improve our ability to characterize the status and trends of managed reef fishes, but with sufficient sampling intensity

(Bryan et al. 2016), also provide the flexibility to quantify population-level responses to various natural and anthropogenic stressors at various spatial and temporal scales. This effort will also allow three previously independent surveys to be conducted under a unified and optimized design, increasing the precision of analyses and ultimately providing improved management advice regarding managed reef fishes in the Gulf of Mexico.

Although multiple potential approaches to statistical survey design have been taken, a stratified random sampling design as developed in the current study has two advantages. First, stratification generally improves the precision of parameter estimates by subdividing a heterogeneous population into relatively homogeneous strata (Cochran 1977; Kimura and Somerton 2006). Second, stratification assures that sampling effort is assigned to all strata of interest. Stratification of fishery surveys can be based on a variety of biological or physical processes, including depth, geographical boundaries, time of day, habitat, or even acoustically derived measures of biomass (Switzer et al. 2009; Smith et al. 2011; Hanselman et al. 2012; Richards et al. 2016). Based on results from this study, we chose to proceed with a stratification scheme that combined space and habitat, both of which are important predictors of the distribution of fishes associated with hard-bottom habitats (Pittman and Brown 2011) and have previously been used as the basis of stratification schemes for surveys of reef-associated fishes (Smith et al. 2011; Richards et al. 2016).

For spatial distribution, the resultant stratification scheme included depth strata as well as broad regional designations. Regional stratum boundaries, which divided the eastern Gulf of Mexico into three regions, broadly corresponded to previously identified ichthyofaunal breaks (Saul et al. 2013; Matheson et al. 2017) as well as spatial breaks in underlying habitat quality and quantity (Keenan et al. 2022). Three distinct depth strata were also identified. Depth is a key driver of biological and ecological processes critical to reef fish populations, and assemblage composition as well as population-level attributes such as abundance and size composition often vary with depth (Chester et al. 1984; Misa et al. 2013; Saul et al. 2013; Boland et al. 2020). In addition, complexes of recreationally and commercially important reef fishes vary markedly with depth (Farmer et al. 2016). Of depth strata delineated in this study, the nearshore stratum isolated regions in which reef fish assemblages likely are somewhat connected to estuarine habitats (McEachran and Fechhelm 1998), especially those known to use estuarine nursery grounds, such as Gag and Gray Snapper (Flaherty-Walia et al. 2015; Switzer et al. 2015; Schrandt et al. 2021). The nearshore stratum also includes many of the habitats targeted by the recreational fishery and so is subject to increased fishing

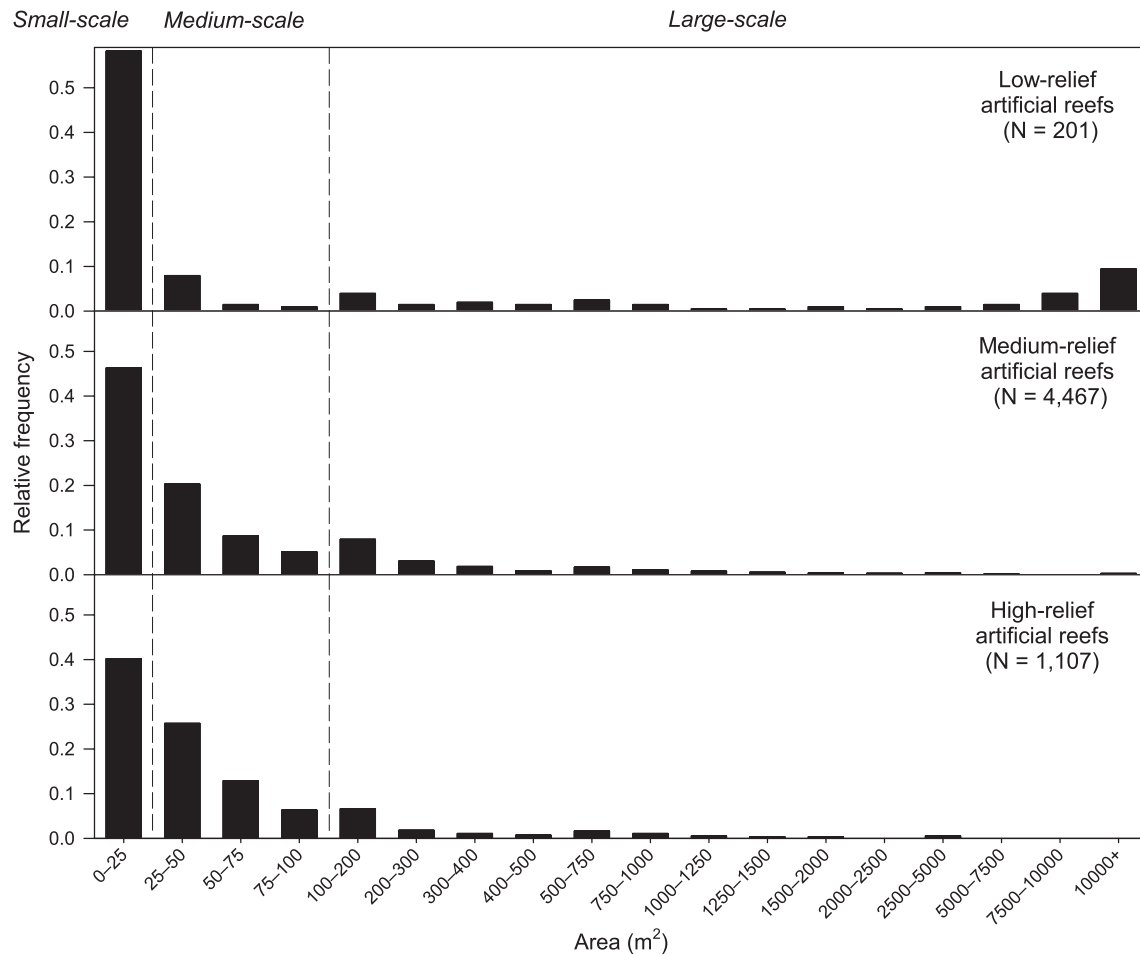


FIGURE 7 Frequency distribution of individual artificial reef features identified through the classification of side-scan sonar habitat-mapping data collected by Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute. Relief categories (low, moderate, and high) and scale categories (small, medium, and large) correspond to the final artificial reef habitat stratification scheme.

pressure (Garner and Patterson 2015; Cross et al. 2018). In contrast, much of the commercial vertical-line fishery operates in the offshore stratum, whereas the commercial longline fishery operates primarily in the deep stratum (Scott-Denton et al. 2011). The deep stratum also includes ecologically important mesophotic reef habitats (Jaap 2015; Locker et al. 2016; Harter et al. 2017), as well as habitats critical to spawning for several economically important reef fishes (Coleman et al. 1996; Farmer et al. 2017; Lowerre-Barbieri et al. 2020). Overall, the spatial stratification scheme ensures a broad distribution of annual sampling effort while implicitly accounting for key biological, ecological, and socioeconomic factors that determine populations of managed reef fishes.

Habitat stratification for both natural and artificial reef habitats was developed by integrating measures of relief and scale or size of individual reef features. Vertical relief is one of the most important factors influencing reef populations, and multiple authors have documented notable differences in the abundance, size composition, and diversity of reef fishes among natural and artificial

reef habitats of varying relief (Parker et al. 1994; Sluka et al. 2001; Ault et al. 2006; Misa et al. 2013; Campbell et al. 2019; Ilich et al. 2021). Accordingly, measures of vertical relief have often been incorporated into the statistical design of reef fish surveys (Smith et al. 2011; Richards et al. 2016). Vertical relief might also reduce detection probability for many species, especially in visual surveys (Green et al. 2013; Bacheler et al. 2014). Because habitat-mapping data were collected with side-scan sonar, a quantitative determination of reef-specific relief was impractical. Nevertheless, relative measures of vertical relief were implicit in our habitat classification, and earlier studies verified the utility of acoustically derived habitat classes in structuring reef fish assemblages in the eastern Gulf (Keenan et al. 2018; Switzer et al. 2020). In contrast, the influence that size of individual reef features may have on reef fish assemblages is generally less well understood, especially for hard-bottom reefs, although measures of habitat extent (e.g., patchy versus continuous reefs) have been incorporated into surveys of coral reefs in the Florida Keys and the U.S. Caribbean (Smith et al. 2011; Bryan

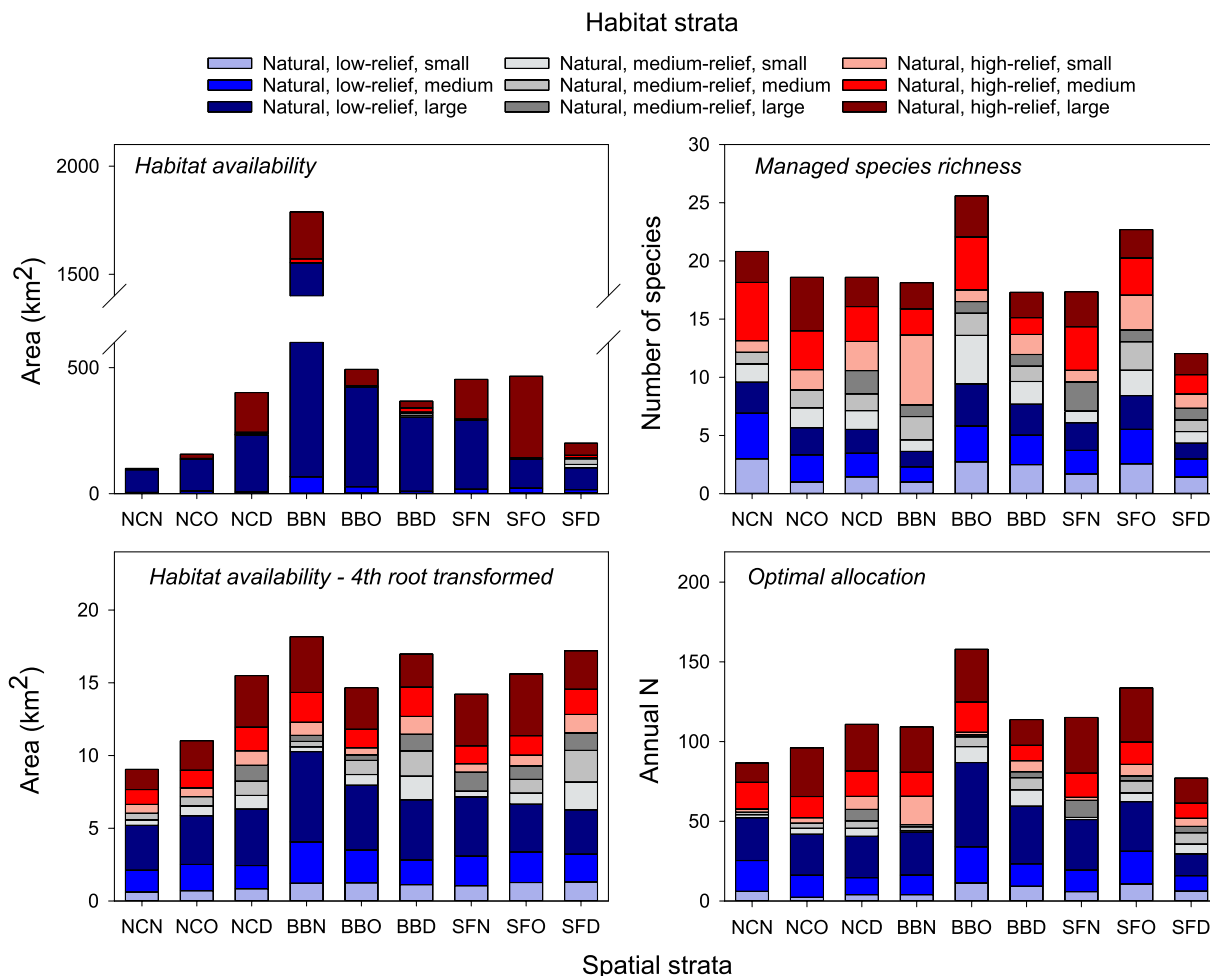


FIGURE 8 Optimal allocation of annual sampling effort ($N=1000$) among sampling strata for natural reef surveys in the eastern Gulf of Mexico. The upper left panel represents estimates of natural reef habitat, and the upper right panel represents average managed-species richness by habitat type for each spatial stratum. Habitat estimates were first fourth-root transformed (lower left panel) so that sampling effort could be more equitably distributed among strata. Annual sampling effort was then allocated optimally (lower right panel) based on the proportional product of managed-species richness and fourth-root-transformed habitat availability for each sampling stratum. Spatial-stratum labels represent a combination of region (first two characters; NC = north-central Gulf, BB = Big Bend, SF = south Florida) and depth (third character; N = nearshore, O = offshore, D = deep).

et al. 2016). Artificial reef size has been shown to influence abundance, size, and species richness of reef-associated assemblages (Bohnsack et al. 1994; Gregalis et al. 2012; Jaxion-Harm et al. 2018), as well as differences in species richness (Chittaro 2002; Stier et al. 2014) and rates of settlement and mortality (Nanami and Nishihira 2003) between small, isolated, and continuous reef habitats. The incorporation of small-scale reef strata is especially important for the eastern Gulf of Mexico, since these features, often associated with Red Grouper or other ecosystem engineers (Coleman et al. 2010; Ellis et al. 2017), support unique reef fish assemblages (Harter et al. 2017; Ellis 2019; Grasty et al. 2019). Given the nearly four orders of magnitude difference in the size of natural and artificial reef features identified in the eastern Gulf, data provided by this survey design should facilitate an improved

understanding of essential fish habitat at multiple spatial scales (Anderson and Yoklavich 2007) for a variety of economically and ecologically important reef fishes, while enhancing our ability to better integrate habitat science into fisheries management (Thorson et al. 2021).

Our approach to optimizing effort allocation involved allocating proportionally more sampling effort to strata with higher managed-species richness and to strata that covered a larger total extent. Although most surveys use some measure of habitat availability in their allocation schemes, the use of managed-species richness as an optimization criterion is less common. For single-species surveys, optimal allocation often involves allocating effort to strata to minimize the variance of the abundance metric being estimated (Cochran 1977; Kimura and Somerton 2006). This approach can be modified to

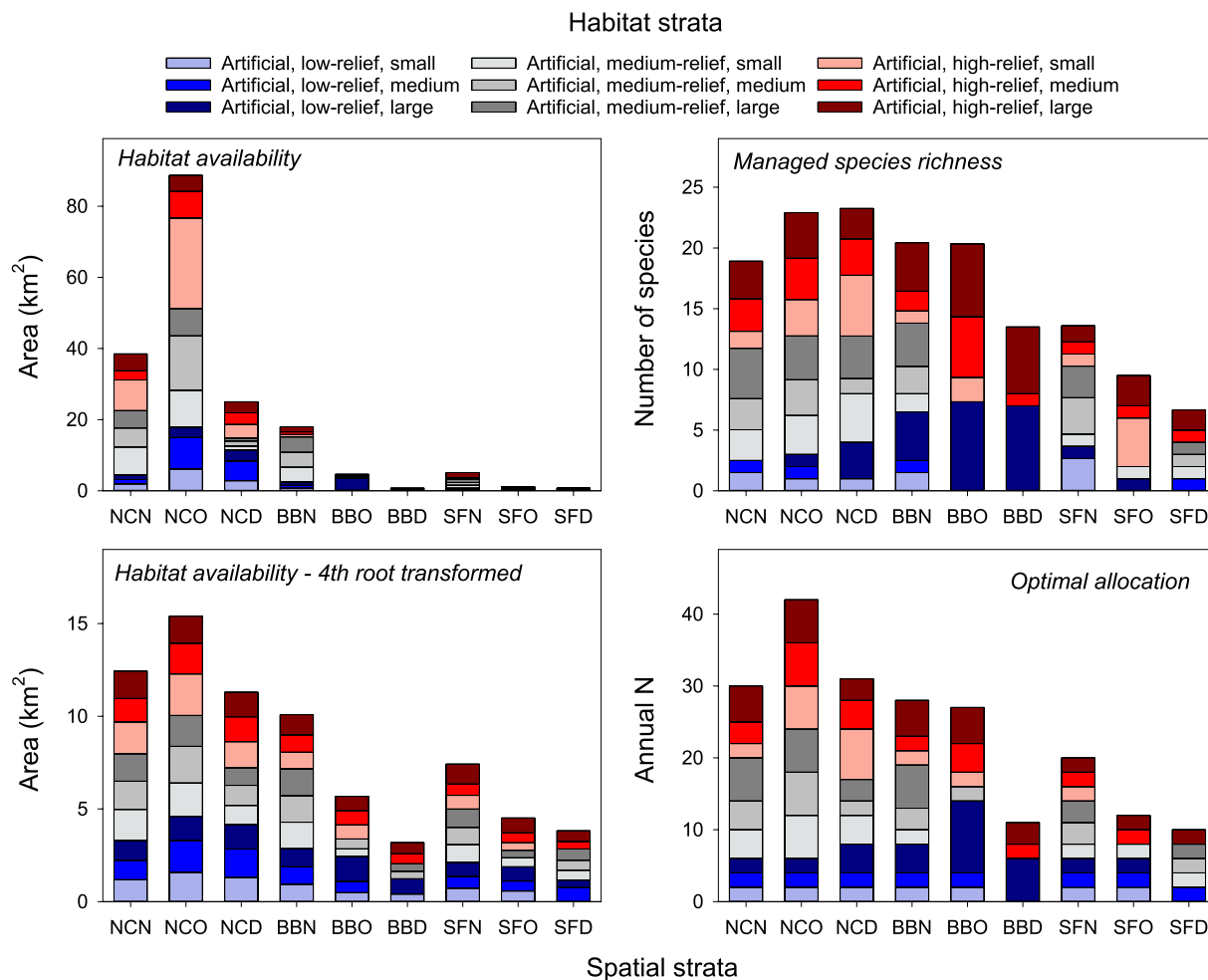


FIGURE 9 Optimal allocation of annual sampling effort ($N=200$) among sampling strata for artificial reef surveys in the eastern Gulf of Mexico. The upper left panel represents estimates of artificial reef habitat, and the upper right panel represents average managed-species richness by habitat type for each spatial stratum. Habitat estimates were first fourth-root transformed (lower left panel) so that sampling effort could be more equitably distributed among strata. Annual sampling effort was then allocated optimally (lower right panel) based on the proportional product of managed-species richness and fourth-root-transformed habitat availability for each sampling stratum. Spatial strata labels represent a combination of region (first two characters; NC = north-central Gulf, BB = Big Bend, SF = south Florida) and depth (third character; N = nearshore, O = offshore, D = deep).

optimize allocation for several parameters simultaneously (for example, abundance estimates of several species), often by independently calculating optimal allocations for each parameter and then calculating overall average allocations. But this approach generally works best when only a few parameters are optimized (Cochran 1977), although novel applications of spatiotemporal models to optimize both spatial stratification and effort allocation for multiple species simultaneously show tremendous promise (Oyafuso et al. 2021). To date, video survey data have been used in the assessment of 11 reef fishes in the Gulf of Mexico, and it is likely that many others could be assessed under enhanced survey efforts and as requested by the Gulf of Mexico Fisheries Management Council. For many of these species, available data were insufficient to conduct single-species optimization analyses. Instead,

allocation of sampling effort was optimized using species richness, which is considered an effective proxy for variance for the purposes of effort allocation (Steel and Torrie 1960; Parker et al. 1994).

The optimal survey design developed in this study generally performed as well as or better than the simple random or spatially stratified designs when considering unweighted means, with estimated biases $<|10\%$ and estimated imprecision $<30\%$ for most species examined. Measures of bias and imprecision have increasingly been recognized as essential criteria in assessing the performance of sampling designs (Seavy and Reynolds 2007). Survey stratification approaches as developed in the present study generally result in reduced bias and imprecision of estimates of key population parameters, although the improvements may depend on the choice of an

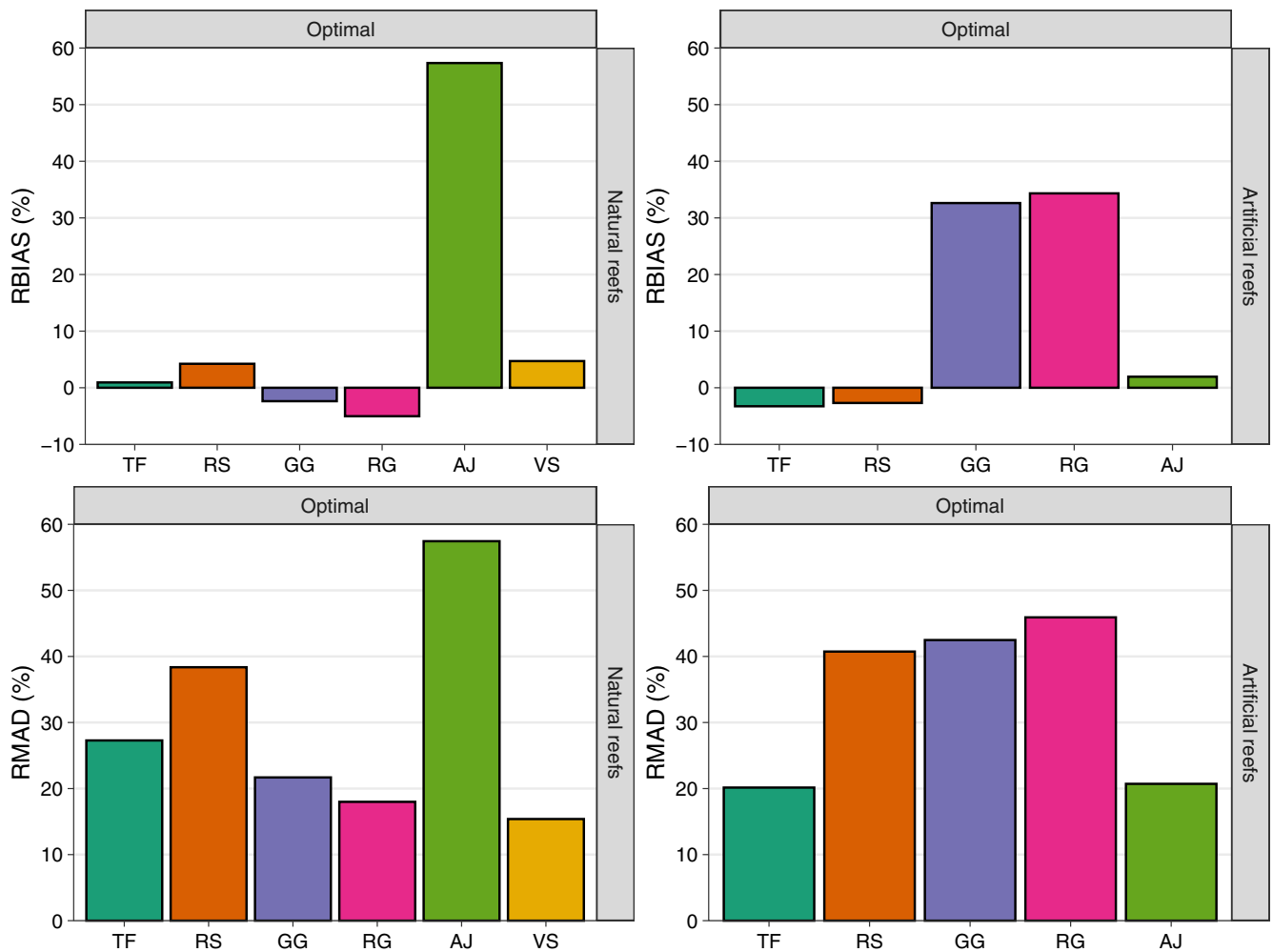


FIGURE 10 Median relative bias (RBIAS) and relative median absolute deviation (RMAD) associated with species-specific, systemwide weighted mean relative abundance estimates in natural reefs (left panels) and artificial reefs (right panels) for the optimum allocation scenario based on 1000 simulation replicates across species (AJ = Greater Amberjack, GG = Gag, RG = Red Grouper, RS = Red Snapper, TF = Gray Triggerfish, VS = Vermilion Snapper).

appropriate stratification scheme (Wang et al. 2018). On natural reef habitats, the optimal design performed well for all species simulated except Greater Amberjack; the high values of weighted estimated bias and RMAD for that species largely result from exceptionally high variability in one or two strata that, because they cover such a large part of the study area, were especially influential in weighted analyses. For artificial reef habitats, performance of the optimal design was poorest for species with relatively high proportion of zero counts (e.g., Red Grouper, Gag). Further reductions to the bias and imprecision of key population parameters for such species could likely be improved through the implementation of a multiframe sampling design (Haines and Pollock 1998). As expected, the performance of all three survey designs improved greatly when weighting factors were applied that adjusted for the total area of habitat that occurred within each sampling strata (Maunder et al. 2020). It is important to note that the interpretation of simulation results relies heavily on

the assumption that each analysis was fit with the correct species-specific distribution. Our simulations were limited to some extent by the quantity of available data; for some strata, only a handful of empirical observations were available from which to simulate new survey data; other strata were excluded due to lack of data. Survey performance will be reevaluated when more robust data become available (~5 years). Nevertheless, there were no indications of large-scale systematic bias in the optimal survey design that would preclude its implementation. Thus, in 2020 the design was implemented as the Gulf Fishery Independent Survey of Habitat and Ecosystem Resources (G-FISHER).

Although not presented here, results from this study were used to implement a similar change in survey design for the western Gulf of Mexico. But key limitations in data availability have complicated those efforts. Unlike the eastern Gulf of Mexico, survey efforts in the western Gulf have been restricted primarily to deep reefs near

the shelf break (Campbell et al. 2019), so data needed to delineate spatial strata, especially in relation to depth, is limited. Data needed to delineate artificial reef habitat strata are also lacking because long-term surveys in the western Gulf have exclusively targeted natural reef habitats, although some insights could be gleaned from focused studies (Bolser et al. 2020, 2021). Finally, available habitat mapping data are restricted largely to multibeam sonar data collected in association with well-known reef features (i.e., not collected under a randomized design) and so cannot be used to provide the unbiased estimates of habitat quantity and composition necessary for allocating sampling effort, particularly for natural reef habitats. Nevertheless, we have developed and implemented an initial design for the western Gulf that largely mimics that developed in the eastern Gulf. We anticipate iteratively revising the design for the western Gulf as new information is collected over the coming years. Key to these efforts are randomized habitat mapping surveys using a combination of side-scan (in shallow waters) and multibeam sonar (in deeper waters) to provide unbiased estimates of habitat availability and possible sampling sites, particularly on the shelf, where recent efforts have identified a substantial number of undocumented reef anomalies (Stunz et al. 2021).

Modifying long-term monitoring programs should not be undertaken lightly, especially given the time needed to effectively detect population-level trends for most species (White 2019). But with careful consideration, long-term surveys can be modified to improve the quality of data provided, while maintaining connectivity to data collected in earlier surveys (Smith et al. 2011; Schrandt et al. 2021). In this study, several factors motivated efforts to develop and implement a new sampling design. First, combining survey efforts from three earlier surveys into a unified sampling design will greatly simplify approaches to generating time series of relative abundance and size composition, along with associated measures of precision, as required for conducting single-species stock assessments (Thompson et al. 2022). Second, interest has been increasing in fishery-independent data from artificial reef habitats because of the heavy recreational fishing pressure associated with these habitats (Garner and Patterson 2015; Cross et al. 2018), as well as uncertainty in the contribution of these habitats to overall stock productivity (Glenn et al. 2017; Karnauskas et al. 2017). Third, managers clearly need additional data for several managed reef fishes (e.g., Black Grouper, Mutton Snapper, Yellowtail Snapper) from depths greater than those at which the ongoing diver-based visual census survey is conducted (Smith et al. 2011). Fourth, enhanced spatial coverage of survey data is essential to quantifying any climate-induced shifts in the distribution of reef fishes (Morley et al. 2018) and characterizing ecosystem-level impacts of

broad-scale environmental perturbations that may influence stock assessment parameterization, projection of future stock productivity, and final management recommendations (Harford et al. 2018; Ward et al. 2018). Finally, and perhaps most important, our research team received long-term funding to significantly expand upon annual survey efforts, which greatly facilitated our ability to address multiple survey objectives. In summary, these efforts should ultimately improve our ability to characterize the status and trends of managed reef fishes, while providing robust data needed in addressing a variety of emerging ecologically relevant questions at multiple spatial scales.

ACKNOWLEDGMENTS

We gratefully acknowledge present and former staff of Fisheries Independent Monitoring group at the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute and the reef fish survey teams for the NMFS Pascagoula and NMFS Panama City laboratories for their dedication to field sampling, data collection, and analyses of video and habitat mapping data. We also appreciate the insightful comments of S. Allen, R. Ellis, B. Crowder, the associate editor, and three anonymous reviewers who greatly improved this manuscript. Data collection and analyses for this project were supported in part by funding from the National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Monitoring and Assessment Program (grant numbers NA11NMF4350047 and NA16NMF4350165), the U.S. Fish and Wildlife Service, Federal Aid in Sportfish Restoration (grant numbers F14AF00328, F15AF01222, F16AF00898, and F17AF00932), and the National Fish and Wildlife Foundation Gulf Environmental Benefit Fund (grant numbers FL 40624, FL 45766, FL 50347, FL 54269, and FL 58101) and from the sale of state of Florida saltwater recreational fishing licenses. This paper is also a product of research funded by National Oceanic and Atmospheric Administration's RESTORE Science Program under award NA19NOS4510192 to FWRI. The statements, findings, views, conclusions, and recommendations contained in this document are those of the authors and do not necessarily reflect the views of the U.S. Department of the Interior, the U.S. Department of Commerce, or the National Fish and Wildlife Foundation and should not be interpreted as representing the opinions or policies of the U.S. Government or the National Fish and Wildlife Foundation. Mention of trade names or commercial products does not constitute their endorsement by the U.S. Government or the National Fish and Wildlife Foundation.

CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

All data are available upon request to the corresponding author.

ETHICS STATEMENT

No specific permission for sampling was required, as sampling was conducted using nonextractive video camera systems.

REFERENCES

- Anderson, T. A., & Yoklavich, M. M. (2007). Multiscale habitat associations of deepwater demersal fishes off central California. *U.S. National Marine Fisheries Service Fishery Bulletin*, 105(2), 168–179.
- Ault, J. S., Smith, S. G., Bohnsack, J. A., Luo, J., Harper, D. E., & McClellan, D. B. (2006). Building sustainable fisheries in Florida's coral reef ecosystem: Positive signs in the Dry Tortugas. *Bulletin of Marine Science*, 78(3), 633–654.
- Ault, J. S., Smith, S. G., Richards, B. L., Yau, A. J., Langseth, B. J., O'Malley, J. M., Boggs, C. H., Seki, M. P., & DiNardo, G. T. (2018). Towards fishery-independent biomass estimation for Hawaiian Islands deepwater snappers. *Fisheries Research*, 208, 321–328. <https://doi.org/10.1016/j.fishres.2018.08.012>
- Bacheler, N. M., Berrane, D. J., Mitchell, W. A., Schobernd, C. M., Schobernd, Z. H., Teer, B. Z., & Ballenger, J. C. (2014). Environmental conditions and habitat characteristics influence trap and video detection probabilities for reef fish species. *Marine Ecology Progress Series*, 517, 1–14. <https://doi.org/10.3354/meps11094>
- Bohnsack, J. A., Harper, D. E., McClellan, D. B., & Hulsbeck, M. (1994). Effects of reef size on colonization and assemblage structure of fishes at artificial reef off southeastern Florida, U.S.A. *Bulletin of Marine Science*, 55(2–3), 796–823.
- Boland, R. C., Hyrenbach, K. D., DeMartini, E. E., Parrish, F. A., & Rooney, J. J. (2020). Comparing mesophotic and shallow reef fish assemblages in the Au'au channel, Hawai'i: Fish size, feeding guild composition, species richness, and endemism. *Bulletin of Marine Science*, 96(4), 577–591. <https://doi.org/10.5343/bms.2019.0031>
- Bolser, D. G., Egerton, J. P., Grüss, A., & Erisman, B. E. (2021). Optic-acoustic analysis of fish assemblages at petroleum platforms. *Fisheries*, 46(11), 552–563. <https://doi.org/10.1002/fsh.10654>
- Bolser, D. G., Egerton, J. P., Grüss, A., Loughran, T., Beyea, T., McCain, K., & Erisman, B. E. (2020). Environmental and structural drivers of fish distributions among petroleum platforms across the U.S. Gulf of Mexico. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 12(2), 142–163. <https://doi.org/10.1002/mcf2.10116>
- Bryan, D. R., Smith, S. G., Ault, J. S., Feeley, M. W., & Menza, C. W. (2016). Feasibility of a regionwide probability survey for coral reef fish in Puerto Rico and the U.S. Virgin Islands. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 8(1), 135–146. <https://doi.org/10.1080/19425120.2015.1082520>
- Bryan, M. D., & McCarthy, K. (2015). *Standardized catch rates for Red Grouper from the United States Gulf of Mexico vertical line and longline fisheries* (SEDAR42-AW-02). SouthEast Data, Assessment, and Review.
- Campbell, M. D., Pollack, A. G., Driggers, W. B., & Hoffmayer, E. R. (2014). Estimation of hook selectivity of Red Snapper (*Lutjanus campechanus*) and Vermilion Snapper (*Rhomboplites aurorubens*) from fishery independent surveys of natural reefs of the northern Gulf of Mexico. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 6(1), 260–273. <https://doi.org/10.1080/19425120.2014.968302>
- Campbell, M. D., Rademacher, K. R., Hendon, M., Felts, P., Noble, B., Caillouet, R., Salisbury, J., & Moser, J. (2017). *SEAMAP reef fish video survey: Relative indices of abundance of Grey Snapper* (SEDAR 51-DW-07). SouthEast Data, Assessment, and Review.
- Campbell, M. D., Rademacher, K. R., Noble, B., Salisbury, J., Felts, P., Moser, J., Caillouet, R., Hendon, M., & Driggers, W. B. (2019). Status and trends of Marbled Grouper in the north-central Gulf of Mexico. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 11(2), 114–124. <https://doi.org/10.1002/mcf2.10066>
- Cappo, M., Harvey, E., & Shortis, M. (2007). Counting and measuring fish with baited video techniques—An overview. In J. M. Lyle, D. M. Furlani, & C. D. Buxton (Eds.), *Cutting-edge technologies in fish and fisheries science*. Australian Society for Fish Biology Workshop Proceedings, Hobart, Tasmania, August 2006 (pp. 101–114). Australian Society for Fish Biology.
- Chester, A. J., Huntsman, G. R., Tester, P. A., & Manooch, C. S., III. (1984). South Atlantic Bight reef fish communities as represented in hook-and-line catches. *Bulletin of Marine Science*, 34(2), 267–279.
- Chittaro, P. (2002). Species–area relationships for coral reef fish assemblages of St. Croix, U.S. Virgin Islands. *Marine Ecology Progress Series*, 233, 253–261. <https://doi.org/10.3354/meps233253>
- Christiansen, H. M., Solomon, J. J., Switzer, T. S., & Brodie, R. B. (2022). Assessing the size selectivity of capture gears for reef fishes using paired stereo-baited remote underwater video. *Fisheries Research*, 249, Article 106234. <https://doi.org/10.1016/j.fishres.2022.106234>
- Christiansen, H. M., Switzer, T. S., Keenan, S. F., Tyler-Jedlund, A. J., & Winner, B. L. (2020). Assessing the relative selectivity of multiple sampling gears for managed reef fishes in the eastern Gulf of Mexico. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 12(5), 322–338. <https://doi.org/10.1002/mcf2.10129>
- Clarke, K. R., & Gorley, R. N. (2015). *PRIMER v7. User manual/tutorial*. PRIMER-E, Plymouth Marine Laboratory.
- Clarke, K. R., Gorley, R. N., Somerfield, P. J., & Warwick, R. M. (2014). *Change in marine communities: An approach to statistical analysis and interpretation* (3rd ed.). PRIMER-E.
- Clarke, K. R., Somerfield, P. J., & Chapman, M. G. (2006). On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded samples. *Journal of Experimental Marine Biology and Ecology*, 330(1), 55–80. <https://doi.org/10.1016/j.jembe.2005.12.017>
- Clarke, K. R., Somerfield, P. J., & Gorley, R. N. (2008). Testing of null hypotheses in exploratory community analyses: Similarity profiles and biota–environment linkage. *Journal of Experimental Marine Biology and Ecology*, 366(1–2), 56–69. <https://doi.org/10.1016/j.jembe.2008.07.009>

- Cochran, W. G. (1977). *Sampling techniques* (3rd ed.). John Wiley and Sons.
- Coleman, F. C., Koenig, C. C., & Collins, L. A. (1996). Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environmental Biology of Fishes*, 47, 129–141. <https://doi.org/10.1007/BF00005035>
- Coleman, F. C., Koenig, C. C., Scanlon, K. M., Heppell, S., Heppell, S., & Miller, M. W. (2010). Benthic habitat modification through excavation by Red Grouper, *Epinephelus morio*, in the north-eastern Gulf of Mexico. *Open Fish Science Journal*, 3, 1–15. <https://doi.org/10.2174/1874401X01003010001>
- Cross, T. A., Sauls, B., Germeroth, R., & Mille, K. (2018). Methods to quantify recreational angling effort on artificial reefs off Florida's Gulf of Mexico coast. In S. A. Bortone (Ed.), *Marine artificial research and development: Integrating fisheries management objectives* (Symposium 86, pp. 265–277). American Fisheries Society.
- De'ath, G. (2002). Multivariate regression trees: A new technique for modeling species-environment relationships. *Ecology*, 83(4), 1105–1117. [https://doi.org/10.1890/0012-9658\(2002\)083\[1105:MRTANT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1105:MRTANT]2.0.CO;2)
- Driggers, W. B., III, Campbell, M. D., Hannan, K. M., Hoffmayer, E. R., Jones, C. M., Jones, L. M., & Pollack, A. G. (2017). Influence of bait type on catch rates of predatory fish species on bottom longline gear in the northern Gulf of Mexico. *U.S. National Marine Fisheries Service Fishery Bulletin*, 115(1), 50–59. <https://doi.org/10.7755/FB.115.1.5>
- Ellis, D. M., & DeMartini, E. E. (1995). Evaluation of a video camera technique for indexing abundances of juvenile Pink Snapper, *Pristipomoides filamentosus*, and other Hawaiian insular shelf fishes. *U.S. National Marine Fisheries Service Fishery Bulletin*, 93(1), 67–77.
- Ellis, R. D. (2019). Red Grouper (*Epinephelus morio*) shape faunal communities via multiple ecological pathways. *Diversity*, 11(6), Article 89. <https://doi.org/10.3390/d11060089>
- Ellis, R. D., Coleman, F. C., & Koenig, C. C. (2017). Effects of habitat manipulation by Red Grouper, *Epinephelus morio*, on faunal communities associated with excavations in Florida Bay. *Bulletin of Marine Science*, 93(4), 961–983. <https://doi.org/10.5343/bms.2017.1002>
- Farmer, N. A., Heyman, W. D., Karnauskas, M., Kobara, S., Smart, T. I., Ballener, J. C., Reichert, M. J. M., Wyanski, D. M., Tishler, M. S., Lindeman, K. C., Lowerre-Barbieri, S. K., Switzer, T. S., Solomon, J. J., McCain, K., Marefka, M., & Sedberry, G. R. (2017). Timing and locations of reef fish spawning off the southeastern United States. *PLOS ONE*, 12(3), Article e0172968.
- Farmer, N. A., Malinowski, R. P., McGovern, M. M., & Rubec, P. J. (2016). Stock complexes for fisheries management in the Gulf of Mexico. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 8(1), 177–201. <https://doi.org/10.1080/19425120.2015.1024359>
- Federal Geographic Data Committee. (2012). *Coastal and marine ecological classification standard* (FGDC-STD-18-2012I). Federal Geographic Data Committee.
- Flaherty-Walia, K. E., Switzer, T. S., Winner, B. L., Tyler-Jedlund, A., & Keenan, S. F. (2015). Improved ability to characterize recruitment of Gray Snapper *Lutjanus griseus* in three Florida estuaries along the Gulf of Mexico through targeted sampling of polyhaline seagrass beds. *Transactions of the American Fisheries Society*, 144(5), 911–926. <https://doi.org/10.1080/00028487.2015.1054516>
- Gardner, C. L., DeVries, D. A., Overly, K. E., & Pollack, A. G. (2017). Gray Snapper *Lutjanus griseus*: Findings from the NMFS Panama City laboratory camera fishery-independent survey 2005–2015 (SEDAR 51-DW05). SouthEast Data, Assessment, and Review.
- Garner, S. B., & Patterson, W. F. (2015). Direct observation of fishing effort, catch, and discard rates of charter boats targeting reef fishes in the northern Gulf of Mexico. *U.S. National Marine Fisheries Service Fishery Bulletin*, 113(2), 157–166. <https://doi.org/10.7755/FB.113.2.4>
- Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7(4), 457–472. <https://doi.org/10.1214/ss/1177011136>
- Gledhill, C., & David, A. (2004). Survey of fish assemblages and habitat within two marine protected areas on the West Florida Shelf. *Proceedings of the Gulf and Caribbean Fisheries Institute*, 55, 614–653.
- Glenn, H. D., Cowan, J. H., Jr., & Powers, J. E. (2017). A comparison of red snapper reproductive potential in the northwestern Gulf of Mexico: Natural versus artificial habitats. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 9(1), 139–148. <https://doi.org/10.1080/19425120.2017.1282896>
- Goodrich, B., Gabry, J., Ali, I., & Brilleman, S. (2020). rstanarm: Bayesian applied regression modeling via Stan. R package version 2.21.1. <https://mc-stan.org/rstanarm>
- Grasty, S. F., Wall, C. C., Gray, J. W., Brizzolara, J., & Murawski, S. (2019). Temporal persistence of Red Grouper holes and analysis of associated fish assemblages from towed camera data in the steamboat lumps marine protected area. *Transactions of the American Fisheries Society*, 148(3), 652–660. <https://doi.org/10.1002/tafs.10154>
- Green, S. J., Tamburello, N., Miller, S. E., Akins, J. L., & Côté, I. M. (2013). Habitat complexity and fish size affect the detection of indo-Pacific lionfish on invaded coral reefs. *Coral Reefs*, 32, 413–421. <https://doi.org/10.1007/s00338-012-0987-8>
- Gregalis, K. C., Schlenker, L. S., Drymon, J. M., Mareska, J. F., & Powers, S. P. (2012). Evaluating the performance of vertical longlines to survey reef fish populations in the northern Gulf of Mexico. *Transactions of the American Fisheries Society*, 141(6), 1453–1464. <https://doi.org/10.1080/00028487.2012.703154>
- Haines, D. E., & Pollock, K. H. (1998). Estimating the number of active and successful bald eagle nests: An application of the dual frame method. *Environmental and Ecological Statistics*, 5, 245–256. <https://doi.org/10.1023/A:1009673403664>
- Hanselman, D. H., Spencer, P. D., McKelvey, D. R., & Martin, M. H. (2012). Application of an acoustic-trawl survey design to improve estimates of rockfish biomass. *U.S. National Marine Fisheries Service Fishery Bulletin*, 110(4), 379–396.
- Harford, W. J., Gruss, A., Schirripa, M. J., Sagarese, S. R., Bryan, M., & Karnauskas, M. (2018). Handle with care: Establishing catch limits for fish stocks experiencing episodic natural mortality events. *Fisheries*, 13(10), 463–471. <https://doi.org/10.1002/fsh.10131>
- Harter, S. L., Moe, H., Reed, J. K., & David, A. W. (2017). Fish assemblages associated with Red Grouper pits at Pulley Ridge, a mesophotic reef in the Gulf of Mexico. *U.S. National Marine Fisheries Service Fishery Bulletin*, 115(3), 419–432. <https://doi.org/10.7755/FB.115.3.11>

- Hartig, F. (2021). DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3.3.0. <https://CRAN.R-project.org/package=DHARMA>
- Hilborn, R., & Walters, C. J. (1992). *Quantitative fisheries stock assessment: Choice, dynamics, and uncertainty*. Chapman and Hall. <https://doi.org/10.1007/978-1-4615-3598-0>
- Ilich, A. R., Brizzolara, J. L., Grasty, S. E., Gray, J. W., Hommeyer, M., Lembke, C., Locker, S. D., Silverman, A., Switzer, T. S., Vivlamore, A., & Murawski, S. A. (2021). Integrating towed underwater video and multibeam acoustics for marine benthic habitat mapping and fish population estimation. *Geosciences*, 11(4), Article 176. <https://doi.org/10.3390/geosciences11040176>
- Jaap, W. C. (2015). Stolid coral (Milleporidae and Scleractinia) communities in the eastern Gulf of Mexico: A synopsis with insights from the Hourglass collections. *Bulletin of Marine Science*, 91(2), 207–253. <https://doi.org/10.5343/bms.2014.1049>
- Jaxion-Harm, J., Szedlmayer, S. T., & Mudrak, P. A. (2018). A comparison of fish assemblages according to artificial reef attributes and seasons in the northern Gulf of Mexico. In S. A. Bortone (Ed.), *Marine artificial research and development: Integrating fisheries management objectives* (Symposium 86, pp. 23–45). American Fisheries Society.
- Karnauskas, M., Walter, J. F., III, Campbell, M. D., Pollack, A. G., Drymon, J. M., & Powers, S. (2017). Red Snapper distribution on natural habitats and artificial structures in the northern Gulf of Mexico. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 9(1), 50–67. <https://doi.org/10.1080/19425120.2016.1255684>
- Keenan, S. F., Switzer, T. S., Knapp, A., Weather, E. J., & Davis, J. (2022). Spatial dynamics of the quantity and diversity of natural and artificial hard bottom habitats in the eastern Gulf of Mexico. *Continental Shelf Research*, 233, Article 104633. <https://doi.org/10.1016/j.csr.2021.104633>
- Keenan, S. F., Switzer, T. S., Thompson, K. A., Tyler-Jedlund, A. J., & Knapp, A. R. (2018). Comparison of reef-fish assemblages between artificial and geologic habitats in the northeastern Gulf of Mexico: Implications for fishery-independent surveys. In S. A. Bortone (Ed.), *Marine artificial research and development: Integrating fisheries management objectives* (Symposium 86, pp. 141–163). American Fisheries Society.
- Kimura, D. K., & Somerton, D. A. (2006). Review of statistical aspects of survey sampling for marine fishes. *Reviews in Fisheries Science*, 14(3), 245–283. <https://doi.org/10.1080/10641260600621761>
- Langlois, T., Goetze, J., Bond, T., Monk, J., Abesamis, R. A., Asher, J., Barrett, N., Bernard, A. T. F., Bouchet, P. J., Birt, M. J., Cappel, M., Currey-Randall, L. M., Driessen, D., Fairclough, D. V., Fullwood, L. A. F., Givvons, B. A., Harasti, D., Heupel, M. R., Hicks, J., ... Harvey, E. S. (2020). A field and video annotation guide for baited remote underwater stereo-video surveys of demersal fish assemblages. *Methods in Ecology and Evolution*, 11(11), 1401–1409. <https://doi.org/10.1111/2041-210X.13470>
- Locker, S. D., Reed, J. K., Farrington, S., Harter, S., Hine, A. C., & Dunn, S. (2016). Geology and biology of the “sticky grounds,” shelf-margin carbonate mounds, and mesophotic ecosystem in the eastern Gulf of Mexico. *Continental Shelf Research*, 125, 71–87. <https://doi.org/10.1016/j.csr.2016.06.015>
- Lowerre-Barbieri, S., Menendez, H., Bickford, J., Switzer, T. S., Barbieri, L., & Koenig, C. (2020). Testing assumptions about sex change and spatial management in the protogynous Gag Grouper, *Mycteroperca microlepis*. *Marine Ecology Progress Series*, 639, 199–214. <https://doi.org/10.3354/meps13273>
- Matheson, R. E., Jr., Flaherty-Walia, K. E., Switzer, T. S., & McMichael, R. H., Jr. (2017). The importance of time of day in structuring demersal ichthyofaunal assemblages on the West Florida Shelf. *Bulletin of Marine Science*, 93(2), 407–437. <https://doi.org/10.5343/bms.2016.1047>
- Maunder, M. N., Thorsen, J. T., Xu, H., Oliveros-Ramos, R., Hoyle, S. D., Tremblay-Boyer, L., Hua Lee, H., Kai, M., Chang, S. K., Kitakado, T., Albertsen, C. M., Minte-Vera, C. V., Lennert-Cody, C. E., Aires-da-Silva, A. M., & Piner, K. R. (2020). The need for spatio-temporal modeling to determine catch-per-unit effort based indices of abundance and associated composition data for inclusion in stock assessment models. *Fisheries Research*, 229, Article 105594. <https://doi.org/10.1016/j.fishres.2020.105594>
- McEachran, J. D., & Fechhelm, J. D. (1998). *Fishes of the Gulf of Mexico. Volume 1: Myxiniiformes to Gasterosteiformes*. University of Texas Press. <https://doi.org/10.7560/752061>
- Misa, W. F. X. E., Drazen, J. C., Kelley, C. D., & Moriwake, V. N. (2013). Establishing species-habitat associations for 4 eteline snappers with the use of a baited stereo-video camera system. *U.S. National Marine Fisheries Service Fishery Bulletin*, 111(4), 293–308. <https://doi.org/10.7755/FB.111.4.1>
- Morley, J. W., Selden, R. L., Latour, R. J., Frölicher, T. L., Seagraves, R. J., & Pinsky, M. L. (2018). Projecting shifts in thermal habitat for 686 species on the North American continental shelf. *PLOS ONE*, 13(5), Article e0196127. <https://doi.org/10.1371/journal.pone.0196127>
- Nanami, A., & Nishihira, M. (2003). Population dynamics and spatial distribution of coral reef fishes: Comparison between continuous and isolated habitats. *Environmental Biology of Fishes*, 68, 101–112. <https://doi.org/10.1023/B:EBFI.0000003799.77382.de>
- Oyafuso, Z. S., Barnett, L. A. K., & Kotwicki, S. (2021). Incorporating spatiotemporal variability in multispecies survey design optimization addresses trade-offs in uncertainty. *ICES Journal of Marine Science*, 78(4), 1288–1300. <https://doi.org/10.1093/icesjms/fsab038>
- Parker, R. O., Jr., Chester, A. J., & Nelson, R. S. (1994). A video transect method for estimating reef fish abundance, composition, and habitat utilization at Gray's Reef National Marine Sanctuary, Georgia. *U.S. National Marine Fisheries Service Fishery Bulletin*, 92(4), 787–799.
- Pittman, S. J., & Brown, K. A. (2011). Multi-scale approach for predicting fish species distributions across coral reef seascapes. *PLOS ONE*, 6(5), Article e20583. <https://doi.org/10.1371/journal.pone.0020583>
- Powers, S. P., Drymon, J. M., Hightower, C. L., Spearman, T., Bosarge, G. S., & Jefferson, A. (2018). Distribution and age composition of Red Snapper across the inner continental shelf of the north-central Gulf of Mexico. *Transactions of the American Fisheries Society*, 147(5), 791–805. <https://doi.org/10.1002/tafs.10081>
- Richards, B. L., Smith, J. R., Smith, S. G., Ault, J. S., DiNardo, G. T., Kobayashi, D., Domokos, R., Anderson, J., Taylor, J., Misa, W., Giuseffi, L., Rollo, A., Merritt, D., Drazen, J. C., Clarke, M. E., & Tam, C. (2016). *Design and implementation of a bottom-fish fishery-independent survey in the main Hawaiian Islands* (Technical Memorandum NMFS-PIFSC-53). National Oceanic and Atmospheric Administration.

- Saul, S. E., Walter, J. F., III, Die, D. J., Naar, D. F., & Donahue, B. T. (2013). Modeling the spatial distribution of commercially important reef fishes on the West Florida Shelf. *Fisheries Research*, 143, 12–20. <https://doi.org/10.1016/j.fishres.2013.01.002>
- Schrandt, M. N., Shea, C. P., Kurth, B. N., & Switzer, T. S. (2021). Amending survey design to improve statistical inferences: Monitoring recruitment of juvenile reef fish in the eastern Gulf of Mexico. *Fisheries Research*, 241, Article 106015. <https://doi.org/10.1016/j.fishres.2021.106015>
- Scott-Denton, E., Cryer, P. F., Gocke, J. P., Harrelson, M. R., Kinsella, D. L., Pulver, J. R., Smith, R. C., & Williams, J. A. (2011). Descriptions of the U.S. Gulf of Mexico reef fish bottom long-line and vertical line fisheries based on observer data. *Marine Fisheries Review*, 73(2), 1–26.
- Seavy, N. E., & Reynolds, M. H. (2007). Is statistical power to detect trends a good assessment of population monitoring? *Biological Conservation*, 140(1–2), 187–191. <https://doi.org/10.1016/j.biocon.2007.08.007>
- Siegfried, K. I., Williams, E. H., Shertzer, K. W., & Coggins, L. G. (2016). Improving stock assessments through data prioritization. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(12), 1703–1711. <https://doi.org/10.1139/cjfas-2015-0398>
- Sluka, R. D., Chiappone, M., & Sullivan Sealey, K. M. (2001). Influence of habitat on grouper abundance in the Florida Keys, U.S.A. *Journal of Fish Biology*, 58(3), 682–700. <https://doi.org/10.1111/j.1095-8649.2001.tb00522.x>
- Smith, M. W., Goethel, D., Rios, A., & Isley, J. (2015). *Standardized catch rate indices for Gulf of Mexico Gray Triggerfish (Balistes capriscus) landed during 1993–2013 by the commercial hand-line fishery (SEDAR43-WP-05)*. SouthEast Data, Assessment, and Review.
- Smith, S. G., Ault, J. S., Bohnsack, J. A., Harper, D. E., Luo, J., & McClellan, D. B. (2011). Multispecies survey design for assessing reef-fish stocks, spatially explicit management performance, and ecosystem condition. *Fisheries Research*, 109(1), 25–41. <https://doi.org/10.1016/j.fishres.2011.01.012>
- SouthEast Data, Assessment, and Review. (2014a). *SEDAR 33 – Gulf of Mexico Gag stock assessment report*. SEDAR.
- SouthEast Data, Assessment, and Review. (2014b). *SEDAR 33 – Gulf of Mexico Greater Amberjack stock assessment report*. SEDAR.
- SouthEast Data, Assessment, and Review. (2015). *SEDAR 43 – Gulf of Mexico Gray Triggerfish stock assessment report*. SEDAR.
- SouthEast Data, Assessment, and Review. (2016a). *SEDAR 33U – Gulf of Mexico Gag update stock assessment report*. SEDAR.
- SouthEast Data, Assessment, and Review. (2016b). *SEDAR 33U – Gulf of Mexico Greater Amberjack update stock assessment report*. SEDAR.
- SouthEast Data, Assessment, and Review. (2018a). *SEDAR 51 – Gulf of Mexico Gray Snapper stock assessment report*. SEDAR.
- SouthEast Data, Assessment, and Review. (2018b). *SEDAR 52 – Gulf of Mexico Red Snapper stock assessment report*. SEDAR.
- Steel, R. G. D., & Torrie, J. H. (1960). *Principles and procedures of statistics*. McGraw-Hill.
- Stier, A. C., Hanson, K. M., Holbrook, S. J., Schmitt, R. J., & Brooks, A. J. (2014). Predation and landscape characteristics independently affect reef fish community organization. *Ecology*, 95(5), 1294–1307. <https://doi.org/10.1890/12-1441.1>
- Stunz, G. W., Patterson, W. F., III, Powers, S. P., Cowan, J. H., Jr., Rooker, J. R., Ahrens, R. A., Boswell, K., Carleton, L., Catalano, M., Drymon, J. M., Hoenig, J., Leaf, R., Lecours, V., Murawski, S., Portnoy, D., Saillant, E., Stokes, L. S., & Wells, R. J. D. (2021). *Estimating the absolute abundance of age-2+ Red Snapper (Lutjanus campechanus) in the U.S. Gulf of Mexico*. Mississippi–Alabama Sea Grant Consortium.
- Switzer, T. S., Chesney, E. J., & Baltz, D. M. (2009). Habitat selection by flatfishes in the northern Gulf of Mexico: Implications for susceptibility to hypoxia. *Journal of Experimental Marine Biology and Ecology*, 381(Supplement 1), S51–S64. <https://doi.org/10.1016/j.jembe.2009.07.011>
- Switzer, T. S., Keenan, S. F., Stevens, P. W., McMichael, R. H., Jr., & MacDonald, T. C. (2015). Incorporating ecology into survey design: Monitoring recruitment of age-0 Gags in the eastern Gulf of Mexico. *North American Journal of Fisheries Management*, 35(6), 1132–1143. <https://doi.org/10.1080/02755947.2015.1082517>
- Switzer, T. S., Tyler-Jedlund, A. J., Keenan, S. F., & Weather, E. J. (2020). Benthic habitats, as derived from classification of side-scan-sonar mapping data, are important determinants of reef-fish assemblage structure in the eastern Gulf of Mexico. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 12(1), 21–32. <https://doi.org/10.1002/mcf2.10106>
- Thompson, K. A., Switzer, T. S., Christman, M. C., Keenan, S. F., Gardner, C., Overly, K. E., & Campbell, M. D. (2022). A novel habitat-based approach for combining indices of abundance from multiple fishery-independent video surveys. *Fisheries Research*, 247, Article 106178. <https://doi.org/10.1016/j.fishres.2021.106178>
- Thompson, K. A., Switzer, T. S., & Keenan, S. F. (2017). *Indices of abundance for Gray Snapper (Lutjanus griseus) from the Florida [Fish and Wildlife Conservation Commission's] Fish and Wildlife Research Institute (FWRI) video survey on the West Florida Shelf (SEDAR 51-DW-10)*. SouthEast Data, Assessment, and Review.
- Thorson, J. T., Hermann, A. J., Siwicke, K., & Zimmermann, M. (2021). Grand challenge for habitat science: Stage-structured responses, nonlocal drivers, and mechanistic associations among habitat variables affecting fishery productivity. *ICES Journal of Marine Science*, 78(6), 1956–1968. <https://doi.org/10.1093/icesjms/fsaa236>
- Wang, J., Xu, B., Ahang, C., Xue, Y., Chen, Y., & Ren, Y. (2018). Evaluation of alternative stratifications for a stratified random fishery-independent survey. *Fisheries Research*, 207, 150–159. <https://doi.org/10.1016/j.fishres.2018.06.019>
- Ward, E. J., Oken, K. L., Rose, K. A., Sable, S., Watkins, K., Holmes, E. E., & Scheuerell, M. D. (2018). Applying spatiotemporal models to monitoring data to quantify fish population responses to the Deepwater Horizon oil spill in the Gulf of Mexico. *Environmental Monitoring and Assessment*, 190, Article 530. <https://doi.org/10.1007/s10661-018-6912-z>
- White, E. R. (2019). Minimum time required to detect population trends: The need for long-term monitoring programs. *Bioscience*, 69(1), 40–46. <https://doi.org/10.1093/biosci/biy144>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.