**Cooperative monitoring, assessment, and management of fish spawning aggregations and associated fisheries in the U.S. Gulf of Mexico**

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## Abstract

Many species of inshore, coastal, and reef fishes in the U.S. Gulf of Mexico (GOM) aggregate to spawn at specific sites and times. These fish spawning aggregations (FSAs) can be highly vulnerable to concentrated fishing pressure, which can have detrimental effects on entire stocks and ecosystems. There has been only limited research and management attention on FSAs in the U.S. GOM. We synthesized available information on FSA locations, spawning seasonality, and fisheries management for 28 regionally important species known or likely to form FSAs in the U.S. GOM. We identified and mapped 22 multi-species FSA sites in the region. These FSA sites fall within areas predicted from recently published FSA distribution models, but the number of known sites is probably far less than the number that actually exist. Only three of the 22 (13%) FSA sites were located within no-take marine protected areas and none were in state waters. Management measures (e.g., seasonal closures or gear restrictions) to protect species from fishing during their spawning season are also limited, particularly in state waters. We recommend expanded cooperative research efforts with fishers and other stakeholders to characterize FSAs in the U.S. GOM in order to assist managers in prioritizing sites and seasons for additional protection. Important multi-species FSAs can be incorporated in a network of monitored and managed “sentinel" sites. These efforts should build stakeholder engagement in the management process, generate data that can be used to improve fisheries stock assessments, contribute to developing ecosystem-based fisheries management approaches, and confer resilience to important fisheries stocks and ecosystems of the U.S. GOM.

## 1. Introduction

Many species of marine fishes are known to reproduce in fish spawning aggregations (FSAs), temporary gatherings of large numbers of conspecifics that form for the sole purpose of reproduction (Domeier and Colin 1997; Claydon 2004). From both ecological and management perspectives, FSA sites serve as productivity hotspots, small areas of the ocean that are dictated by interactions between physical processes and geomorphology that attract multiple species to spawn in large numbers (Heyman and Kjerfve 2008; Kobara et al. 2013; Erisman et al. 2017). FSAs comprise the main, if not the entire, source of reproductive output for all of the wide-ranging stocks that use this life history strategy (Coleman et al. 1999; Erisman et al. 2012; Sadovy de Mitcheson and Erisman 2012). In the U.S., many federally managed species reproduce in FSAs, yet the majority of these species have not been assessed or have only limited data available for stock assessments. Managing these species could be improved by 1) protecting their FSAs in the absence of, or in addition to, other management measures and 2) applying data-limited assessment methods that can make use of data collected at FSA sites (e.g., size composition).

These productivity hotspots are also pressure points, and numerous aggregation-forming species have undergone severe declines in response to overfishing of their FSAs (Claro et al. 2009; Sadovy de Mitcheson and Erisman 2012; Russell et al. 2014). Some species are currently classified as threatened or endangered by the International Union for Conservation of Nature (IUCN), with FSA fishing listed as a principal threat to their recovery. In an extreme example, Nassau grouper, (*Epinephelus striatus*) was listed as threatened under the U.S. Endangered

Species Act (ESA) citing that the number and size of FSAs has been reduced by overfishing (C.F.R. 2016). The most recent and comprehensive report on the global status of FSAs revealed that the current status of 52% of the nearly 900 documented FSAs is unknown, and that less than 35% of documented FSAs have any form of management in place (Russell et al. 2014). More than half of the FSAs with known status are in decline, while 10% have disappeared altogether (Russell et al. 2014).

The vulnerability of FSAs to fishing and the rate of decline of FSA-forming populations in response to fishing pressure are linked to the spatial, temporal, and behavioral characteristics of spawning (Erisman et al. 2011; Sadovy de Mitcheson and Erisman 2012; Lowerre-Barbieri et al. 2017). The literature differentiates between two main types of FSAs, resident and transient, based on the duration of spawning, the distribution of FSA sites, whether or not fish migrate to these sites, and the overall abundance and density of fish at individual FSA sites (Domeier and Colin 1997; Claydon 2004). Resident FSAs take place daily over extended time-periods (sometimes year-round), within or in proximity to normal adult residence areas. Therefore, migration distances are very short (meters to a few kilometers), and a species typically has many individual FSAs that involve tens to a few hundred fish. By contrast, transient FSAs form at a much more limited number of sites located outside of normal adult home ranges, often requiring fish to migrate long distances (up to hundreds of kilometers in some species) to spawn within a brief period of time. Transient FSAs involve hundreds to tens of thousands of fish densely aggregated at a single FSA site. Once transient FSAs are located, heavy fishing pressure can result in their rapid depletion or elimination (Johannes 1998; Sadovy de Mitcheson et al. 2013). Since transient FSAs may attract the majority of spawning fish from a catchment area of tens to

100s of kilometers (Nemeth 2009), the extirpation of fish from FSA sites effectively removes stocks from a much larger surrounding area and causes population-scale declines (Erisman et al. 2012). Thus, there is an urgent need to focus conservation and management efforts on FSAs (Heyman 2014; Russel et al. 2014, Sadovy de Mitcheson 2016; Erisman et al. 2017). In the Gulf of Mexico (GOM), a large marine region bordered by the U.S., Mexico, and Cuba, many economically important species form transient FSAs which are the primary focus of this study.

Finfish resources in the U.S. GOM support coastal economies via tens of thousands of jobs in commercial and recreational fisheries and generate billions of dollars in economic impacts. In 2015, over 74,000 people were employed in commercial capture fisheries in the U.S. GOM, generating landings worth over $200 million in sales (NMFS 2017). Grouper sales alone accounted for $28 million. Recreational fishers generated $10.4 billion in direct expenditures on durable equipment and trip sales (NMFS 2017). Many of the species that are targeted in these recreational and commercial fisheries are known to or presumed to reproduce in spawning aggregations (Grüss et al. 2018; Kobara et al. 2019).

In the U.S. GOM, several economically and ecologically important FSA-forming species, particularly groupers, have experienced significant declines. Goliath grouper (*Epinephelus itajara*), for example, was severely depleted from extensive fishing that began in the late 1800s and culminated in the 1970s and 1980s. Goliath grouper FSAs were fished extensively while they still formed. By the late 1980s, all FSAs for goliath grouper in U.S. waters had been nearly extirpated (SEDAR 2011). In response to the observed declines, the National Oceanic and Atmospheric Administration (NOAA) enacted a complete closure of the goliath grouper fishery in the Southeast in 1990 and the U.S. Caribbean in 1993 (Koenig et al. 2011; SEDAR 2011, 2016a). However, because these declines occurred prior to formal and quantitative stock assessments, the details of the decline and subsequent recovery after the Goliath grouper fishery closure have been difficult to document with certainty (Koenig et al. 2011). Other species believed to have declined in the U.S. GOM due to vulnerability to fishing associated with aggregative behavior include gag (*Mycteroperca microlepis*) (Koenig et al. 2012) and red drum (*Sciaenops ocellatus*) (SEDAR 2016b).

Similar declines of aggregation-forming species have occurred in other regions and have been attributed, in large part, to intensive harvest at FSA sites (e.g., Claro et al. 2009). Yet, in spite of the presumed contribution of FSAs to ecosystem health (Nemeth 2009, 2012) and economy in the U.S. GOM, and the potentially large negative impacts of FSA fishing, scientists and managers have very limited information on the timing, location and status of FSAs in the region (Koenig et al. 2000; Burton et al. 2005; Coleman et al. 2011; Biggs et al. 2017c; Kobara et al. 2017; Feeley et al. 2018). In fact, Russell et al. (2014)'s study on the global status of FSAs identified the GOM as one of the world's least studied areas for the biology and management of FSAs. Further biological and fisheries information on FSAs in the U.S. GOM would assist state, federal and regional efforts to monitor, assess, restore, and maintain healthy, productive stocks for the benefit of fisheries and ecosystems.

The objectives of this study were to evaluate and synthesize information on the spatial, temporal, and management aspects of FSAs in the U.S. GOM and to identify priorities for research and management. First, we gathered all available information on FSA locations in the U.S. GOM, mapped these locations in relation to bathymetry, and compared the maps with model-based maps of FSA locations produced in previous studies (Grüss et al. 2018a, 2018b). Next, we compiled all available information on the spawning seasons of priority FSA-forming species and evaluated the overlap with federal (commercial and recreational) closed seasons for each species. We evaluated the overall level of spawning protection or management in place for each species. Finally, we generated a comprehensive list of recommendations for research, monitoring, and fisheries management related to FSAs.

## 2. Materials and Methods

Recognizing resource limitations we selected 28 species of primary management concern that were known or likely to form FSAs in the GOM for the focus of this study (Table 1; Biggs et al. 2017d). Existing biological, reproductive, and fisheries information for these species in the U.S. GOM were then compiled and synthesized using over 800 references (Biggs et al. 2017a). For each of the 28 focal species, the following steps were carried out: 1) FSA locations were mapped, 2) identified FSA locations were compared to the potential spawning areas predicted by species distribution models (SDMs) fitted to independent data, 3) spawning seasons for each species were compared with seasonal closures, and 4) management status was summarized.

We relied on the following three primary resources to map FSA locations in the U.S. GOM: 1) the existing literature for the 28 selected species, 2) reliable accounts from mostly commercial fishers, and 3) unpublished data from the co-authors. In some cases, FSAs could be verified based on direct observations of spawning or through documenting hydrated oocytes or postovulatory follicles in the gonads of fishes collected at the presumed FSA sites during the spawning season (Domeier and Colin, 1997; Heyman et al. 2017a). In the absence of direct evidence, several indirect methods were employed to document the presence of FSAs (Domeier and Colin 1997; Heyman et al. 2017a). If site coordinates were available, they were entered into a geographic information system (GIS) database. In cases where the coordinates of FSA sites were not available (i.e., only descriptions were provided), coordinates were visually estimated and extracted using Google Earth Pro. In all cases, FSA site location coordinates were transformed to decimal degrees using the WGS 84 (World Geodetic System 1984) datum. For presentation in this study, however, FSA site locations were mapped at a coarse scale and with a random centroid to deliberately mask the exact locations, given that most of the FSA sites identified remain open to fishing.

In a recent study (Grüss et al. 2018a), multiple fisheries-independent and fisheries-dependent datasets were employed to develop SDMs, which were then used to predict the potential spawning areas of 17 of the 28 focal species of this study (Table 1). The data sources employed to create the SDMs in Grüss et al. (2018a) were completely independent from the data used in the present study to identify FSA sites. To gauge consistency between SDM predictions and the locations of FSA sites documented in this study, we employed Z-scores following Farmer et al. (2017). All SDM predictions were converted into Z-scores centered at zero, and Z-scores underlying the locations of FSA sites documented in the present study were retained for analysis. The greater the proportion of retained Z-scores above zero, the higher the consistency between SDM predictions and the FSA site locations documented in this study (Farmer et al. 2017).

Grüss et al. (2018b) also used multiple fisheries-independent and fisheries-dependent datasets to fit a SDM for goliath grouper (all life stages combined), to then generate an annual distribution map for the species. Mapping potential goliath grouper spawning areas was not possible, because monitoring data for goliath grouper spawners during the spawning season were extremely scarce. The annual distribution map for goliath grouper produced in Grüss et al. (2018b) was overlayed with FSA locations identified empirically for the species. Then, Z-scores underlying the locations of goliath grouper FSA sites documented in this study were calculated and analyzed.

Spawning season data were derived from published literature sources and summarized in Biggs et al. (2017a). Published sources used acceptable protocols and criteria to define spawning season, which included elevated gonosomatic index (GSI) levels and the presence of spawning capable or actively spawning females (Brown-Peterson et al. 2011; Lowerre-Barbieri et al. 2011). Similarly, peak spawning period was defined by maximum monthly levels in GSI, spawning fractions (% of actively spawning females), fish abundance at spawning sites, observed spawning activity (e.g., courtship rates), or some combination of these parameters (Erisman et al. 2010). When the data were available, the peak spawning time was plotted as a distinct subset of the entire spawning period for each focal species.

To summarize the status of management for FSAs in the U.S. GOM, we reviewed and compiled existing fisheries regulations from publications of the Gulf of Mexico Fishery Management Council (GMFMC; for federal waters) and from relevant state fisheries management agencies (for state waters) within the period 2016-2017. There are five states in the U.S. GOM (Florida, Alabama, Mississippi, Louisiana, and Texas; Fig. 1) each with its own set of regulations. These were used to develop proxies for the relative amount of protection afforded to each species in relation to spawning seasons, locations, and gears used for harvest (Biggs et al. 2018). Data were collected and grouped into four categories for each species: catch and effort limits, gear measures, seasonal restrictions, and site closures (marine protected areas or MPAs). For each category, we used an ordinal (ranked) scoring system to streamline comparisons, with scores of 1-4 scaling from complete protection (1) to no protection (4). Restrictions placed on both commercial and recreational fishing were included separately when compiling information (e.g., species that are banned from commercial harvest). However, information on recreational and commercial fisheries regulations was combined when tallying scores because the objective of the exercise was to determine overall protection rather than to compare regulations between fishing sectors.

The scoring rubric was consistent when applied to federal and state regulations with a few exceptions. The average number of regulations across the five U.S. GOM states was used to generate a proxy score for the level of management provided via catch and effort limits and for gear measures in state waters. Federal gear measures were scored separately for recreational and commercial fishing and averaged to generate an overall score. Federal seasonal restriction scores reflect the least restrictive value of recreational and commercial scores. For seasonal closures in state waters, the criteria for a score of 2 reflected that only part of the spawning season is closed in some or all U.S. GOM states. There are no site closures for FSAs in state waters, so that category received a score of 4 for all species except for goliath and Nassau groupers (scored as 1) because harvest of those species is entirely closed.

## 3. Results and Discussion

This study evaluated and synthesized information on the spatial, temporal, and management aspects of 28 species in the U.S. GOM to identify priorities for research and management associated with spawning. We identified two primary data gaps from our review. First, there is a near total lack of information on the locations of FSAs for most of the focal species in the U.S. GOM (with a few notable exceptions; e.g., Coleman et al. 1996, 2011; Koenig et al. 2000, 2011, 2017; Burton et al. 2005; Lowerre-Barbieri et al. 2009, 2013, 2016; Feeley et al. 2018). Second, data on the behavioral dynamics of FSAs (e.g., timing and periodicity, dimensions, duration, abundance, fish movements) and fine-scale, spatio-temporal interactions between FSAs and fisheries are lacking for many species of recreational, commercial, or conservation importance.

### *Spatial Patterns of FSAs*

To map the known locations of FSAs in the GOM, we used reliable accounts from fishers, unpublished data from our authors, and a survey of over 800 references (Biggs et al. 2017a). Information was extracted to map the locations of all known, verified FSAs in the U.S. GOM (Fig. 1). Using both direct and indirect methods, we documented a total of 22 FSA sites including 9 coastal, 7 shelf edge and 6 mid shelf sites (Fig. 1; Table 2). In some cases, verification required inference from the literature and reports that pre-dated any efforts to formally characterize FSAs.

Coastal and inshore species, including spotted seatrout (*Cynoscion nebulosus*), red drum, black drum (*Pogonias cromis*) and sheepshead (*Archosargus probatocephalus*), aggregate for reproduction in coastal channel passes and associated jetties (Fig. 1; Table 2). Early studies documented these types of FSAs in various U.S. GOM coastal passes (e.g. Pearson 1928; Overstreet 1983; Saucier and Baltz 1993). More recent studies detailed these dynamics for spotted seatrout (Lowerre-Barbieri et al. 2009; 2013) and red drum (Lowerre-Barbieri et al. 2016) in Tampa Bay. The degree to which these FSAs occur at various jetties and passes is a critical research question due to the easy accessibility of these sites for fishers and their proximity to nearshore anthropogenic stressors (Luczkovich et al. 2008; Becker et al. 2013).

Reef-associated species in the snapper-grouper-jack complex generally aggregate near the continental shelf edge (*ca.* 30-200 m water depth) in association with abrupt discontinuities in bottom structure (Fig. 1; Table 2). Members of the snapper-grouper-jack complex that have documented FSAs in this study include: mutton snapper (*Lutjanus analis*), cubera snapper (*L. cyanopterus*), gag, yellowmouth grouper (*Mycteroperca interstitialis*), scamp (*M. phenax*), black grouper (*M. bonaci*), and greater amberjack (*Seriola dumerili*). As an example, the principal spawning habitat for gag, one of the most important grouper species in U.S. commercial and recreational catches (Koenig and Coleman 2012), is high relief, hard bottom habitat along the continental West Florida Shelf edge (70-90 m deep; Coleman et al. 1996; Koenig et al. 2000).

In addition to the coastal and shelf edge sites mentioned above, seven of the eight documented FSAs of goliath grouper were associated with shipwrecks or radio towers off southwest Florida (Fig. 1; Table 2). Many of these sites also serve as FSA sites for permit (*Trachinotus falcatus*)

(Don DeMaria, pers. comm.). The eight goliath grouper FSA sites identified in this study are within one of the goliath grouper hotspot areas predicted by Grüss et al. (2018b) (Fig. 2). Similarly, museum records indicate goliath grouper historically occupied inshore (estuarine), coastal, and reef habitats throughout the northern, western, and southern U.S. GOM (Robertson and van Tassell 2015). Goliath grouper was once an important target species for recreational and commercial fisheries of the U.S. GOM. According to fishers from Galveston, Texas (B. Guindon and S. Hickman, pers. comm.), goliath grouper were caught routinely in the waters off Texas as late as the 1970s. Heavy exploitation of goliath grouper by recreational and commercial fishers caused a range reduction and localized extirpations, and they resulted in goliath grouper being listed as "critically endangered" by the IUCN. The U.S. goliath grouper fishery was closed to harvest in the early 1999s (Sadovy and Eklund 1999). After nearly 30 years of closure, goliath grouper populations have begun to recover in the U.S. GOM (Koenig et al. 2011), to the point that reopening the fishery has been contemplated (SEDAR 2016a).

The size of FSAs and the number of fish at each one varied by species and location. Some FSAs are highly discrete, with large numbers of fish in a concentrated area, such as the mutton snapper FSA at Riley's Hump in the Dry Tortugas, Florida (Burton et al. 2005, Feeley et al. 2018). This aggregation reaches ~ 4,000 individuals and is found within a core area of ~1 km$^2$ on the upper slope of the convex curving reef, in 35-50 m water depth (Feeley et al. 2018). By contrast, gag FSAs were reported to occur as a series (two aggregations every 1.8 km) of small (<100 individuals) aggregations along a 12.9 km long, rocky, shelf-edge ridge (2-8 m relief) within the Madison Swanson MPA (Coleman et al. 2011). Variations in the behavioral dynamics among FSAs suggest that FSA types should be considered along a series of continua between resident and transient, based on migration distance, aggregation size, the numbers of individuals participating in the aggregation, spawning duration, and other factors (following Claydon 2004; Nemeth 2009; Claydon et al. 2014).

We classified FSA type for each of the 28 focal species and determined that at least 22 species form FSAs. FSA types were defined along the continuum between transient and resident with Nassau grouper, goliath grouper, black grouper, yellowfin grouper, mutton snapper, and cubera snapper at the transient end of the spectrum (Biggs et al. in review). The six remaining species - Spanish mackerel (*Scomberomorus maculatus*), king mackerel (*S. cavalla*), red grouper, (*Epinephelus morio*), snowy grouper (*Hyporthodus niveatus*), tilefish (*Lopholatilus chamaeleonticeps*) and speckled hind (*Epinepheulus drummondhayi*) either did not form FSAs or had insufficient information with which to characterize them.

The locations of FSA sites documented in this study show a similar distribution to the potential FSA areas predicted from SDMs fitted to independent data sources (Grüss et al. 2018a, 2018b; Fig. 2). The median Z-score standardized FSA indices and Z-score standardized probabilities of encounter were substantially greater than 0 (Fig. 3), confirming that the locations of FSA sites documented herein are highly consistent with those predicted from independent data sources in Grüss et al. (2018a, 2018b). The SDMs predicted a suite of FSAs along the coast and another along the shelf edge (Fig. 2). The SDM predictions are contained within the broad Essential Fish Habitat (EFH) for each species as defined in their respective fishery management plans. EFH is defined as those habitats that are necessary to the species for spawning, breeding, feeding, or growth to maturity. However, there are extensive areas of potential FSA sites identified in the

SDMs, in which there are no documented FSA sites, particularly in the western U.S. GOM These results suggest that information on spawning sites in the GOM is incomplete and can be used to prioritize efforts to identify additional spawning sites.

Our results indicate that the majority (13 of 22) of the documented FSA sites in the U.S. GOM occur on the West Florida shelf. The concentration of known sites is likely due to the relatively high surface area of suitable FSA habitat, particularly for species of the snapper-grouper-jack complex, e.g., an extensive rocky shelf edge favored by species such as gag for spawning (Coleman et al. 2011) and extensive areas of ledges and high-relief bottoms suitable for scamp FSAs (Harris et al. 2002). It may also be due to the density of observations from fishers and scientists in that specific area of the U.S. GOM. Both recreational and commercial fishing effort is higher from west Florida than any other U.S. GOM state (NMFS 2017). Additionally, there are over a dozen marine graduate school programs in Florida, at least 10 more than any other U.S. GOM state. Finally, the Florida Fish and Wildlife Research Institute, which conducts large-scale monitoring of reef fish along the shelf, has a long history of assessing reef fish reproduction (Moe 1969; Bullock et al. 1992; Bullock et al. 1996; McBride et al. 2008; Lowerre-Barbieri et al. 2009, 2013, 2016). While the relatively high density of documented FSA sites on the west Florida shelf is likely related to suitable habitat, the relatively high proportion of the documented sites in this study may be inflated by the disproportionate amount of fishing and scientific effort in that region. This is supported by the numerous multi-species FSA sites of snappers and groupers (e.g., cubera snapper, yellowedge grouper (*Hyporthodus flavolimbatus*) that have been anecdotally reported to the authors by commercial fishers in the northern and western U.S. GOM (Helies et al. 2016, W. Werner, B. Guindon, pers. comm.); these sites have yet to be characterized.

***Seasonal Patterns of FSAs***

Spawning seasons for the 28 focal species in the U.S. GOM were compiled from available literature (Biggs et al. 2017b; Table 3). Spawning seasons ranged from 3 to 12 months in duration (mean = 5.9 months). The highest number of species (n = 21; 75%) spawned during June, and the fewest in December (n = 5; 18%). Nassau grouper (*Epinephelus striatus*) and sheepshead have the shortest spawning seasons (3 months), whereas yellowedge grouper (10 months) and yellowmouth grouper (12 months) have the longest seasons. Groupers (Epinephelidae) show no consistent pattern in the seasonal timing or duration of spawning, as species spawn from 3 to 12 months (mean = 6.6 months) and at varying times of the year. Snappers spawn from 4 to 6 months (mean = 4.8 months), with peak spawning occurring consistently during the summer (June-August). Focal species of sciaenids that spawn inshore and/or in channel passes also show no discernible seasonal pattern (mean = 5.7 months; range = 4 to 7 months): spotted seatrout spawning occurs from April to September, red drum from August-November, and black drum spawn during two seasons (winter-spring and fall) (Table 3).

The protracted spawning seasons (i.e. > 4 months) of many species would indicate a relatively high resilience to disturbance. This is based on reproductive resilience theory that predicts that species with higher lifetime spawning opportunities are less vulnerable to environmental (e.g., climate change) and anthropogenic (e.g., fishing) disturbances (Lowerre-Barbieri et al. 2017). For example, a 12-month spawning season in yellowmouth grouper suggests the species may be resilient to fishing peaks during certain months of the year or the contraction of the spawning season resulting from climate change (Asch and Erisman 2018). By contrast, Nassau grouper, which is listed as "Threatened" under the U.S. Endangered Species Act, only spawns a few days a month during 3 months of the year, and not all females participate in all spawning events (as observed in Cuba in the southeastern GOM; Sadovy and Eklund 1999; Claro et al. 2009; Biggs et al. 2017b). Therefore, based on gross comparisons, reproductive resilience theory (Lowerre-Barbieri et al. 2017) would predict Nassau grouper to be more vulnerable to disturbance than yellowmouth grouper. However, a more accurate estimate of the number of annual reproductive opportunities per year (annual fecundity or total egg production) requires information on spawning periodicity at the population scale (Lowerre-Barbieri et al. 2013; Erisman et al. 2014) and estimates of spawning frequency for individual females (Lowerre-Barbieri et al. 2011; Lowerre-Barbieri et al. 2016). Unfortunately, information on spawning periodicity of FSAs and spawning frequency of individuals during individual FSA periods is non-existent for most species and regions of the U.S. GOM, making it challenging to accurately assess the resilience of stocks to fishing and environmental impacts. Nonetheless, the same suite of focal species in this study show a range of vulnerability and resilience to fishing. Those species with spawning behaviours at the transient end of the continuum of FSA types (i.e., characterized by long migrations, large changes in density, and spawning in short durations) (Claydon 2014) were more likely to be overfished than those species closer to the "resident" end of the continuum. Further, a recent principle components analysis revealed that spawning behaviours were a better indicator of overfished status than life history traits alone (Biggs et al., in review).

### *Management of FSAs*

We developed a rubric to describe the relative levels of management for each of our study species (Table 4). Overall, existing management regulations in the GOM offer very little protection for spawning fish (mean score of 3.1 of 4; where a score of 4 means no protection), and regulations preventing FSA overfishing are nearly absent (Table 5). No clear difference was identified in the average amount of protection provided in federal (3.0) versus state (3.2) waters. Catch and effort limits during the spawning season in federal (mean = 2.5) and state (mean = 2.8) waters offered the highest level of protection, consistent with the implementation of the Magnuson-Stevens Fishery Management and Conservation Act, which limits fisheries through single-species management measures designed around sustainable catch limits (NMFS 2007).

Nassau grouper (overall score = 1), goliath grouper (overall score = 1), and red drum (overall score = 2) received the highest level of protection from fishing. Recreational and commercial harvest and possession of Nassau and goliath grouper was prohibited in both federal and state waters of the U.S GOM (NMFS 2007), mainly in response to the overfishing of their FSAs (Sadovy and Eklund 1999; Koenig et al. 2011). Fisheries-dependent data is a primary source for stock assessments and, therefore, when a fishery is closed, it is difficult to obtain samples. Sampling individuals during scientific endeavors on FSAs could provide critical data (e.g., size composition and maturity data) that would enable data-limited assessment methods and could, therefore, move managed stocks into higher, more data-rich tiers. In addition such studies can help identify ‘critical habitat’ for ESA-listed species such as Nassau grouper, as mandated by the ESA.

Red drum is also protected from commercial and recreational harvest in federal waters. In state waters, the commercial fishery is closed everywhere except Mississippi, where the fishery is regulated by annual catch limits. Recreational fisheries in state waters primarily target large juveniles (e.g., 20-28 inches total length) that reside in estuaries, which are regulated by daily catch limits and size limits (e.g., slot limits). All U.S. GOM states except Florida allow a limited take of large adults (e.g. 1 fish per year, > 28 inches total length). Recreational fishing effort for red drum in state waters peaks between September and November when anglers and guides target "bull reds" (i.e., individuals >30 inches in total length) near coastal passes during the peak spawning season (Table 3A; Kobara et al. 2017) and warrants analysis.

Only three of the 22 documented FSAs in the U.S. GOM receive some form of spatial protection: the Madison Swanson Marine Reserve, the Tortugas South Ecological Reserve on the West Florida Shelf, and Warsaw Hole along the Florida reef tract (Fig. 1; Table 2). The remaining 19 documented FSA sites are unprotected aside from species-specific state and federal fisheries regulations (e.g., bag and size limits, and seasonal restrictions). One additional FSA was identified in the Flower Garden Banks National Marine Sanctuary (FGBNMS). Helies et al. (2016) offered indirect evidence (courtship behavior and color changes) of crevalle jack (*Caranx hippos*) and horse-eye jack (*C. latus*) FSAs at the West Flower Garden Bank. Since these species were not among our focal species, the FGBNMS FSA site was not considered explicitly in this study, yet warrants future investigation. The FGBNMS FSA site benefits from some anchoring and gear restrictions though fishing is still permitted. It is worthwhile to note that the FGBNMS is in the process of boundary expansion which is likely to include several additional banks in the NW GOM including 29 Fathom Bank, MacNeil; Rezak and Sidner Banks; Rankin, Bright Bank; Geyer Bank, McGrail Bank, Bouma Bank, Sonnier Bank, Alderice Bank, and Jakkula Bank (labelled as FGB area in Fig. 1). These banks form abrupt discontinuities in the seafloor (consistent with other multi-species sites) and fall within the priority area identified through modeling (Fig. 1) and thus warrant further investigation.

There are no FSA-based MPAs in the state waters of the U.S. GOM (Table 2). However, other U.S. states have enacted spatial and temporal closures to protect spawning marine fishes. In California for example, the commercially and economically important white seabass (*Atractoscion nobilis*) fishery was nearly destroyed in large part from commercial fishers targeting spawning aggregations at coastal headlands (Allen et al., 2007). By banning the use of nearshore gill nets in 1994, the California Marine Resources Protection Act effectively removed commercial harvest from white seabass spawning aggregations which in turn lead to the recovery of the species and its fishery (Allen et al., 2007; Pondella et al. 2008). Management of U.S. Atlantic herring (*Clupea harengus*) provide another example. Atlantic herring spawn in the state waters of Massachusetts, New Hampshire and Maine and adjacent federal waters (> 3 miles from shore). The Atlantic States Marine Fisheries Commission (ASMFC) coordinates efforts with the New England Fishery Management Council (NEFMC) via complementary fishery management plans that include 4 – 6 week seasonal and spatial spawning closures. The timing of these closures is chosen adaptively each year, based on the measured onset of spawning and the duration of the spawning season (ASMFC 2019).

In order to analyze the effectiveness of closed seasons for spawning fish, we overlaid federal closed seasons for recreational fisheries (GMFMC 2018a; Table 3A) and for commercial fisheries (GMFMC 2018b; Table 3B) on spawning seasons. Three species have year-round, federal harvest restrictions for both recreational and commercial fisheries including Nassau grouper, goliath grouper and red drum (Tables 3A and B). The commercial harvest of 12 of our focal species is presently managed using an Individual Fishing Quota (IFQ) system rather than seasonal closures [i.e., red snapper (*Lutjanus campechanus*), red grouper, gag, scamp, yellowedge grouper, speckled hind, Warsaw grouper (*H. nigritus*), snowy grouper, black grouper, and yellowfin grouper (*Mycteroperca venenosa*)] (GMFMC 2019; Table 1). IFQ management does not restrict fishing during spawning seasons. For those species commercially harvested in federal waters that are managed with seasonal closures [gray triggerfish (*Balistes capriscus*) and greater amberjack] closed seasons protect the entire peak spawning period for those species (June - July and March - May, respectively) (Table 3B).

Seven of our 28 focal species are regulated in part via recreational closed seasons, although their alignment with peak spawning is uneven. In the most restrictive case, the recreational fishery for gag is closed January-May and encompasses the entire spawning season (Table 3A). Gag spawning is further protected from recreational and commercial fishing within the year-round MPA in Madison Swanson (GMFMC 2018b). The peak gray triggerfish spawning period (June – July) is also protected. Other species have partial protection for the spawning period, including red grouper and yellowfin grouper (one of their three month spawning periods, respectively), scamp (one of two peak months), and black grouper (two of three peak months) (Table 3A). The recreational closed season for greater amberjack was recently updated to restrict fishing during 8 months of the year but allowing fishing during May (one of three peak spawning months) (GMFMC 2018a; Table 3A). The management of red snapper, the most sought-after species in the U.S. GOM (NMFS 2017) has undergone substantial changes in recent years. Private recreational fishing for red snapper in federal waters was only permitted during June and July, effectively concentrating the effort during two of the three peak spawning months (Table 3A). Due to recent changes, each Gulf state (Texas, Louisiana, Mississippi, Alabama, and Florida) is now responsible for setting private recreational fishing seasons for red snapper from state and federal waters, landed within their state, creating uneven seasonal closures in the region. In situations where spatial management would be politically contentious or ecologically inefficient, data provided herein could be used to adjust and harmonize temporal closures to protect spawning in the U.S. GOM.

***Recommendations for Research and Monitoring***

To address the data gaps identified in this study and their management implications, we propose a set of recommendations. We recommend using cooperative research to engage constituents from all sectors to verify and characterize important FSAs in the U.S. GOM. The map of documented multi-species FSA constructed in the present study (Fig. 1) and the maps of the potential multi-species FSA areas in the U.S. GOM produced in Grüss et al. (2018a) (Fig. 2) can be employed to prioritize verification and characterization efforts at the regional scale. The western U.S. GOM is a clear priority, given the vast area of potential spawning grounds and the relative paucity of documented FSA sites in that region. Similarly, the area north of Pulley Ridge (PR) on the southwest Florida Shelf (Fig. 1) appears to be a hotspot for reproduction for multiple species of reef fishes and also a priority for further characterization (Grüss et al. 2018a). Though fishers have reported the presence of gag FSAs there, no FSAs have been verified in the Pulley

Ridge area to date (Hallock, 2007; Grüss et al. 2017). Finally, we recommend FSA characterizations within coastal passes, which are easily accessible but also vulnerable to both fishing and upland impacts (Luczkovich et al. 2008; Becker et al. 2013). While various methods are available, Heyman et al. (2017a) offers techniques that can be used in cooperative research programs to identify and characterize FSAs throughout the U.S. GOM.

Given limited resources for research and assessments, we offer further criteria for prioritizing areas and species for application of cooperative research protocols. From an ecosystem management standpoint, sites identified as multi-species FSAs are always high priority for characterization (van Overzee and Rijnsdorp 2015; Erisman et al. 2017; Grüss et al. 2019). Setting priorities for individual species is more subjective and based on perspective. State-managed coastal species are all high priorities for those jurisdictions (e.g., red drum, black drum, spotted sea trout). Federally managed species are all priority for federal managers (Table 1). Those with pending assessments are of particular priority given that uncertainty can be reduced by including data generated from cooperative research at FSAs (e.g., scamp; Table 1). Species that have never been assessed are also a priority. Commercially important and recreationally important species are a priority for each of those sectors, respectively. Species managed under Individual Fishing Quotas (IFQ) are a great priority for those fishers with catch share allocations since they have a direct and personal stake in the sustainable management of those species (Table 1).

Priority can also be assessed based on species vulnerability. Highly vulnerable species should be prioritized, e.g. those listed by IUCN as critically endangered (e.g. goliath grouper, Nassau grouper) or on the U.S. Endangered Species list (e.g. Nassau grouper) (C.F.R. 2016). While goliath grouper is still considered critically endangered by IUCN, its range is expanding north and west into areas it once inhabited (Koenig et al. 2011; K. Guindon, pers. comm). If goliath FSAs have formed in the central and western U.S. GOM, they should be identified, characterized and protected, prior to decisions regarding the possible reopening of the fishery (SEDAR 2016a). A full assessment of the factors governing the vulnerability of the species considered herein, is the subject of a forthcoming manuscript (Biggs et al., in review). The study uses various criteria to assess vulnerability including migration distance, aggregation size (number of fish present), aggregation type (e.g., transient, resident, non-aggregating), and spawning season duration.

We have shown herein that multi-species FSA sites occur at geomorphologically distinctive and predictable features. Coastal species aggregate to spawn in or near coastal passes. Snapper, grouper and jack species aggregate to spawn at shelf edges and ridges adjacent to deep waters (Figs. 1 and 2). The geomorphological and oceanographic factors create suitable conditions, where multiple species aggregate to spawn (Kobara et al. 2013). The biophysical attractiveness of such sites is further enforced by evidence that FSA sites can be re-colonized after extirpation (Kadison et al. 2010; Nemeth 2012). The general shape, location, and depth of these natural features have remained largely unchanged for hundreds of years. These factors suggest that persistent multi-species FSA sites may continue to attract spawning fishes in spite of projected changes in temperature and sea level over the next 100 years. While Asch and Erisman (2018) suggest that FSAs serve as a bottleneck to climate change adaptation for Nassau grouper, the suite of species that spawn at FSA sites (through colonization) may shift with climate change. These hypotheses could be tested using long-term biophysical monitoring at a network of multi-species FSA sites.

We posit that FSA sites serve as ecosystem integrators. In fact, physical geomorphology and hydrodynamics may dictate where multi-species FSAs are likely to form (Kobara et al. 2013). These transient, dense concentrations of spawning fish in turn attract aggregations of migratory apex predators (e.g., sharks, billfishes, dolphins, and tunas) that feed on spawning adults, and mega-planktivores [e.g., whale shark (*Rhincodon typus*) and ESA-listed manta rays (*Manta birostris*)] that feed on spawned eggs (Heyman et al. 2001; Nemeth 2012; Fuiman et al., 2015). This scenario creates concentrated hotspots of primary and secondary productivity that cascade into diverse coastal and pelagic food webs, fostering ecosystem connectivity and stability through trophic interactions (Nemeth et al. 2011). Therefore, FSA declines are equated with apex predator loss, which can have detrimental effects on ecosystem health in marine areas throughout the world (Jackson et al. 2001; Burke and Maidens 2004; Estes et al. 2011). By contrast, effective FSA management can have umbrella effects that support complex food webs and populations of apex predators that are critical in the maintenance of healthy ecosystem function and structure (Pauly et al. 1998; Nemeth 2009; Heithaus et al. 2008; Sadovy 2016). FSAs are natural nexus points of multi-species, biophysical ecosystem integration.

In addition to the natural FSA sites described herein, some fishes are attracted to artificial reefs for spawning. Goliath grouper aggregate around anomalous hard structures (e.g., wrecks and radio towers) within otherwise relatively featureless areas of flat bottom (Koenig et al. 2011, 2017; Don DeMaria, pers. comm.; Table 2; Fig. 1). Sheepshead aggregate to spawn at oil and gas platforms in nearshore waters off Texas (Gallaway and Martin 1980; Table 2; Fig. 1; Site 4).

The U.S. GOM maintains the largest artificial reef system in the world. There have been 7,093 oil and gas platforms installed in the U.S. GOM in the last 50 years, but many have reached the end of their productive lives and have been decommissioned and removed. In 2018, there remained 2,026 standing oil and gas platforms in the U.S. GOM (BOEM 2018). Similar to coastal passes, jetties and shelf edge promontories, oil and gas platforms are abrupt discontinuities in the localized geomorphology. We posit that many FSA-forming species in the U.S. GOM may have adopted oil and gas platforms as spawning locations. We recommend evaluating if oil and gas platforms serve as multi-species FSA sites, and if so, it would be important to determine the interaction and connectivity among FSA sites at natural and artificial sites. The presence of FSAs should be considered when evaluating platform decommissioning options since full removal will displace or eliminate the FSA whereas 'reefing in place' may sustain them.

We propose creation of a network of "sentinel sites" at managed locations where large, transient multi-species FSAs have persisted for many years. Because these sites have a significant ecological contribution and serve as sites of ecosystem integration, monitoring a regional network of such sites could serve as a baseline, integrated measure of ecosystem health (Heyman 2014). These sentinel sites should be equipped with long-term, multi-sensor monitoring stations, which should include video and passive acoustic recorders, telemetry receivers, CTDs, current meters, oxygen probes, and other relevant equipment as appropriate. Data should be collected at these sites using a standardized protocol and made public via one or more public data portals. Long-term bio-physical monitoring at a network of sentinel FSA sites would allow for status and trend analysis of reproductive phenology, spawning activity, and overall productivity in relation to variations in environmental conditions both within and among FSA sites. In turn, these analyses would allow testing for effects of chronic and acute, natural (e.g., hurricanes) and anthropogenic (e.g., fishing and oil spills) stressors on multi-species to ecosystem scales. Over the long-term, results of such a monitoring network could provide key insights on the fisheries and ecosystem impacts of regional climate change along with sub-regional spatial variations in productivity that would require different management responses at different locations.

Some sites are already well suited to serve as sentinel FSA sites in that they have been mapped, protected and are relatively well-studied, e.g., Riley's Hump (Site 21 on Fig. 1 and Table 2) and Madison Swanson (Site 11 on Fig. 1 and Table 2). However, the dearth of known existing FSA sites, particularly in the western U.S. GOM suggests that extensive exploratory efforts are needed to document, characterize, select, monitor, and effectively manage a representative network of sentinel sites in the U.S. GOM.

***Recommendations for Inclusion of FSAs into Stock Assessments and Fisheries Management***

This study provides several ways in which data from FSAs might assist fisheries managers. Data collected from FSAs could provide guidance for spatial and temporal management measures, data for stock assessments, and increased stakeholder engagement in the management process. More broadly, FSA metrics could be employed to hone measures of reproductive resilience (Lowerre-Barbieri et al. 2017) and provide insights on the appropriate management benchmark proxies for use, when estimates of maximum sustainable yield are unavailable. That is, detailed information on the distribution of spawning sites, the timing and duration of individual aggregation periods, spawning periodicity of regional populations, sexual patterns (e.g., sequential hermaphroditism), sex ratios and size frequency distributions, and spawning frequency of individual females within aggregations would allow for realistic estimates of annual and lifetime reproductive output. In turn, such information would greatly improve our understanding of resilience and productivity for each species and allow managers to set regulations accordingly.

Most species addressed herein span various management jurisdictions. The GMFMC has traditionally relied on single species management measures, IFQs and closed seasons. Other jurisdictions such as the SAFMC, the Caribbean Fishery Management Council (CFMC), and even neighboring Mexico, Cuba and Belize have employed seasonal closures, but have also shown more willingness/interest in supporting time/areas closures areas to manage FSAs.

FSA data were recently used to guide spatial management measures to protect spawning fishes. The SAFMC worked with federal fisheries managers, conservation leaders, scientists and fishers to identify a suite of key FSA sites within their jurisdiction (Farmer et al. 2017). Confirming knowledge and accounts from and with expert fishers and data from state and federal agencies, spawning was documented at sites such as Georgetown Hole off South Carolina (Heyman 2016; Farmer et al. 2017). As a result, the SAFMC developed Amendment 36 to the snapper-grouper fishery management plan that set up a framework for protecting spawning fishes and designating the first five such sites as Spawning Special Management Zones, in which bottom fishing is now restricted (SAFMC 2017). The CFMC set a regional precedent by creating MPAs to protect FSAs in both the U.S. Virgin Islands and Puerto Rico, including the Red Hind Marine

Conservation District, Grammanik Bank, El Seco, Lang Bank, Bajo de Sico, and Mona Island (Nemeth 2005; Kadison et al. 2010; Schärer et al. 2010). Recovery has been uneven yet dramatic where fishers observed the closure and enforcement has been consistent (Nemeth 2005; Hamilton et al. 2011). In Belize, using cooperative research results as a basis, the nation created a network of 11 MPAs to protect multispecies FSAs in 2003 (Heyman 2011). In Mexico, after participating in the characterization of FSAs with scientists, fishers urged and successfully persuaded Mexico to create three new MPAs to protect FSAs along the Caribbean coast (Fulton et al. 2018).

Following the precedent set in the U.S. South Atlantic, U.S. Caribbean, Belize, Mexico and other countries that share FSA-forming species with the GOM, the GMFMC could develop a framework for evaluating key FSA sites within their jurisdiction for possible spatial, temporal or other warranted management measures. Spatial closures can be effective for species with FSA types on the the transient end of the spectrum and that form relatively few large FSAs. Temporal closures can be effective for species that form large numbers of resident FSAs. Indeed, current temporal closures for several species could be better aligned with their spawning seasons in the U.S. GOM (e.g. red snapper, red grouper, black grouper, Yellowmouth grouper, yellowfin grouper and greater amberjack) (Table 3A).

Fish stocks in the U.S. GOM are managed based on stock assessments, which in turn, are based on various sources of data and traditional stock assessment models (NMFS 2007). These assessment models have been used effectively to guide managing and rebuilding many of the nation’s highest value and largest volume, single-stock fisheries (NRC 2014; NMFS 2017).

However, for many smaller scale, multi-species fisheries, including many stocks in the U.S. GOM, existing data are insufficient to conduct traditional stock assessments (NRC 2014; Sagarese et al. 2016). Data-limited techniques have been developed to address some of these species, though, for many species, data are insufficient to conduct assessments (SEDAR 2016b; SEDAR 2017). There is growing recognition that traditional and data-limited stock assessments could be improved by incorporating additional information, including environmental data (SEDAR 2013; Schirippa and Methot et al. 2013; Newman et al. 2015; Sagarese et al. 2016), as well as length data and life history information that could be derived from FSAs (Erisman et al. 2014; Lowerre-Barbieri et al. 2017). Length data could help elucidate selectivity patterns (e.g., are there bigger fish than the fishery harvests?) or enable length-based data-limited assessment models.

Traditional stock assessments model reproductive success using spawner-recruit relationships (SRRs) that link reproductive potential with subsequent recruit abundance. Stock reproductive potential is typically quantified as spawning stock biomass (SSB), a measure of egg production. Stock resilience is measured using steepness ($h$), i.e., the slope of the SRR curve near the origin (Myers et al. 1999; Mangel et al. 2013). Steepness is an emergent property of the SRR estimated within the model, yet, in U.S. GOM fish, it is often inestimable or estimated to be close to one, implying no SRR. Thus, steepness may have little biological meaning for many species, failing to capture the processes driving reproductive success. A species' reproductive compensatory ability depends on the selection pressures under which it evolved (Garrod and Horwood 1984), and there is a range of reproductive traits expected to affect reproductive success, two of the best recognized being reproductive lifespan (Hixon et al. 2014; Barneche et al. 2018) and spawning site density and diversity (Lowerre-Barbieri et al. 2015). For total spawners (which spawn only once per breeding season) fecundity is expected to increase exponentially with length (Hixon et al. 2014; Barneche et al. 2018); however, most warm-water species spawn in multiple batches and have indeterminate fecundity (Ganias et al. 2015). In these species, older females typically exhibit larger batches, longer spawning seasons, and more spawning events, greatly increasing their reproductive contribution (Lowerre-Barbieri et al. 2011).

Assessment practices based on SSB to recruitment relationships and steepness strongly rely on the assumption of density-dependent population growth and do not integrate emerging understanding of spawner-recruit ecology and how a range of traits can affect reproductive resilience to fishing and other stressors (Lowerre-Barbieri et al., 2017). Taking an ecosystem-based fisheries management approach to understanding spawner-recruit systems and key traits affecting resilience is needed to predict productivity in this time of changing ocean conditions. This will require collaboration between fisheries ecologists, geneticists, early life history scientists, oceanographers, and stock assessment scientists. Therefore, we recommend teams of stock assessment scientists to work with biologists that study FSAs to guide this effort (e.g., developing spatially-explicit measures of reproductive value associated with FSA sites).

Engaging stakeholders in cooperative research to characterize and monitor FSAs will increase their support for active stewardship and sustainable management initiatives (Heyman 2011; SEDAR 2013; Grüss et al. 2014; Fulton et al. 2018). Key stakeholders include commercial, for-hire recreational fishing guides, and recreational fishers, dive operators and recreational divers.

Each of these groups can participate in cooperative research as citizen scientists in various ways. Fishers that catch female fish with hydrated oocytes can provide direct evidence of spawning (Colin et al. 2003; Farmer et al. 2017; Heyman et al. 2017a). Diver observations of courtship behavior and coloration can help identify FSA places and times. In the future, these observations might be provided by citizen scientists, using, for example, the anecdotal data sheet in the cooperative monitoring protocol (Heyman et al. 2017a). This confidential information must be carefully safeguarded to avoid unintended use. Further, the presence of cooperative monitoring teams at the time and location of FSAs will provide an on-the-water presence and, thus, deter illegal fishing. Nonetheless, there exists a critical need to enact effective enforcement and monitor compliance for any type of FSA management, in order for policies and regulations to have their desired effects (Russell et al. 2012).

FSA characterization can contribute data for several species and species complexes as described herein, decreasing uncertainty on stock status and vulnerability and, thus, ultimately contributing to sustainable harvest and increased access for all resource users. As with any proposed management measures, the impacts of FSA management will require socio-economic impact analysis which in turn must be considered in any final ruling. Many species' life histories include species ranges and migrations, spanning the jurisdictions of federal and state waters in the U.S., as well several neighboring countries. Management focus on FSAs throughout the region could help managers harmonize management approaches and enforcement.

***Conclusions***

This study represents a comprehensive synthesis of existing information on spawning times, spawning locations, and associated management for 28 species of fishery and conservation importance in the U.S. GOM. Our results are consistent with habitat suitability models that illustrate three distinctive bands of multi-species FSAs: 1) coastal passes and jetties for croakers and drum, 2) shelf edges and ridges for snapper-groupers-jacks, and 3) mid-shelf obstructions for goliath grouper and related species. We highlight that, while many species are known to reproduce in multi-species FSAs and FSA sites serve as productivity hotspots, managers lack sufficient information on the spatio-temporal dynamics of FSAs in the U.S. GOM to assess their status and to manage them effectively. However, fisheries resources are also being impacted by natural stressors (e.g., hurricanes, red tide and flood events) and anthropogenic forces (e.g., pollution and climate change) (Halpern et al. 2008), though these linkages are often poorly understood. The geographic ranges of marine fishes can shift in response to climate change (e.g. Perry et al. 2005; Nye et al. 2009; Pinsky et al. 2013). Likewise, the phenology, migration timing, and diversity of species that use each FSA site may be affected and altered by climate change (Asch and Erisman 2018). Growing human populations coupled with a decline in available management and research funds dictate that investments in fisheries management and marine conservation be efficient, enforceable, and provide measurable benefits to both biodiversity and fisheries (Grüss et al. 2014; Erisman et al. 2017).

We conclude that cooperative monitoring of a network of sentinel FSA sites will offer a new data stream that can enable and improve stock assessments, guide spatial and temporal management measures for many of the U.S. GOM's most important fisheries species, increase stakeholder involvement in fisheries management, contribute to developing ecosystem-based fisheries management approaches, and create unique opportunities to evaluate physical and biological effects of climate change on fisheries stocks and their resilience.

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**Table 1.** Species known or likely to form fish spawning aggregation (FSAs) in the U.S. Gulf of Mexico considered in this study.

| Common Name | Scientific Name | Family | [1]Modelled | [2]Assessment Year | [2]SEDAR No. | [3]Managed under IFQ | [4]Prohibited |
|---|---|---|---|---|---|---|---|
| Speckled Hind | *Epinephelus drummondhayi* | Epinephelidae | No | 2016 | 49 | Yes | |
| Goliath Grouper | *Epinephelus itajara* | Epinephelidae | [1]No | 2016 | 47 | Yes | Total |
| Red Grouper | *Epinephelus morio* | Epinephelidae | No | 2017 | 42 | Yes | |
| Nassau Grouper | *Epinephelus striatus* | Epinephelidae | [1]No | | | | Total |
| Yellowedge Grouper | *Hyporthodus flavolimbatus* | Epinephelidae | Yes | 2011 | 22 | Yes | |
| Warsaw Grouper | *Hyporthodus nigritus* | Epinephelidae | Yes | | | Yes | |
| Snowy Grouper | *Hyporthodus niveatus* | Epinephelidae | No | 2016 | 49 | Yes | |
| Black Grouper | *Mycteroperca bonaci* | Epinephelidae | Yes | 2010 | 19 | Yes | |
| Yellowmouth Grouper | *Mycteroperca interstitialis* | Epinephelidae | [1]No | 2016 | 49 | Yes | |
| Gag Grouper | *Mycteroperca microlepis* | Epinephelidae | Yes | 2017 | 33 | Yes | |
| Scamp | *Mycteroperca phenax* | Epinephelidae | Yes | 2021 | 68 | Yes | |
| Yellowfin Grouper | *Mycteroperca venenosa* | Epinephelidae | [1]No | | | Yes | |
| Mutton Snapper | *Lutjanus analis* | Lutjanidae | Yes | 2008 | 15 | | |
| Red Snapper | *Lutjanus campechanus* | Lutjanidae | No | 2018 | 52 | | |
| Cubera Snapper | *Lutjanus cyanopterus* | Lutjanidae | [1]No | | | | |
| Vermilion Snapper | *Rhomboplites aurorubens* | Lutjanidae | No | 2020 | 67 | | |
| Gray Triggerfish | *Balistes capriscus* | Balistidae | No | 2019 | 62 | | |
| Greater Amberjack | *Seriola dumerili* | Carangidae | Yes | 2016 | 33 | | |
| Almaco Jack | *Seriola rivoliana* | Carangidae | Yes | 2016 | 49 | | |
| Hogfish | *Lachnolaimus maximus* | Labridae | No | 2018 | 37 | | |
| Tilefish | *Lopholatilus chamaeleonticeps* | Malacanthidae | No | 2011 | 22 | Yes | |
| King Mackerel | *Scomberomorus cavalla* | Scombridae | No | 2014 | 38 | | |
| Spanish Mackerel | *Scomberomorus maculatus* | Scombridae | No | 2013 | 28 | | |
| Southern Flounder | *Paralichthys lethostigma* | Paralichthyidae | Yes | NFM | | | |
| Black Drum | *Pogonias cromis* | Sciaenidae | Yes | NFM | | | |
| Red Drum | *Sciaenops ocellatus* | Sciaenidae | Yes | 2016 | 49 | | Commercial |

| | | | | |
|---|---|---|---|---|
| Spotted Seatrout | *Cynoscion nebulosus* | Sciaenidae | No | NFM |
| Sheepshead | *Archosargus probatocephalus* | Sparidae | Yes | NFM |

[1] Species marked yes were modelled or considered in Grüss et. al. (2018a) but those footnoted had insufficient data to model.

[2] Year (and number) of most recent SEDAR stock assessment for GOM stock; NFM indicates species that are not federally managed.

[3] Species managed under Individual Fishing Quotas (IFQ) in the GOM.

[4] Species for which fishing is prohibited totally, or only for commercial harvest.

**Table 2.** Documented fish spawning aggregations in the U.S. Gulf of Mexico. Sites are mapped by number in Fig. 1.

| Site Number (Fig. 1) | Site Name | Shelf position | Management status | Characterization status | Goliath grouper | Black grouper | Gag | Scamp | Mutton snapper | Cubera snapper | Greater amberjack | Spotted seatrout | Black drum | Red drum | Sheepshead | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Documented FSAs: Species at Sites | | | | | | | | | | | |
| 1 | Corpus Christi Pass, TX | C | 3 | 3 | | | | | | | | | X | X | | 1 |
| 2 | Port Aransas | C | 3 | 2 | | | | | | | | X | X | X | X | 2 |
| 3 | Galveston Channel, TX | C | 3 | 2 | | | | | | | | X | X | X | X | 3 |
| 4 | Bucaneer Rig, TX | MS | 3 | 2 | | | | | | | | | | | X | 4 |
| 5 | Barataria Pass, LA | C | 3 | 3 | | | | | | | | X | X | | | 5 |
| 6 | East Timbalier Pass, LA | C | 3 | 3 | | | | | | | | X | X | | | 5 |
| 7 | Caminada Pass, LA | C | 3 | 3 | | | | | | | | X | X | | | 5 |
| 8 | Mobile Point, AL | C | 3 | 3 | | | | | | | | | X | X | | 6 |
| 9 | Tampa Bay, FL | C | 3 | 1 | | | | | | | | X | | X | | 7, 8 |
| 10 | Wayne's Lump | SE | 3 | 2 | | | | | | X | | | | | | 3 |
| 11 | Madison Swanson | SE | 1 | 1 | | | X | X | | | | | | | | 9, 10, 11 |
| 12 | Fantastico wreck | MS | 3 | 3 | X | | | | | | | | | | | 12, 13, 14 |
| 13 | Stoney ferry boat wreck | MS | 3 | 3 | X | | | | | | | | | | | 13, 14 |
| 14 | Patrol boat wreck | MS | 3 | 3 | X | | | | | | | | | | | 13 |
| 15 | Shrimp boat wreck | MS | 3 | 3 | X | | | | | | | | | | | 13 |
| 16 | Tower | MS | 3 | 3 | X | | | | | | | | | | | 13 |
| 17 | Californian wreck | MS | 3 | 3 | X | | | | | | | | | | | 13 |
| 18 | Western Dry Rocks, FL | SE | 3 | 3 | X | | | | X | | | | | | | 13,15 |
| 19 | Warsaw Hole | SE | 1 | 3 | | | | | | | X | | | | | 16, 17 |
| 20 | Tortugas Banks | SE | 3 | 3 | | X | | | | | | | | | | 13, 18 |
| 21 | Riley's Hump | SE | 1 | 1 | | X | | | X | X | | | | | | 18, 19, 20 |
| 22 | Shrimp boat wreck | MS | 3 | 3 | X | | | | | | | | | | | 12, 13 |

**Legend**

| Shelf position | Management Status (1-3) | Characterization status (1-3) |
|---|---|---|
| C = Coastal | 1 Site closed all year | 1 Site well mapped and characterized |
| MS = Mid Shelf | 2 Site closed part of the year | 2 Some recent mapping or characterization |
| SE = Shelf Edge | 3 No spatial closure | 3 Poor or outdated map or characterization |
| | X Documented FSA | |


**References**

1 Pearson 1928
2 Holt 2008; Erisman unpublished data
3 W. Werner, pers. comm.; Heyman unpublished
4 Gallaway and Martin 1980
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7 Lowerre-Barbieri et al. 2013; 2016
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9 Coleman et al. 1996
10 Coleman et al. 2011
11 Koenig et al. 2000
12 Mann et al. 2009
13 D. DeMaria log book
14 Koenig et al. 2016
15 Bullock histology samples; D. DeMaria log book
16 B. Venura, pers. comm.
17 SAFMC 2017
18 Lindeman et al. 2000
19 Burton et al. 2005
20 Feeley et al. 2018

**Table 3.** Spawning season of 28 species of marine and coastal fish species from the U.S. Gulf of Mexico (GOM). Grey indicates the extent of the spawning season while black indicates the peak spawning months. The red outlines indicate seasonal fisheries closures for A) the recreational sector and B) the commercial sector.

Table 3A. Spawning seasons in relation to recreational seasonal closures in the U.S. GOM.

## Recreational Seasonal Closures

| Family | Common Name | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Epinephelidae | Speckled Hind | | | | | | | | | | | | |
| Epinephelidae | Goliath Grouper | | | | | | | | | | | | |
| Epinephelidae | Red Grouper | | | | | | | | | | | | |
| Epinephelidae | Nassau Grouper | | | | | | | | | | | | |
| Epinephelidae | Yellowedge Grouper | | | | | | | | | | | | |
| Epinephelidae | Warsaw Grouper | | | | | | | | | | | | |
| Epinephelidae | Snowy Grouper | | | | | | | | | | | | |
| Epinephelidae | Black Grouper | | | | | | | | | | | | |
| Epinephelidae | Yellowmouth Grouper | | | | | | | | | | | | |
| Epinephelidae | Gag | | | | | | | | | | | | |
| Epinephelidae | Scamp | | | | | | | | | | | | |
| Epinephelidae | Yellowfin Grouper | | | | | | | | | | | | |
| Lutjanidae | Mutton Snapper | | | | | | | | | | | | |
| Lutjanidae | Red Snapper | | | | | | | | | | | | |
| Lutjanidae | Cubera Snapper | | | | | | | | | | | | |
| Lutjanidae | Vermilion Snapper | | | | | | | | | | | | |
| Balistidae | Gray Triggerfish | | | | | | | | | | | | |
| Carangidae | Greater Amberjack | | | | | | | | | | | | |
| Carangidae | Almaco Jack | | | | | | | | | | | | |
| Labridae | Hogfish | | | | | | | | | | | | |
| Malacanthidae | Tilefish | | | | | | | | | | | | |
| Scombridae | King Mackerel | | | | | | | | | | | | |
| Scombridae | Spanish Mackerel | | | | | | | | | | | | |
| Paralichthyidae | Southern Flounder | | | | | | | | | | | | |
| Sciaenidae | Black Drum | | | | | | | | | | | | |
| Sciaenidae | Red Drum | | | | | | | | | | | | |
| Sciaenidae | Spotted Seatrout | | | | | | | | | | | | |
| Sparidae | Sheepshead | | | | | | | | | | | | |

Table 3B. Spawning seasons in relation to commercial seasonal closures in the U.S. GOM

## Commercial Seasonal Closures

| Family | Common Name | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Epinephelidae | Speckled Hind | | | | | | | | | | | | |
| Epinephelidae | Goliath Grouper | | | | | | | | | | | | |
| Epinephelidae | Red Grouper | | | | | | | | | | | | |
| Epinephelidae | Nassau Grouper | | | | | | | | | | | | |
| Epinephelidae | Yellowedge Grouper | | | | | | | | | | | | |
| Epinephelidae | Warsaw Grouper | | | | | | | | | | | | |
| Epinephelidae | Snowy Grouper | | | | | | | | | | | | |
| Epinephelidae | Black Grouper | | | | | | | | | | | | |
| Epinephelidae | Yellowmouth Grouper | | | | | | | | | | | | |
| Epinephelidae | Gag | | | | | | | | | | | | |
| Epinephelidae | Scamp | | | | | | | | | | | | |
| Epinephelidae | Yellowfin Grouper | | | | | | | | | | | | |
| Lutjanidae | Mutton Snapper | | | | | | | | | | | | |
| Lutjanidae | Red Snapper | | | | | | | | | | | | |
| Lutjanidae | Cubera Snapper | | | | | | | | | | | | |
| Lutjanidae | Vermilion Snapper | | | | | | | | | | | | |
| Balistidae | Gray Triggerfish | | | | | | | | | | | | |
| Carangidae | Greater Amberjack | | | | | | | | | | | | |
| Carangidae | Almaco Jack | | | | | | | | | | | | |
| Labridae | Hogfish | | | | | | | | | | | | |
| Malacanthidae | Tilefish | | | | | | | | | | | | |
| Scombridae | King Mackerel | | | | | | | | | | | | |
| Scombridae | Spanish Mackerel | | | | | | | | | | | | |
| Paralichthyidae | Southern Flounder | | | | | | | | | | | | |
| Sciaenidae | Black Drum | | | | | | | | | | | | |
| Sciaenidae | Red Drum | | | | | | | | | | | | |
| Sciaenidae | Spotted Seatrout | | | | | | | | | | | | |
| Sparidae | Sheepshead | | | | | | | | | | | | |

**Table 4.** Rubric for the scaled levels of management used in Table 5. Scores range between 1 (high), 2 (medium), 3 (low), to 4 (no management).

| Management Type | Measure of management | Scoring Rubric | | | |
|---|---|---|---|---|---|
| Catch and Effort Limits | Number of regulations | 5 | 4 | 1-3 | 0 |
| Gear Limitations | Number of legal gear types | 0-1 | 3-5 | 6-8 | 9+ |
| Seasonal Restrictions | Catch restrictions during spawning | Full spawning season closure | Seasonal closure during peak spawning | Seasonal closure not during spawning | No seasonal closures |
| Site Closures | Spatial closure of spawning sites | Site closed all year | Site closed part of the year | Restricted gear in designated sites | No site closures |
| Level of Management (score) | | High (1) | Medium (2) | Low (3) | None (4) |

**Table 5**. Management status for the 28 species evaluated in this study. Values reported are scaled from 1 (high level of management) to 4 (no management) based on the scoring rubric provided in Table 4. Values in federal columns are based on totals, while values in the state columns are calculated as the average from each of the five U.S. Gulf of Mexico states.

| | | | Federal Management Measures | | | | State Management Measures (Mean Value of 5 Gulf States) | | | | Overall Level of Management | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| FMP Category | Common Name | Scientific Name | Catch and Effort | Gear | Seasonal | Site Closures | Catch and Effort | Gear | Seasonal | Site Closures | Federal (Mean) | State (Mean) | Overall (Mean) |
| Reef Fish | Speckled Hind | *Epinephelus drummondhayi* | 3 | 3 | 4 | 3 | 3 | 3 | 4 | 4 | 3 | 4 | 3 |
| Reef Fish | Goliath Grouper | *Epinephelus itajara* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Reef Fish | Red Grouper | *Epinephelus morio* | 2 | 3 | 4 | 3 | 3 | 3 | 2 | 4 | 3 | 3 | 3 |
| Reef Fish | Nassau Grouper | *Epinephelus striatus* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Reef Fish | Yellowedge Grouper | *Hyporthodus flavolimbatus* | 3 | 3 | 4 | 3 | 4 | 3 | 4 | 4 | 3 | 4 | 4 |
| Reef Fish | Warsaw Grouper | *Hyporthodus nigritus* | 3 | 3 | 4 | 3 | 4 | 3 | 4 | 4 | 3 | 4 | 4 |
| Reef Fish | Snowy Grouper | *Hyporthodus niveatus* | 3 | 3 | 4 | 3 | 4 | 3 | 4 | 4 | 3 | 4 | 4 |
| Reef Fish | Black Grouper | *Mycteroperca bonaci* | 2 | 3 | 4 | 3 | 3 | 3 | 2 | 4 | 3 | 3 | 3 |
| Reef Fish | Yellowmouth Grouper | *Mycteroperca interstitialis* | 3 | 3 | 4 | 3 | 4 | 3 | 4 | 4 | 3 | 4 | 4 |
| Reef Fish | Gag Grouper | *Mycteroperca microlepis* | 2 | 3 | 4 | 3 | 2 | 3 | 2 | 4 | 3 | 3 | 3 |
| Reef Fish | Scamp | *Mycteroperca phenax* | 2 | 3 | 4 | 3 | 3 | 3 | 4 | 4 | 3 | 4 | 3 |
| Reef Fish | Yellowfin Grouper | *Mycteroperca venenosa* | 2 | 3 | 4 | 3 | 3 | 3 | 2 | 4 | 3 | 3 | 3 |
| Reef Fish | Mutton Snapper | *Lutjanus analis* | 3 | 3 | 4 | 3 | 3 | 3 | 4 | 4 | 3 | 4 | 3 |
| Reef Fish | Red Snapper | *Lutjanus campechanus* | 2 | 3 | 4 | 3 | 2 | 3 | 4 | 4 | 3 | 3 | 3 |
| Reef Fish | Cubera Snapper | *Lutjanus cyanopterus* | 3 | 3 | 4 | 3 | 3 | 3 | 4 | 4 | 3 | 4 | 3 |
| Reef Fish | Vermilion Snapper | *Rhomboplites aurorubens* | 3 | 3 | 4 | 3 | 3 | 3 | 4 | 4 | 3 | 4 | 3 |
| Reef Fish | Gray Triggerfish | *Balistes capriscus* | 1 | 4 | 2 | 3 | 2 | 3 | 2 | 4 | 3 | 3 | 3 |
| Reef Fish | Greater Amberjack | *Seriola dumerili* | 1 | 4 | 3 | 3 | 3 | 3 | 2 | 4 | 3 | 3 | 3 |
| Reef Fish | Almaco Jack | *Seriola rivoliana* | 4 | 4 | 4 | 3 | 4 | 3 | 4 | 4 | 4 | 4 | 4 |
| Reef Fish | Hogfish | *Lachnolaimus maximus* | 3 | 4 | 4 | 3 | 3 | 3 | 4 | 4 | 4 | 4 | 4 |
| Reef Fish | Tilefish | *Lopholatilus chamaeleonticeps* | 4 | 4 | 4 | 3 | 4 | 3 | 4 | 4 | 4 | 4 | 4 |
| Coastal Migratory Pelagics | King Mackerel | *Scomberomorus cavalla* | 1 | 2 | 4 | 3 | 2 | 3 | 4 | 4 | 3 | 3 | 3 |
| Coastal Migratory Pelagics | Spanish Mackerel | *Scomberomorus maculatus* | 2 | 2 | 4 | 3 | 3 | 3 | 4 | 4 | 3 | 4 | 3 |
| Not Federally Managed | Southern Flounder | *Paralichthys lethostigma* | 4 | 4 | 4 | 4 | 3 | 3 | 4 | 4 | 4 | 4 | 4 |
| Not Federally Managed | Black Drum | *Pogonias cromis* | 4 | 4 | 4 | 4 | 3 | 3 | 4 | 4 | 4 | 4 | 4 |
| Red Drum | Red Drum | *Sciaenops ocellatus* | 1 | 1 | 1 | 1 | 1 | 2 | 4 | 4 | 1 | 3 | 2 |
| Not Federally Managed | Spotted Seatrout | *Cynoscion nebulosus* | 4 | 4 | 4 | 4 | 1 | 2 | 4 | 4 | 4 | 3 | 3 |
| Not Federally Managed | Sheepshead | *Archosargus probatocephalus* | 4 | 4 | 4 | 4 | 3 | 3 | 4 | 4 | 4 | 4 | 4 |

## Figure Captions

**Fig. 1.** Documented fish spawning aggregation (FSA) sites in the U.S. Gulf of Mexico. Site numbers and species at each site are detailed in Table 2. Locations are approximate and randomly offset to obscure the actual locations. The FSAs are divided into three main groups: coastal, shelf edge, and mid-shelf goliath grouper (*Epinephelus itajara*) sites. Coastal species, including sheepshead (*Archosargus probatocephalus*), spotted seatrout (*Cynoscion nebulosus*), red drum (*Sciaenops ocellatus*), and black drum (*Pogonias cromis*), form FSAs at or near the mouths of coastal embayments and river systems (green dots; FSA sites 1-9). Goliath grouper aggregate around mid-shelf structures such as radio towers and shipwrecks (orange dots; FSA sites 12-18 and 22). Shelf-edge spawning species include cubera snapper (*Lutjanus cyanopterus*), mutton snapper (*L. analis*), black grouper (*Mycteroperca bonaci*), gag (*M. microlepis*), and scamp (*M. phenax*) (red dots, FSA sites 10, 11; 19-21). The existing and expansion area of the Flower Garden Banks National Marine Sanctuary is marked as FGB area and the area near Pulley Ridge is labelled at PR.

**Fig. 2.** Areas of fish spawning aggregations (FSAs) of coastal species and snappers-groupers-jacks predicted by the species distribution models (SDMs) developed in Grüss et al. (2018a), and probabilities of encounter of goliath grouper (*Epinephelus itajara*) predicted by the SDM developed in Grüss et al. (2018b). Likelihood of FSA occurrence is scaled as an index ranging from 1 (low) to 6 (high) for coastal species and snappers-groupers-jacks. Coastal species modeled include red drum (*Sciaenops ocellatus*), black drum (*Pogonias cromis*), sheepshead (*Archosargus probatocephalus*) and southern flounder (*Paralichthys lethostigma*). Snappers-groupers-jacks modeled include mutton snapper (*Lutjanus analis*), yellowedge grouper

(*Hyporthodus flavolimbatus*), Warsaw grouper (*H. nigritus*), scamp (*Mycteroperca phenax*), gag (*M. microlepis*), black grouper (*M. bonaci*), greater amberjack (*Seriola dumerili*) and almaco jack (*S. rivoliana*). Probability of encounter rather than likelihood of FSA occurrence is mapped for goliath grouper (*Epinephelus itajara*), because the data available for the species did not allow to distinguish between spawners and non-spawners. FSA sites documented empirically in this study (Fig.1; Table 2) are overlaid on prediction maps.

**Fig. 3.** Boxplot of model-predicted Z-score standardized fish spawning aggregation (FSA) indices for coastal species and snappers-groupers-jacks and boxplot of model-predicted Z-score standardized probabilities of encounter for goliath grouper (*Epinephelus itajara*). Positive Z-scores indicate consistency between the locations of FSA sites documented in this study and the potential multi-species FSA areas predicted from species distribution models in Grüss et al. (2018a, 2018b). Higher Z-scores are indicative of higher consistency between empirical results and model predictions.

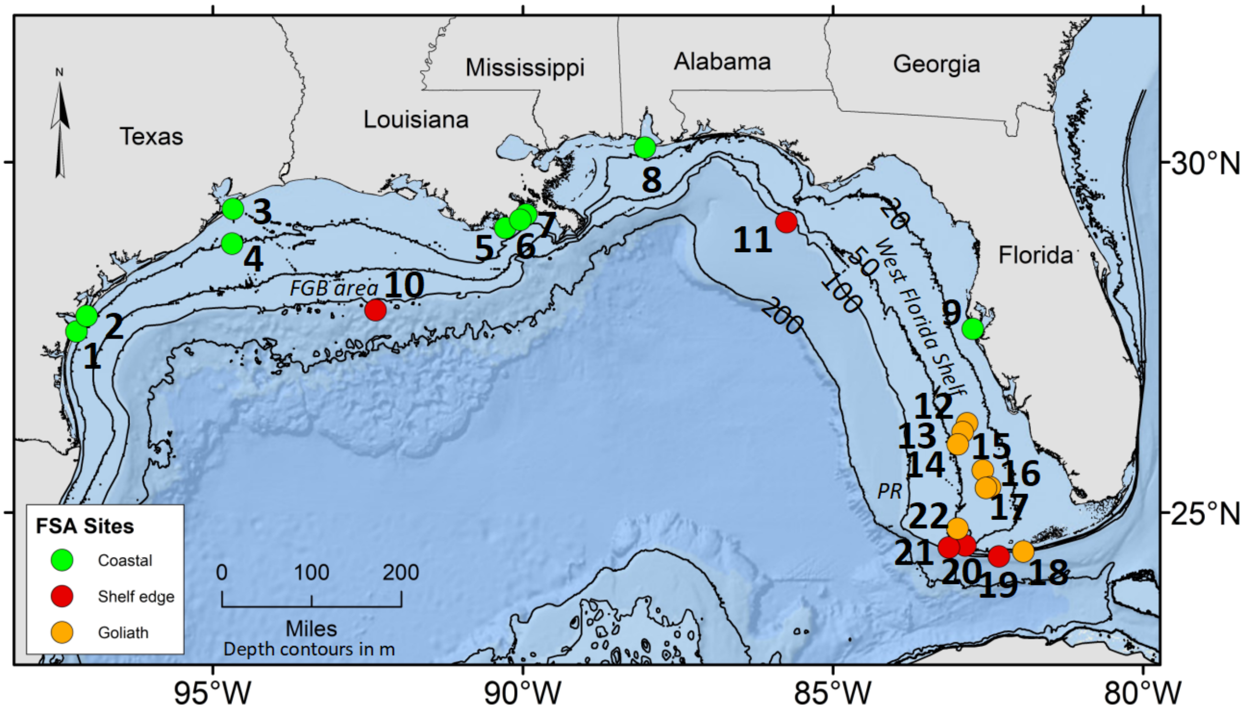
Mississippi
Alabama
Georgia
Texas
Louisiana
Florida
30°N
25°N
95°W
90°W
85°W
80°W
FGB area
West Florida Shelf
PR
20
50
100
200
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
FSA Sites
Coastal
Shelf edge
Goliath
0
100
200
Miles
Depth contours in m
N

**Fig. 1**

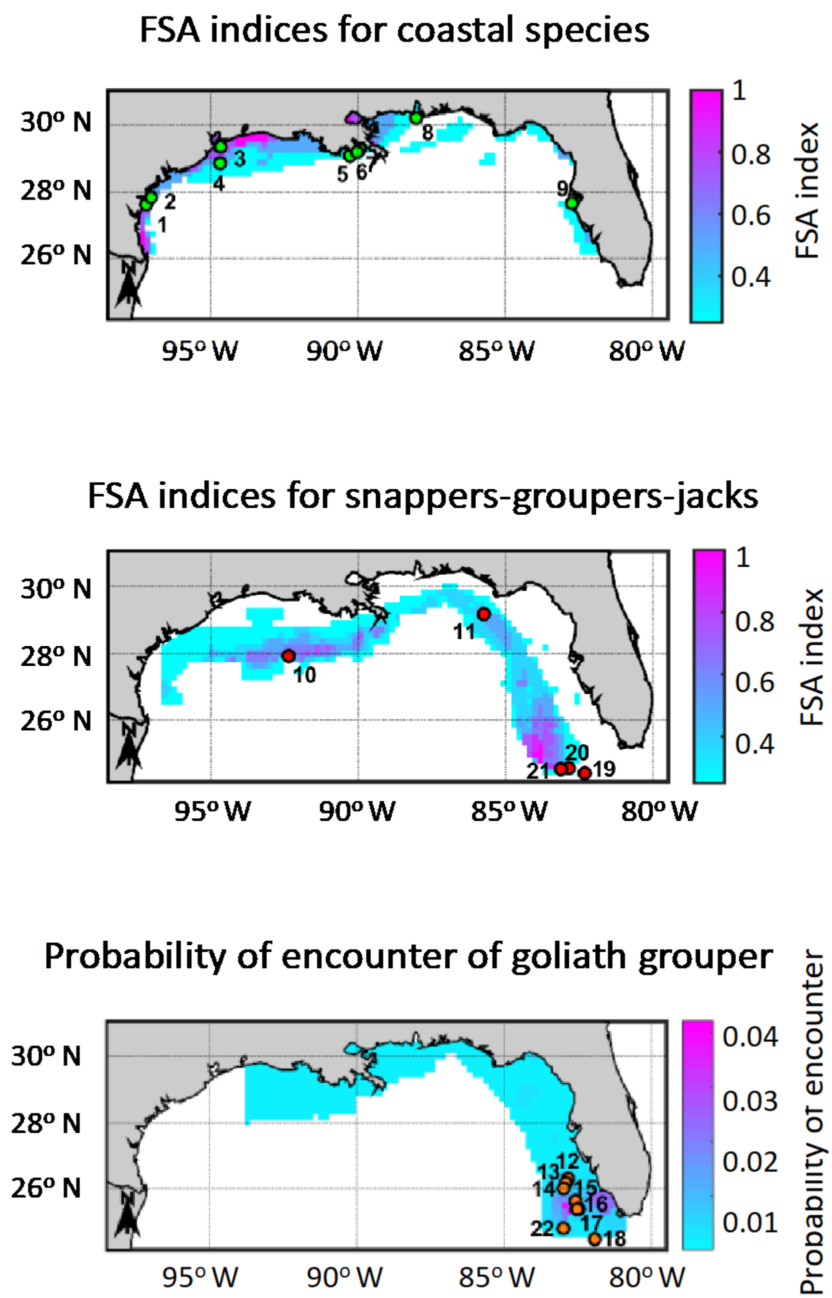
FSA indices for coastal species
30° N
28° N
26° N
95° W
90° W
85° W
80° W
FSA index
1
0.8
0.6
0.4
1
2
3
4
5
6
7
8
9
FSA indices for snappers-groupers-jacks
30° N
28° N
26° N
95° W
90° W
85° W
80° W
FSA index
1
0.8
0.6
0.4
10
11
19
20
21
Probability of encounter of goliath grouper
30° N
28° N
26° N
95° W
90° W
85° W
80° W
Probability of encounter
0.04
0.03
0.02
0.01
12
13
14
15
16
17
18
22

**Fig 2.**

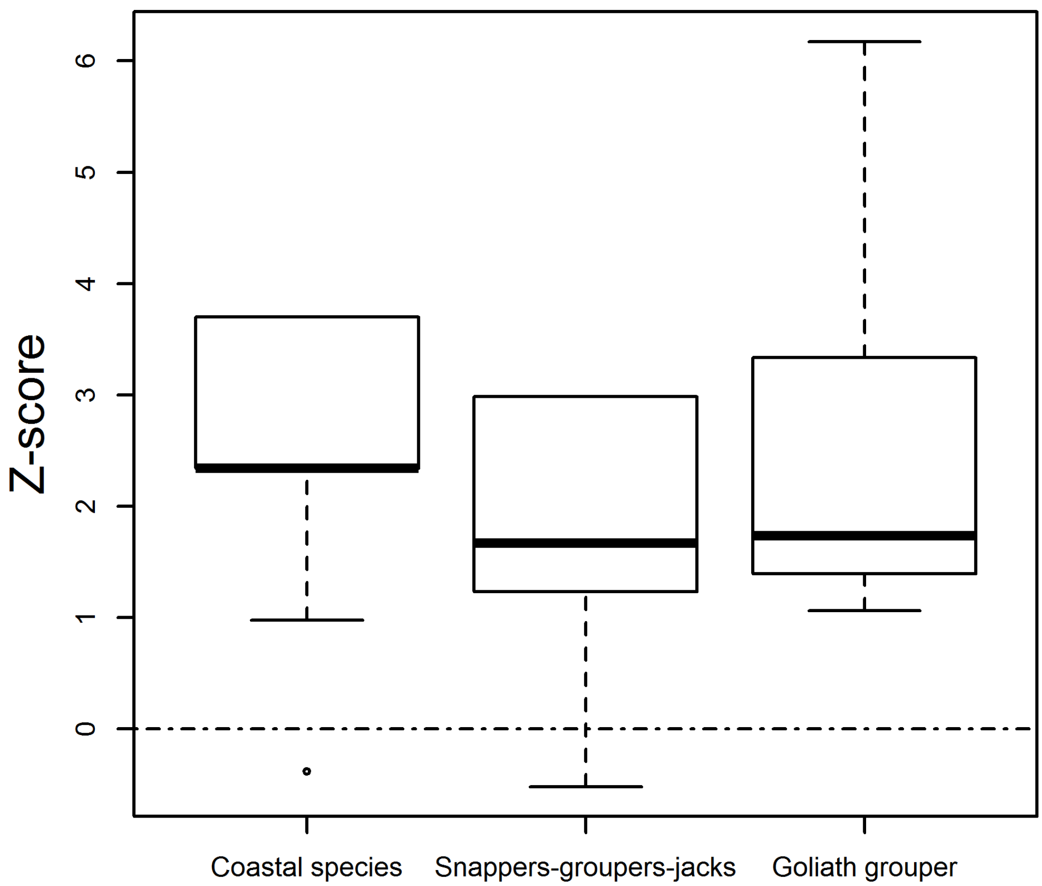
Z-score
0
1
2
3
4
5
6
Coastal species
Snappers-groupers-jacks
Goliath grouper

**Fig. 3**