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Review Article

A Review of Grouper Fisheries Management in the Southeastern and Caribbean U.S.: Challenges, Successes, and Future Directions

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Manuel Coffill-Rivera[1,2]

1. Stokes School of Marine and Environmental Sciences, University of South Alabama, United States; 2. Dauphin Island Sea Lab, Dauphin Island, United States

Groupers (Epinephelidae) are ecologically important mesopredators that support valuable fisheries across the globe. Many groupers display slow growth and maturity, high longevity, ontogenetic habitat shifts, spawning-related migrations and aggregations, and protogynous hermaphroditism, which make them susceptible to overexploitation. In this review, I synthesize available information related to the management of grouper fisheries across the southeastern and Caribbean U.S. I highlight current management challenges, such as managing multispecies reef fish fisheries with growing recreational fishing effort. I discuss management interventions with limited success, such as establishing marine protected areas to increase the abundance of groupers that display protogynous hermaphroditism. I also highlight management successes, such as recovering historically depleted grouper stocks, and ecosystem-based considerations in grouper stock assessments. I discuss how climate change and anthropogenic effects are expected to affect groupers. Lastly, I provide examples of stakeholder involvement in monitoring and management efforts for grouper stocks. The purposes of this review are to demonstrate the complexities of managing grouper fisheries and provide a road map for future research and conservation efforts into these economically and ecologically relevant fishes within and beyond the region.

Corresponding author: Manuel E. Coffill-Rivera, manuelcoffill@gmail.com

1. Introduction

Groupers (Epinephelidae) are highly prized reef-associated mesopredators that support recreational, commercial, and artisanal fisheries across their range. They can also have important ecological roles as ecosystem engineers shaping the physical and biogenic structure[1][2][3]. Many groupers display slow growth, late maturity, high longevity, sequential hermaphroditism, ontogenetic habitat shifts, and spawning-related migrations and aggregations, which make them susceptible to overexploitation[4]. A recent global assessment of groupers indicated that 30% of species are data deficient, 12% risk extinction under current conditions, and 13% are considered near threatened[4]. Their life history, data availability,

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and population trends highlight the need to carefully consider groupers in a fisheries management context.

In this review, I present information regarding the management of grouper fisheries in the southeastern U.S. (SEUS), which is composed of the Caribbean (CAB), Gulf of Mexico (GOM), and South Atlantic (SA) subregions (Figure 1). I provide information on the history of these fisheries across the region, evidence of the complexities of managing grouper fisheries, and case studies of management challenges and successes. Lastly, I discuss the potential effects of climate change and other anthropogenically-driven perturbations on grouper fisheries and highlight technological advances to monitor these stocks. Providing species profiles is not among the goals of this review, but rather to draw enough detail from different species to emphasize the complexities of managing grouper fisheries. This synthesis aims to direct future research and conservation efforts into grouper fisheries within and beyond the SEUS that could be applied to other taxa.

Figure 1. Map depicting the U.S. Caribbean (CAB), Gulf of Mexico (GOM), and South Atlantic (SA) subregions delineated by the U.S. exclusive economic zone.

2. Relevance and Management History of Grouper Fisheries in the SEUS

In the SEUS, groupers support some of the most valuable finfish fisheries with Red Grouper *Epinephelus morio* and Gag *Mycteroperca microlepis* among the most harvested reef fishes in recreational and commercial sectors of the GOM and SA[5][6][7][8]. Harvest of groupers in the GOM can be traced back to the 1800s when settlers from the northeast U.S. traveled south to harvest Red Snapper *Lutjanus campechanus*, and groupers quickly went from bycatch to target species as the Red Snapper population declined[9][10]. In the CAB, Red Hind *E. guttatus* has a high importance in commercial fisheries[11], and Nassau Grouper *E. striatus* supported both recreational and commercial fisheries until the 1970s when severe population declines became evident[12][13][14]. In 1980, groupers were among the three most landed (by weight) families across the CAB[15]. Evidently, groupers distributed across the SEUS (or within any of the included subregions) display varying fishery relevance. As such, their degree of management can range from nonexistent (e.g., Marbled Grouper *Dermatolepis inermis*; Figure 2) to complete harvest moratorium (e.g., Nassau Grouper).

Figure 2. An elusive Marbled Grouper *Dermatolepis inermis* landed off the coast of Alabama, USA. Photo credit: M. E. Coffill-Rivera.

In the U.S., federal marine fishery resources are governed by the Magnuson Stevens Fishery Conservation and Management Act (MSA) and managed by the National Oceanographic and Atmospheric Administration's National Marine Fisheries Service (NMFS). The MSA was first passed in 1976, and among its many objectives are to prevent overfishing, rebuild overfished stocks, increase long-term economic and social benefits, and maintain a safe and sustainable seafood supply[16]. To do so, regional fishery management councils were created and tasked with constructing fishery management plans (FMPs) that comply with MSA guidelines. The MSA has undergone two revisions. First, the Sustainable Fisheries Act of 1996, which recognized the importance of healthy habitats for sustainable fisheries. Second, the MSA reauthorization of 2007, which further improved fisheries science, management, and conservation. It is important to note that the spatial application of federal fisheries management is not uniform across the SEUS subregions, as federal fisheries regulations in the SA start at three miles off the coast, and a mix of three and nine miles off the coast in the GOM and CAB. For the purposes of this review, I will provide a generalized history of FMPs in the SEUS as it pertains to grouper fisheries. Any discussion regarding marine protected areas (MPAs) will be purposely saved for the case studies throughout the review.

In the SA, the Snapper-Grouper FMP was implemented in 1983[17]. At the time, a substantial amount of reef fishes distributed across the SA were exhibiting growth overfishing[17], or harvesting below the size that would produce maximum sustainable yield (MSY) or maximize yield-per-recruit[18]. To alleviate this, the FMP introduced a 12" minimum size limit to a suite of reef fishes, including two groupers (Red Grouper and Nassau Grouper). An amendment implemented in 1999 brought minimum size limits up to ≥20" for many groupers. The amendments listed were selectively picked to highlight some of the management efforts directed at sustainably managing SA grouper stocks. For a comprehensive history of amendments to the SA Snapper-Grouper FMP visit https://www.fisheries.noaa.gov/action/south-atlantic-snapper-grouper-historical-amendments-and-rulemaking-1983-2017.

The GOM Reef Fish FMP was implemented in 1984 and included gear restrictions to assist in rebuilding declining reef fish stocks[19]. In 1990, a 20" minimum size limit was implemented for multiple groupers (Gag, Nassau Grouper, Red Grouper, Black Grouper *M. bonaci*, and Yellowfin Grouper *M. venenosa*). A regulatory amendment implemented in 2000 introduced increases to Gag minimum size limits (from 20” to 22” for recreational and 24” for commercial sectors) and implemented the first two MPAs directed at rebuilding the Gag stock (further discussed in section 3.2). Harvest of multiple groupers during their spawning season was banned for both the commercial and recreational sectors during the 2000s. A significant management change to the commercial grouper fishery was implemented in 2010 through individual fishing quotas (IFQ), which greatly improved data collection in this sector, but has been accompanied by somewhat high levels of concern and dissatisfaction among participants[20]. To date, a substantial number of amendments to the GOM Reef Fish FMP involve changes to grouper stocks, particularly Red Grouper and Gag. For a comprehensive history of the GOM Reef Fish FMP visit https://www.fisheries.noaa.gov/action/gulf-mexico-reef-fish-historical-amendments-and-rulemaking-1983-2017.

The CAB Reef Fish FMP was implemented in 1985 and focused on fish trap requirements and a minimum size limit on Nassau Grouper[15]. The first amendment was implemented in 1990 and included a prohibition on the take and possession of Nassau Grouper and introduced a seasonal spatial closure of a Red Hind spawning area, known as Red Hind Bank Marine Conservation District. This seasonal spatial closure became the first MPA specifically directed at improving population levels of a grouper species in the SEUS and was permanently closed to fishing in 1999[21][22]. Additional seasonal spatial closures during the Red Hind spawning season were implemented across the CAB during 1993, 1996, and 2005 (further discussed in section 4.1). Seasonal harvest closures during the spawning season were implemented for a suite of grouper species in 2005. In 2022, the CAB-wide FMP transitioned to island-based (Puerto Rico, St. Thomas and St. John, and St. Croix) plans. For a comprehensive history of the CAB Reef Fish FMP visit https://www.caribbeanfmc.com/fishery-management/fishery-management-plans.

3. Complexities of Managing Grouper Fisheries

3.1. Multispecies Reef Fish Fisheries

In the SEUS, groupers form part of diverse multispecies reef fish fisheries composed of species with varying life histories and exploitation histories. These open access fisheries provide year-round harvest opportunities for fishers as managed species have varying temporal management measures (e.g., seasonal closures). Due to non-selective (or low selectivity) fishing gear and the diversity of species sharing reef habitats, avoiding species closed to harvest is difficult, resulting in high levels of bycatch and mandatory discards. The latter induces discard mortality, which results from depredation (predators consuming fishers’ hooked fish), physical injury, or handling stress[23]. In high magnitudes, this source of mortality not only undermines minimum size limits but can also prevent meeting stock rebuilding targets. For example, the high discard mortality observed in GOM Gag has been linked to preventing stock rebuilding and potentially inducing recruitment overfishing[24].

Discards can be considered a significant source of mortality in groupers as many species are associated with deep waters either throughout ontogeny (e.g., deepwater groupers) or during adult stages (e.g., Gag), which have been linked to increasing physical injuries (e.g., barotrauma)[25]. The MSA National Standard 9 mandates that bycatch and discard mortality be minimized; however, this has proven extremely difficult to achieve in the SEUS reef fish fisheries. It is worth noting that significant efforts have gone into understanding the mechanisms of discard mortality[26][27][28] and increasing public awareness of the utility of descender devices to mitigate discard mortality (https://returnemright.org/). Recent management changes have made it a requirement for GOM and SA reef fish fishers to carry a descending device on board[29][30], and this action is currently being proposed for the CAB[31].

A substantial increase in recreational effort has been observed across the GOM and Atlantic coasts in the last 40 years (Figure 3). In addition, increases in recreational landings have been reported for both the GOM and SA[32]. Due to recreational sector characteristics, such as large user group size and distributed effort that is difficult to track, recreational data contain much higher uncertainty than that of a commercial sector with mandatory reporting requirements, as observed in the GOM commercial grouper fisheries. Consequently, uncertainty in landings can increase as the recreational sector becomes more relevant unless recreational data collection programs continue to improve. Recent explorations of management strategies to rebuild the

SA Red Snapper stock suggest that restricting recreational effort in the reef fish fishery (spatially and/or temporally) could help meet stock rebuilding goals for Red Snapper and associated reef fishes[33]. In an exploration of management strategies for the overfished SA Black Sea Bass *Centropristis striata* stock, only a reduction in fishing mortality, and by extension effort, would significantly reduce the number of dead discards, which has been identified as an objective to rebuild the stock[34]. Restricting recreational effort continues to be a promising avenue for rebuilding stocks, but, this must be weighed against the socioeconomic benefits that recreational fisheries provide.

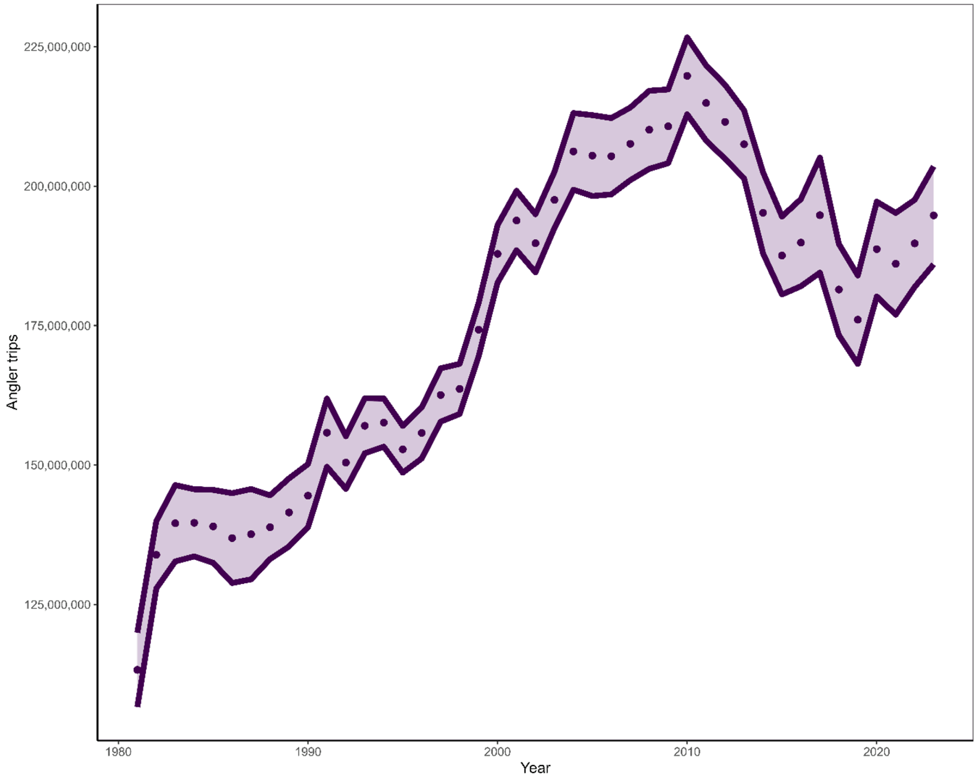

Figure 3. Number of recreational saltwater angler trips across the U.S. Gulf of Mexico and Atlantic coasts. Points denote the yearly estimate while lines bound the 95% confidence intervals. Data are publicly available at https://www.fisheries.noaa.gov/data-tools/recreational-fisheries-statistics-queries.

Allocations (the distribution of the opportunity to participate in a fishery among user groups or individuals) of many SEUS reef fish stocks have changed over time. Increases and decreases in allocation are observed in the recreational and commercial sectors, respectively. This is especially true for GOM Red Grouper and GOM Gag, which have recently undergone increases in the recreational sector[35][36]. As the GOM Red Grouper fishery was historically dominated by the commercial sector, these changes have steered commercial stakeholders to legally prosecute NMFS claiming that multiple MSA National Standards are not being met (https://www.nationalfisherman.com/gulf-south-atlantic/federal-appeals-court-orders-remand-of-red-grouper-allocations). Managing vulnerable groupers within an already complex multispecies reef fish fishery with multiple user groups, discard mortality rates, and uncertainty in recreational landings and effort is a fundamental challenge faced across the region.

3.2. Protogynous Hermaphroditism

Marine reef fishes display diversity in reproductive systems represented by gonochorism, hermaphroditism, and more rarely parthenogenesis[37]. While some species are gonochoristic, hermaphroditism is most prevalent in grouper species distributed across the SEUS (Table 1). Specifically, many of these groupers display monandric protogynous hermaphroditism (protogynous hermaphroditism hereafter), where individuals are born as females, reach sexual maturity, and then transition into males (Figure 4). Environmental variables, local demography, and mortality schedules have been linked to driving/facilitating sex change in this reproductive strategy[38]. In this section, I'll discuss how groupers displaying protogynous hermaphroditism, in conjunction with other life history characteristics, are more conducive to being overexploited.

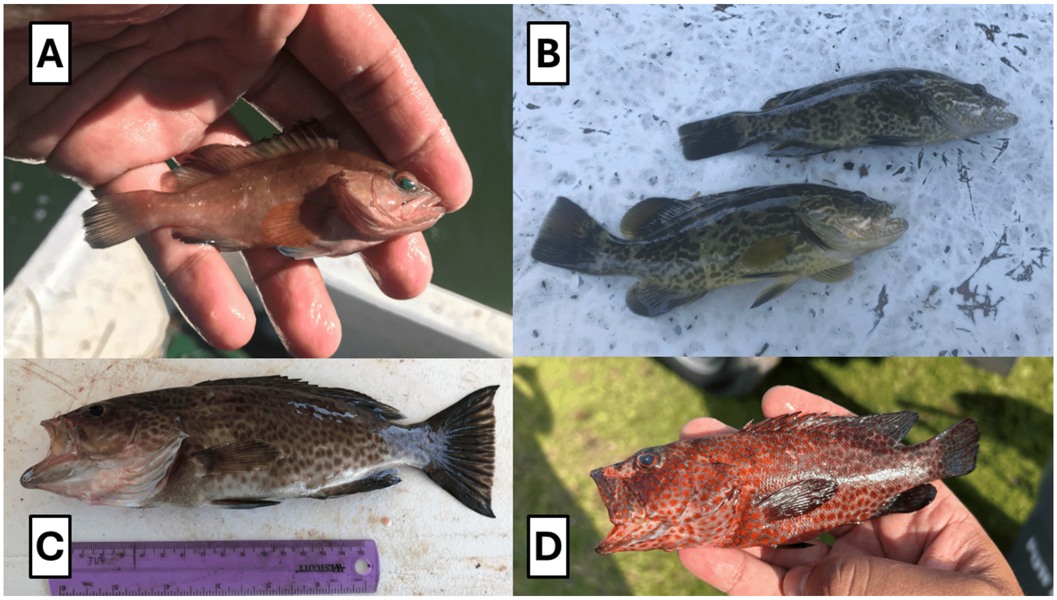

Figure 4. Examples of groupers distributed across the southeastern U.S. that display monandric protogynous hermaphroditism. (A) Juvenile Red Grouper *Epinephelus morio*. (B) Juvenile Gag *Mycteroperca microlepis*. (C) Juvenile Scamp *M. phenax*. (D) Juvenile Graysby *Cephalopholis cruentata*. Photo credits: M. E. Coffill-Rivera.

Common name	Scientific name	Longevity (y)	Reproductive strategy	Managed?	Stock assessment attempted?	Overfished and/or overfishing?
Atlantic Goliath Grouper	*Epinephelus itajara*	>30[39]	G, DPH[40]	CAB, GOM, SA	Y	CAB[41]
Black Grouper	*Mycteroperca bonaci*	>20[42]	MPH[43]	CAB, GOM, SA	Y[44]	-
Comb Grouper	*Mycteroperca acutirostris*	-	-	-	N	-
Coney	*Cephalopholis fulva*	>10[45]	MPH[46]	CAB, SA	N	-
Gag	*Mycteroperca microlepis*	>20[47]	MPH[48]	GOM, SA	Y	GOM[49], SA[50]
Graysby	*Cephalopholis cruentata*	>20[51]	MPH[51]	CAB, SA	N	-
Marbled Grouper	*Dermatolepis inermis*	-	-	-	N	-
Misty Grouper	*Hyporthodus mystacinus*	>100[52]	-	CAB, SA	N	-
Nassau Grouper	*Epinephelus striatus*	>20[13]	G[13]	CAB, GOM, SA	N	-
Red Grouper	*Epinephelus morio*	>20[53]	MPH[43]	CAB, GOM, SA	Y	SA[54]
Red Hind	*Epinephelus guttatus*	>10[11]	MPH[55]	CAB, SA	Y[56]	-
Rock Hind	*Epinephelus adscensionis*	>30[57]	MPH[58]	CAB, SA	N	-
Scamp	*Mycteroperca phenax*	>30[59]	MPH[59]	GOM, SA	Y	SA[60]
Snowy Grouper	*Hyporthodus niveatus*	>50[61]	MPH[62]	GOM, SA	Y	SA[63]
Speckled Hind	*Epinephelus drummondhayi*	>40[64]	MPH[65]	GOM, SA	Y[66]	-
Tiger Grouper	*Mycteroperca tigris*	>10[67]	MPH[68]	CAB	N	-
Yellowedge Grouper	*Hyporthodus flavolimbatus*	>80[69]	MPH[70]	CAB, GOM, SA	Y	GOM[71]
Yellowfin Grouper	*Mycteroperca venenosa*	>30[72]	MPH[73]	CAB	Y[74]	-

Common name	Scientific name	Longevity (y)	Reproductive strategy	Managed?	Stock assessment attempted?	Overfished and/or overfishing?
Yellowmouth Grouper	*Mycteroperca interstitialis*	>20[75]	MPH[75]	CAB, GOM, SA	Y[66]	-
Warsaw Grouper	*Hyporthodus nigritus*	>90[76]	-	GOM, SA	N	-

Table 1. Grouper species distributed across the southeastern and Caribbean U.S. "DPH" denotes diandric protogynous hermaphroditism, "G" denotes gonochorism, and "MPH" denotes monandric protogynous hermaphroditism. "CAB" denotes the Caribbean, "GOM" denotes the Gulf of Mexico, and "SA" denotes the South Atlantic. Integrated assessments directed at providing management advice were exclusively considered as attempted stock assessments. Integrated assessments capable of providing stock status were exclusively considered for the overfished and/or overfishing status. Brackets denote the reference.

It has long been understood that reproductive output (e.g., egg production) increases disproportionately with size/age in fish populations[77][78]. Consequently, fishing-induced size/age truncation has been shown to reduce stock resilience[79]. As such, significant management efforts are directed at conserving larger/older fish (e.g., using slot limits) to maintain sustainable spawning stock biomass levels. Protogynous hermaphrodites display dome-shaped egg production, meaning the oldest females show a reduction in egg production as energy is reallocated into sexual transition[80]. Consequently, protogynous hermaphrodites violate the hypothesis of the largest/oldest females having the highest contributions to reproductive output. Instead, size/age truncation in protogynous hermaphrodites severely depletes male sex ratios in naturally female-skewed populations, creating a unique situation of potential sperm limitation.

Decadal-scale declines in the male sex ratios of two SEUS protogynous hermaphrodites (Gag and Scamp *M. phenax*) have been documented[81][48]. Notably, both groupers display varying degrees of spawning aggregations, and this behavior in conjunction with increasing fishing pressure has been linked to the declines in male sex ratios[81]. Interestingly, another protogynous hermaphroditic grouper with significant fishing pressure (Red Grouper) has shown comparatively lighter declines in the male sex ratio, and this has been linked to its non-aggregating reproductive behavior[81]. In addition, a recent study observed low male gonadosomatic indices and milt reserves in Gag, suggesting they could actually be pair spawners, which would limit fertilization rates at low male sex ratios[48]. Whether this is a trend in other protogynous hermaphroditic groupers across the SEUS remains to be explored.

In response to the reduced GOM Gag population, the Gulf of Mexico Fishery Management Council created two seasonal MPAs in 2000 (Madison-Swanson and Steamboat Lumps) to increase stock size, followed by a third in 2009 (The Edges). Almost 25 years later, the MPAs' primary goal remains unattained. A recent study concluded that GOM Gag male sex ratio is at a historic low (5% in MPAs and 0% outside of protected areas)[48]. In addition, this study also reported increases in the age at 50% transition to male from 10.9 to 13 years, accompanied by the reduced male sex ratio, suggesting the male GOM Gag population is aging while experiencing limited recruitment[48]. Gag sexual transition does not require male presence, thus female groups traveling to shelf break spawning sites can include newly recruited males[48]. Consequently, fishing pressure inshore/mid-shelf can simultaneously remove females during peak egg production and bottleneck male recruitment. This case study highlights that MPA success can depend on its management purpose, spatial extent, species' life history, reproductive strategy, movement ecology, and surrounding context (e.g., fishery behavior and larval dispersal). It is important to note that measuring MPA effectiveness requires doing so at appropriate time frames[82], and success will be affected by enforcement and compliance[83].

Across the world, quantitative assessments are used to assess fish stocks and determine sustainable catch levels. A primary goal of these assessments is to determine reference points, such as MSY, fishing mortality at MSY (F_{MSY}), and stock size at MSY (B_{MSY}). These require knowledge of stock productivity, which is notoriously challenging to measure[84]. Stock-recruit relationships can be used to estimate B_{MSY}. However, there tends to be a lack of reliable data to estimate steepness, the parameter that controls the shape of the stock-recruit relationship and has a strong influence on stock productivity[85][86]. Due to the uncertainty in reference points derived from the stock-recruit relationship, reference point proxies, such as quantities of the spawning potential ratio (SPR; the ratio of the fished stock size compared to unfished conditions), are used[84]. In the SEUS, a 30% SPR value is the most commonly used MSY proxy to derive reference points and is the current regulation for most GOM reef fishes[87]. However, a recent simulation study indicates that F_{MSY} proxies of 40% and 50% SPRs are most probable in achieving long-term MSY for gonochoristic and hermaphroditic stocks, respectively[84]. Due to their complex life histories, protogynous hermaphrodites exhibit numerous additional vulnerabilities to fishing that may necessitate more conservative management approaches.

Recent efforts have gone into considering MSY proxy values >30% SPR for hermaphroditic grouper stocks across the SEUS. The most recent SA Scamp stock assessment, in which the stock was found to be overfished, used an F_{MSY} proxy of 40% SPR[60]. While 30% SPR was historically used for groupers across the region, management has started adopting the use of higher SPR values in assessments. For example, the latest GOM Yellowedge Grouper *H. flavolimbatus* assessment was explored under several SPR values. While the stock was deemed not overfished nor experiencing overfishing at 30% SPR, the terminal year displayed the lowest spawning stock biomass value across the assessed period[88]. Additional projections using MSY proxies of 40% SPR (adopted value) and 50% SPR both resulted in Yellowedge Grouper experiencing overfishing in the terminal year[71]. While there is no “one size fits all” answer to MSY proxy values, management should consider using SPR values ≥40% for hermaphroditic stocks and completely abandon 30%, especially since recent simulations have found that 40% SPR and similar proxies are robust to nonstationary conditions in life history[89].

Protogynous hermaphrodites provide unique case studies where traditional fisheries management techniques can fall short of providing reliable estimates of stock status. Maintaining female-specific spawning stock biomass is of primary interest when managing fish stocks. However, careful consideration must be given to male-specific spawning stock biomass when assessing protogynous hermaphrodites, as is the case with many groupers across the SEUS[90]. Many of these groupers are showing historic declines in male sex ratios, which can result in sperm limitation and stock collapse. Efforts are underway to rebuild these stocks by using MPAs and considering conservative MSY proxies in stock assessments. However, these stocks remain among the most challenging to manage and rebuild. Many SEUS hermaphroditic grouper stocks have experienced historic population declines (Figure 5). Beyond groupers, many reef fishes that support fisheries display protogynous hermaphroditism (e.g., Sparidae and Labridae). Thus, conservative management strategies should be considered for these species while balancing socioeconomic benefits (e.g., economic security).

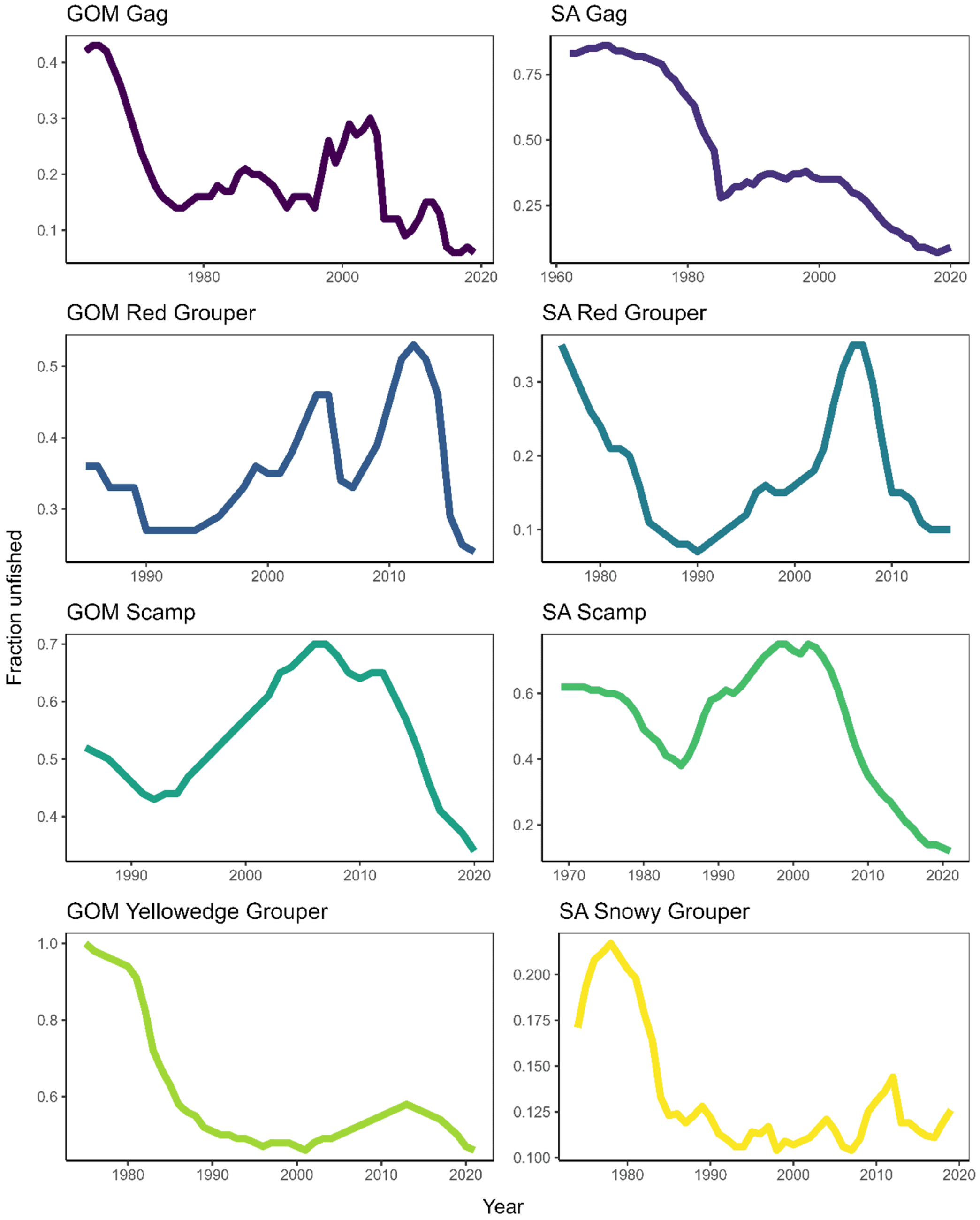

Figure 5. Population trends represented as fraction unfished for U.S. Gulf of Mexico (GOM) and South Atlantic (SA) grouper stocks that display monandric protogynous hermaphroditism assessed with integrated models. Fraction unfished for GOM stocks is measured using spawning stock biomass (except Red Grouper which used the relative number of eggs) while SA stocks are measured using total biomass. Stock assessments are publicly available at https://sedarweb.org/sedar-assessments/.

3.3. Deepwater Groupers

A significant proportion of SEUS groupers can be considered deepwater species occupying habitats at depths >100m. In the GOM and SA, Yellowedge Grouper and Snowy Grouper are the most harvested deepwater groupers (Figure 6). Deepwater groupers are especially susceptible to overexploitation as many of them show comparatively higher longevities, which are associated with slower growth, maturity, and transition rates[62][69][64][76][61]. Consequently, their lower natural mortality rates suggest comparatively lower productivity and fishing pressure can quickly cause severe population declines[91]. Additionally, most of these groupers have been confirmed to display protogynous hermaphroditism[62][70][65]. While little is known about their movement ecology, available information suggests many deepwater groupers display high site fidelity and disproportionate densities of individuals can be observed over small spatial footprints[92].

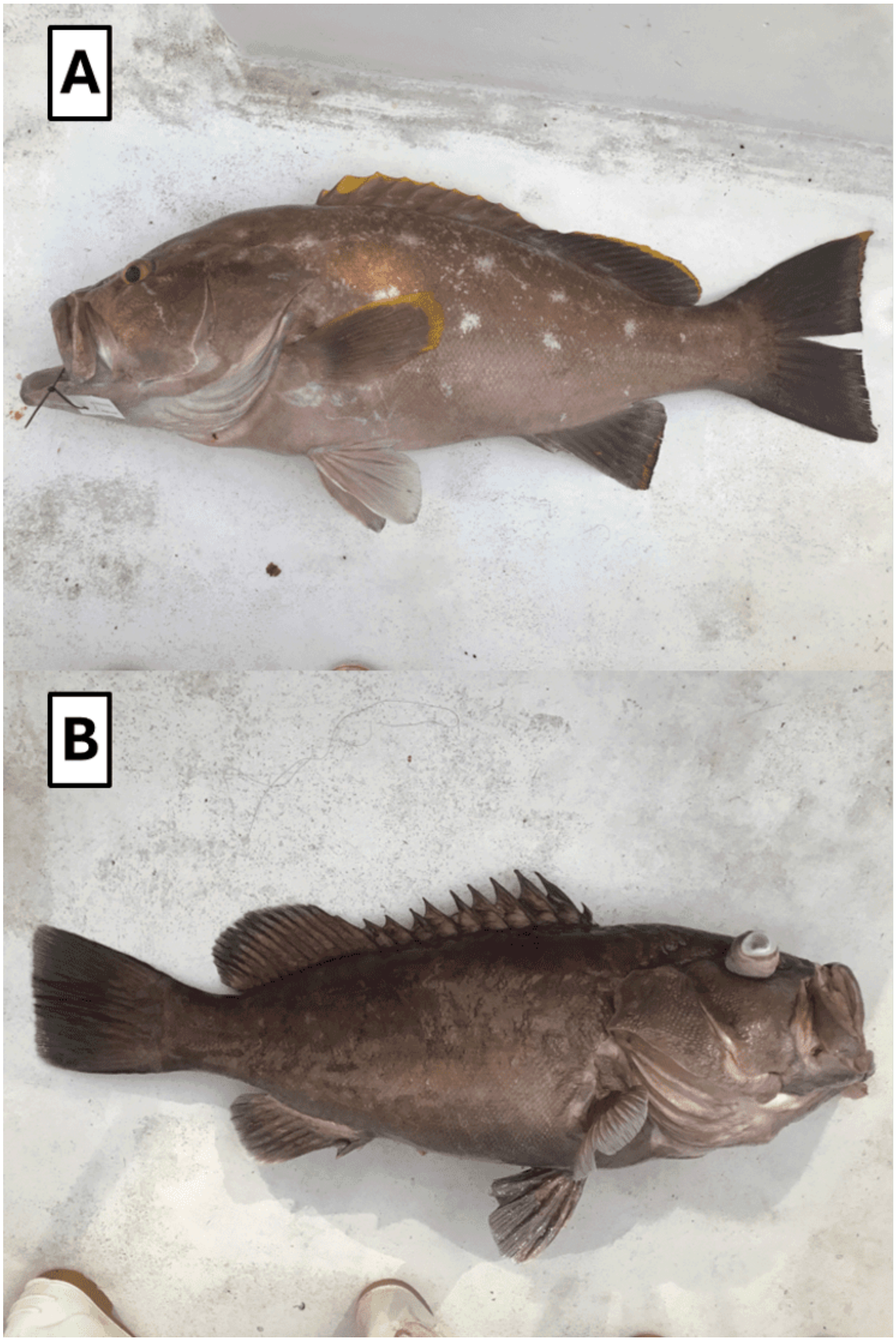

Figure 6. (A) Yellowedge Grouper *Hyporthodus flavolimbatus* and (B) Snowy Grouper *H. niveatus*, the two most landed groupers in the U.S. Gulf of Mexico and South Atlantic's deepwater grouper complex. Both species display monandric protogynous hermaphroditism. Photo credits: M. E. Coffill-Rivera.

Like the shallow-water grouper, The SEUS deepwater grouper fisheries have historically been dominated by the commercial sector but are thought to have started during the late 1900s[6][88]. The later inception is hypothesized to be due to increased management of shallow-water reef fishes in conjunction with increased fishing power (e.g., larger vessels and improved technology)[6][93]. Due to their similarity in habitat use, four species are managed under a combined deepwater grouper complex in both the GOM and SA (Yellowedge Grouper, Snowy Grouper, Speckled Hind *E. drummondhayi*, and Warsaw Grouper *H. nigritus*). Consequently, species-specific landings can vary from year to year without causing any management concerns as long as the stock annual catch limits are not exceeded (Figure 7). A recent assessment of the GOM Yellowedge Grouper, the most landed species in the GOM commercial deepwater grouper fishery (Figure 7), found the species to be experiencing overfishing in the terminal year[88]. Additionally, stakeholder feedback reporting population declines in GOM Yellowedge Grouper suggests it could be due to increased fishing power and recreational effort[94]. This leads to speculate if both of these variables in conjunction with increased harvest restrictions in comparatively "shallower water" reef fishes (e.g., Red Snapper, Greater Amberjack *Seriola dumerili*, Gray Triggerfish *Balistes capriscus*, and Gag) could be leading to increased deepwater grouper recreational landings and effort. As recreational allocations continue to increase in other groupers (e.g., Red Grouper and Gag), should we expect the same patterns for the deepwater grouper complex? These are generally considered "rare event species" in the recreational data partly due to private recreational vessels being missed by sampling programs (e.g., large vessels launching from private ramps rather than public ones where port samplers collect data). Commercial grouper landings are more accurate and precise, leading to smaller buffers between annual catch limits and annual catch targets than the recreational sector[36]. Thus, increases in the recreational deepwater grouper landings would likely be associated with increased uncertainty, and managers should consider approaches to better estimate private recreational landings coming from vessels launching from private ramps.

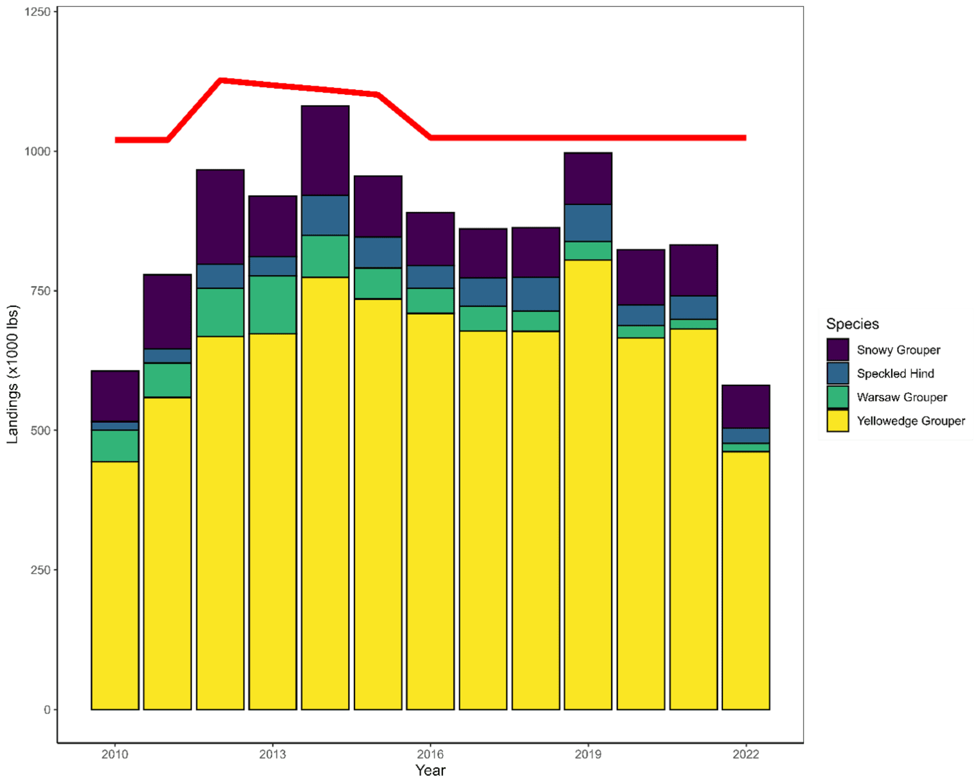

Figure 7. U.S. Gulf of Mexico commercial landings from groupers managed under the deepwater grouper complex during the individual fishing quota era. The red line denotes the complex's yearly sector-specific catch quotas. Landings are publicly available at https://noaa-sero.s3.amazonaws.com/drop-files/cs/2022_GT_AnnualReport_Final.pdf.

As reductions in the GOM Yellowedge Grouper population are evident, how possible is it to observe increased landings in other deepwater groupers, and to what scale? Many of these species have poorly understood life histories, highly uncertain or unobservable recreational landings, and display decadal-scale overexploitation. Misty Grouper *H. mystacinus* and Marbled Grouper are two species distributed across the SEUS for which their population trends are unknown and landings data are scarce. The SA Speckled Hind stock has shown signs of overexploitation since the 1970s, which was followed by reduced bag limits in 1994[65]. However, evidence suggests that the stock continued to be overexploited through the 2000s[65]. Additionally, a recent study reported low population connectivity, limited movement, and high numbers of harvested young fish in the GOM Snowy Grouper stock[95]. In attempts to help rebuild deepwater reef fishes (including groupers), the South Atlantic Fishery Management Council implemented eight deepwater MPAs in 2009[96]. To date, the investigations conducted demonstrate no evidence of the MPAs improving the status of grouper stocks[97][98]. In fact, one of these studies found that community composition within the largest of these MPAs has shifted away from groupers to other reef fishes[98]. Thus, long-term monitoring of MPAs will be important to account for long generation times observed in these long-lived species and to investigate how different fishes respond to the MPA effect.

4. Recovery of Historically Exploited Stocks?

4.1. Nassau Grouper and Red Hind

During the 1900s, Nassau Grouper was considered the most important commercial grouper across the

Caribbean[99]. Due to their aggregating behavior, where 1000s of individuals can be observed at a time, the spawning stock suffered severe fishing mortality, resulting in dramatic population declines[99]. By the 1970s, there was evidence of reductions in the density of individuals at aggregation sites and the number of aggregation sites, followed by reduced landings[99]. To facilitate recovery across the CAB, the Caribbean Fishery Management Council implemented a moratorium on Nassau Grouper in 1990. The species was also listed as threatened under the U.S. Endangered Species Act in 2016[100][101].

In the decades following the moratorium, population trends of CAB Nassau Grouper are poorly understood, but much effort has gone into investigating population dynamics. A genetic study reported evidence of genetic differentiation in Nassau Grouper subpopulations across the Caribbean region, suggesting subpopulations' spawning aggregations may be responsible for self-recruitment[102]. Juvenile Nassau Grouper habitat has not been described across the CAB[103][104][105] compared to other parts of the species' range[106][107][108], and a better understanding could assist in the designation of critical habitats to maximize juvenile recruitment and survival. While current population trends of CAB Nassau Grouper are not well described, subpopulations in other Caribbean jurisdictions are showing signs of recovery. For example, Nassau Grouper spawning aggregation sites in the Cayman Islands have displayed positive responses to >15 years of conservation efforts[14]. Unfortunately, Nassau Grouper has been reported in Puerto Rico recreational landings after the commonwealth's local moratorium, implemented in 2004[109]. Thus, population recovery efforts must include stakeholder involvement to increase compliance and provide local ecological knowledge[110]. Designation under the U.S. Endangered Species Act provides funds to conduct applied research into the species, which can facilitate efforts to conduct an updated population assessment of the CAB Nassau Grouper subpopulation. In the absence of fishery-dependent data in recent times, as is the case for Nassau Grouper, fishery-independent data is exceedingly important to monitor population trends.

Population assessments indicated that the CAB Red Hind was experiencing overexploitation during the 1980s[111][112]. An assessment in 2000 concluded that the Puerto Rico subpopulation continued to experience overexploitation throughout the 1990s[113]. Similar declines were observed in a neighboring jurisdiction[114]. Monitoring efforts during the 30 years following the implementation of the Red Hind Bank Marine Conservation District concluded that the MPA has successfully recovered its Red Hind spawning aggregation[21][115]. While current CAB-wide Red Hind population trends are unknown, a subpopulation of the species is scheduled to undergo an assessment in 2025 (https://sedarweb.org/).

CAB Nassau Grouper and Red Hind populations have suffered historic overexploitation. Management efforts, which have included the use of MPAs, have demonstrated potential in rebuilding these stocks. Telemetry studies report that both of these species undergo dynamic sex-specific movements between protected and non-protected areas during the spawning season[116][117]. Additionally, the Red Hind population recovery rate increased when the Red Hind Bank Marine Conservation District transitioned from seasonal to year-round protection[21]. Thus, extending spatial and temporal MPA closures should be considered to maximize the protection of these and other vulnerable aggregating species[12][117]. The incompatibility in spatial application of federal regulations between CAB jurisdictions (e.g., federal waters starting at different distances from shore) is something to consider during recovery efforts of these species.

4.2. Goliath Grouper

The Atlantic Goliath Grouper *E. itajara* (Goliath Grouper hereafter) is the largest grouper distributed across the Atlantic basin[118]. Interestingly, it was recently confirmed that Goliath Grouper differs from most other economically relevant groupers in the SEUS by displaying gonochorism (single-sex individuals) with the potential for diandric protogyny, where males can arise from birth or sexual transition[40]. The exploitation of this species in the SEUS can be traced back to the early 1900s (Figure 8), and population declines were evident around the 1980s[119]. In other jurisdictions, it is hypothesized that Goliath Grouper populations are currently experiencing overexploitation and/or apparent population declines[120][121].

Figure 8. Atlantic Goliath Grouper *Epinephelus itajara* displayed at Gene Johnson's Tackle Shop, Daytona Beach, Florida, circa 1920. Public domain photograph courtesy of State Archives of Florida, Florida Memory. Available at https://www.floridamemory.com/items/show/140117.

In response to the population declines across the SEUS, NMFS implemented a moratorium across its jurisdiction in 1990. Soon following the moratorium, increases in the population were observed through the following decades[122][123][124]. This was followed by stakeholders expressing frustration reporting increases in Goliath Grouper abundance leading to reduced reef fish communities and increased depredation events[125]. These angler perceptions reduced their satisfaction and led management to consider intervention. After years of consideration, the Florida Fish and Wildlife Conservation Commission opened a limited-access fishery for juvenile Goliath Grouper (https://myfwc.com/fishing/saltwater/recreational/goliath/).

While the juvenile Goliath Grouper fishery provides the state with direct revenue ($10 to apply and ≥$150 if selected) and biological samples, the decision to open the fishery remains controversial. Following the upward trend, the juvenile and adult populations have suffered episodic mortality events (e.g., Red Tide *Karenia brevis* blooms and cold snaps)[123]. In addition, the degradation of Red Mangrove *Rhizophora mangle*, an essential habitat for juvenile Goliath Grouper, has been reported and may lead to reduced recruitment and hindered population recovery efforts[123]. While assessments have been attempted on Goliath Grouper, poor catch records have led to high uncertainty and rejection by peer reviewers[123]. Thus, as the Goliath Grouper population faces other challenges (e.g., episodic mortality events and habitat loss), what effects will the fishery add? Will there be reduced recruitment into an already distressed adult population? The discussion of opening a Goliath Grouper fishery is beyond the scope of this review, but for further dialogue see the following references[123][125][126].

5. Climate Change and Anthropogenically Driven Disturbances

Across the globe, climate change is modifying many mechanisms relating to atmospheric, sea surface, physiochemical, dynamic, seasonal, and regional processes[127]. Investigating the effects of these changes on fish stocks is of primary interest as many have been found to affect fish population dynamics[128][129][130][131][132]. As for groupers, primary processes of concern include oceanographic variables, specifically temperature, and currents. Projected warming is hypothesized to drive changes in maturity and gamete release schedules, as well as transition schedules in sequential hermaphrodites[133][134][135]. Under current climate change projections, grouper spawning dynamics in the southern Gulf of Mexico are expected to be affected in the next 50 years[133]. Changes in current dynamics are also thought to affect larval transport in groupers, which have long pelagic larval duration stages[1][136]. Changes in currents during larval stages may affect where these settle, which can severely affect survival and subsequent recruitment[1]. As many groupers across the SEUS have suffered historic population declines, climate change shall be an important consideration in rebuilding efforts.

Environmental changes have been linked to regime shifts (temporal changes in average recruitment) and recruitment failure (successive poor recruitment events) in fish stocks[128][137]. A recent study found that in many assessed fish stocks, recruitment is more influenced by environmental variables than spawning stock biomass[128]. This same study found that a large proportion of assessed stocks, including GOM Red Grouper, have undergone regime shifts that are often not detected by traditional stock-recruit relationship modeling, and not doing so can lead to biased projections[128]. In the SA, many reef fish stocks are showing signs of recruitment failure[138][139][140]. In addition, there is evidence of a correlation in recruitment failure between these species, suggesting that a common exogenous driver is causing poor recruitment events[140]. Among the species showing signs of recruitment failure in the SA are groupers displaying protogynous hermaphroditism, including Red Grouper, Gag, Scamp, and Snowy Grouper[138][140].

The importance of maintaining healthy habitats for productive fisheries has long been recognized and investigated[141][142][143][144][145]. Many groupers display ontogenetic habitat shifts demonstrated by spending juvenile stages in shallow, inshore habitats followed by deeper, offshore habitats as adults[146][147][148][149]. Primary habitats associated with early life history stages of groupers are Red Mangrove shorelines and seagrass meadows[148][149][150]. These two coastal habitats are among those facing severe impacts due to climate change (e.g., sea level rise and tropicalization) and anthropogenic activities (e.g., nutrient loading)[151][152]. To provide a relevant example, declines in seagrass beds have been reported in the central west and northwest regions of Florida[153][154]. These areas are among the core distribution of GOM Gag, which is currently overfished and experiencing overfishing[49]. Therefore, how will declines in seagrass cover impact Gag recruitment? Additionally, juvenile Goliath Grouper exhibit diel movements between seagrass beds and Red Mangroves[155]. How will Goliath Grouper fare against its essential habitats facing climate- and anthropogenically-driven changes?

Anthropogenic activities have been linked to impacting coastal ecosystems and fisheries. Among the most relevant in the SEUS is eutrophication, nutrient loading which can lead to phytoplankton blooms followed by hypoxic events. In the GOM, Red Tide blooms have been linked to episodic fish kills[156]. While these are naturally occurring, their intensity and duration have increased and have been credited to eutrophication[157]. While it’s difficult to quantify the population effects caused by these episodic events, Gag and Red Grouper have served as model species to describe yearly mortality rates induced on a fish stock by Red Tide blooms[158][159][160][161].

Other anthropogenic activities across the region that can affect fish stocks are pipelines, seismic air guns, and energy exploration[1]. The Deepwater Horizon oil spill (2010) negatively affected a variety of taxa and habitats across the GOM[162][163][164]. An ecosystem model simulating Deepwater Horizon effects found the spill reduced the condition of groupers[162]. Effects caused by the oil spill were considered for the most recent GOM Yellowedge Grouper assessment, but there was no strong evidence to justify including mortality due to the event[88]. Lastly, wind energy development in the GOM has recently been announced (https://www.fisheries.noaa.gov/feature-story/noaa-and-bureau-ocean-energy-management-sign-new-interagency-agreement-wind-energy). The effects of these activities on fisheries have been a recent topic of interest across other regions[165][166][167], and shall be a new line of investigation in the GOM.

Climate change and anthropogenic activities can severely impact fish population dynamics and hinder recovery efforts if left unaccounted for. Groupers are at the forefront of species of concern, as many display complex movement ecology and reproductive dynamics. In addition, their high level of exploitation may affect their sensitivity to upcoming environmental changes[133]. Thus, the effects of climate change and anthropogenic activities should be accounted for when monitoring and managing grouper fisheries.

6. Ecosystem-Based Considerations in Grouper Assessments

Across the globe, there is a push to move from single-species management to ecosystem-based fisheries management (EBFM), a holistic approach that accounts for biotic, abiotic, and human components of ecosystems and their interactions and applies an integrated approach to fisheries within ecologically meaningful boundaries[168][169][170]. In 2016, NMFS released its EBFM policy, in which it declared that EBFM was the preferred way to meet the mandates of sustainably managing the nation's living marine resources[171].

Across the SEUS, efforts to facilitate moving towards EBFM are well underway[172][173][174][175][176]. Groupers have played an important role as case studies to initiate advancing single-species management towards EBFM. In the GOM, the most recent Red Grouper and Gag assessments estimated Red Tide mortality rates (assuming it killed all ages) during years where severe mortality was evident[49][53]. Age-specific estimates of Red Tide mortality rates were estimated from ecosystem models that included many fishing fleets and functional groups as well as environmental variables[160][177]. Although not included in the assessment, the effects of the Deepwater Horizon oil spill were considered in the latest GOM Yellowedge Grouper assessment[88]. While the majority of fish stocks across the SEUS continue to be managed (and assessed) as single stocks, the inclusion of environmental effects moves them closer to EBFM in the model complexity continuum[170], and gets NMFS closer to reaching its EBFM goals.

7. Using Co-Produced Data to Assess Grouper Stocks

Stakeholder involvement is a necessary component for effective and transparent fisheries management as it provides many benefits[178][179][180][181][182]. In the SEUS, stakeholder involvement can be observed at different stages of the management process for grouper fisheries. The Great Goliath Grouper Count was developed to address the data-poor nature of the Goliath Grouper (lacking reliable landings and age/size compositions) by facilitating cost-effective and timely stakeholder visual surveys that inform trends in abundance and size distribution[183]. These data were incorporated into the most recent Goliath Grouper assessment[184], therefore including stakeholders in multiple stages of the management process. Collecting fisher's local ecological knowledge (LEK) has allowed managers to better understand the severity of Red Tide bloom events on fish stocks and validate that groupers are among the species most susceptible to these events regardless of severity[185].

The Gulf of Mexico Fishery Management Council's Fishermen Feedback Tool is used to gather stakeholder perceptions on the status of stocks, which has been used to gather information on the status of Gag, Red Grouper, Scamp, and Yellowedge Grouper (https://gulfcouncil.org/blog/2022/fishy-or-not-we-want-your-feedback/). While the data collected are not directly included in stock assessments, this provides the managers with LEK, which could provide trends not captured by the assessments. In addition, The South Atlantic Fishery Management Council's Citizen Science Program provides research priorities (which currently include grouper sampling) for stakeholders to become involved in the data collection process (https://safmc.net/citizen-science/). To better understand the habitat preferences and population status of threatened groupers in Puerto Rico (e.g., Nassau Grouper and Goliath Grouper), researchers welcome voluntary sighting reports from the public (https://www.merospr.com/).

Stakeholder involvement is a promising avenue for optimizing cost-effective data collection efforts and facilitating stakeholder sense of inclusion in the management process. It is highly recommended by researchers to improve our understanding of spawning aggregations across the SEUS[186][187]. In the Cayman Islands, stakeholder involvement has been a monumental part of the recovery of the Nassau Grouper population[14]. Thus, lessons from this effort could be applied to improve the monitoring and rebuilding efforts of groupers across the SEUS.

8. Emerging Techniques to Monitor Grouper Populations

In recent years, there have been many developments in techniques to improve the management and monitoring of groupers across the SEUS. A promising one for management purposes (including transitioning to EBFM), is management strategy evaluation, in which simulations are used to evaluate management strategies, their associated trade-offs, and uncertainty in achieving management goals[188]. This technique was recently employed in two SA fish stocks to evaluate how different management procedures meet the specific objectives of the recreational and commercial sectors[34]. Currently, the South Atlantic Fishery Management Council is using management strategy evaluation to evaluate procedures in the snapper/grouper fishery (https://safmc-mse.netlify.app/). Results from this effort shall provide important information on how to best meet management objectives in complex multispecies reef fish fisheries that could be applied to the GOM and CAB.

There have also been many improvements to monitor grouper populations. Among these are age validation techniques involving bomb radiocarbon, which have been employed to validate the estimated ages and longevities of multiple groupers in the SEUS[69][61][189][190]. Recently, the use of Fourier transform near-infrared spectroscopy (FT-NIRS) to predict ages from otoliths has shown potential for cost-effective production aging of fishes[191][192][193]. Additionally, recent advances in epigenetic aging, which were validated for Red Grouper, could provide accurate, timely, and non-lethal mass aging of fishes[194][195]. A significant contribution has been recently made by larval dispersal simulations, which have demonstrated that the spawning activity of multiple reef fishes in the GOM, including Scamp, provides a considerable number of larvae to their respective SA stocks[196][197]. These advances shall improve the quantity and quality of assessment inputs and decision-making, therefore decreasing the assessment uncertainty and providing improved catch advice.

Autonomous systems and passive acoustics have been employed to monitor grouper populations. In the CAB, these techniques are used to investigate grouper spawning-related behaviors[198][199][200][201]. These technologies have potentially identified undiscovered grouper spawning areas[199][201], which can assist in directing future management efforts to improve Nassau Grouper and Red Hind recovery efforts. Acoustic telemetry has been employed to investigate movement ecology, spawning dynamics, and post-release mortality of groupers in the SEUS[28][117][202][203][204]. Geochemistry and isotope studies have also provided important information on grouper ontogenetic changes in diet and habitat use, as well as delineating population structure[95][146][205][206]. The utility of environmental DNA for investigating grouper spawning aggregations in the CAB has been recently explored, and while limited success was reported, this remains a powerful tool that could inform population trends of species with depleted population levels, such as Nassau Grouper[207].

Video surveys have become one of the most common methods to monitor reef fish populations across the SEUS[208][209]. These are used to generate fishery-independent relative abundance indices that are directly used in the stock assessments to inform the model on the dynamics of populations[60][49]. In addition to providing species composition and abundance, video surveys can also provide fish measurements to inform size composition[210]. A long-term video survey in the GOM has provided descriptions of Marbled Grouper habitat use, a species poorly understood across its range[211]. Additionally, video surveys conducted across the Caribbean reported a depth range expansion of Misty Grouper, another poorly understood deepwater species[212]. A shortcoming of video surveys is that they don’t provide biological samples (e.g., otoliths and gonads), which are necessary to estimate stock assessment inputs (e.g., growth and age/size at maturity). To circumvent this, video surveys can be paired with other gears, such as traps, as observed in the SA[138][139][208].

9. Conclusions and Future Directions

Groupers have historically supported valuable fisheries across their range, and this continues to be the case. Multiple components make grouper fisheries among the most difficult to manage in the SEUS. First, the dynamics of the multispecies reef fish fisheries in which they are a part of make it extremely difficult for traditional management techniques to maintain sustainable fisheries. Being composed of species with varying life histories and temporal harvest closures, multispecies reef fish fisheries are conducive to high levels of regulatory discards, which can induce severe mortality on fish stocks and undermine the purpose of temporal harvest closures and minimum size limits. Thus, recreational effort restriction (e.g., temporal and/or spatial closure to bottom fishing) should be considered by management while accounting for socioeconomic components.

In addition to being part of complicated fisheries, groupers have complex life histories, demonstrated by protogynous hermaphroditism, high longevities, slow growth, maturity and transition, ontogenetic habitat shifts, as well as spawning-related migrations and aggregations. These make groupers especially vulnerable to overexploitation, especially the poorly understood deepwater stocks with high longevities that will presumably face additional fishing pressure as increases in shallow-water reef fish regulations and recreational effort are observed. In the case studies discussed, there is substantial evidence of declines in protogynous hermaphrodites, demonstrated by decreasing male sex ratios and limited recruitment. There was also evidence of rebuilding stocks by using harvest moratoriums and MPAs. In the GOM and SA, the expansion of MPAs could have benefits but may be hindered by the ever-growing recreational fleet. Thus, long-term monitoring will be essential to evaluate MPA effects. As for the CAB, MPAs have shown signs of success, but MPA effectiveness may be dependent on the surrounding context[213]. Given there is evidence of both self-sustaining and dependent grouper subpopulations across the Gulf of Mexico and the Caribbean regions[102][113][214], an international collaboration to implement effective conservation plans should be considered. An example of this is the recently proposed Caribbean-wide Nassau Grouper and Mutton Snapper *Lutjanus analis* fish spawning aggregation FMP[215]. Additionally, conservative approaches should be considered when assessing grouper stocks and determining their reference points.

Climate change and anthropogenic impacts are expected to take their toll on grouper stocks. Particularly, changing oceanographic conditions are expected to alter the reproductive phenology and larval survival of groupers. Additionally, declines in nursery habitats are expected to affect juvenile condition and recruitment into adult populations. Some grouper stocks have served as models to transition from single-species management towards EBFM. Efforts shall continue to progress by exploring ecosystem models, as currently done to estimate grouper red tide mortality rates, to identify interactions that can be appropriately modeled under current stock assessment platforms (e.g., environmental effects on recruitment). As regime shifts and poor recruitment for some grouper stocks are evident, assessment techniques should account for exogenous mechanisms driving these.

Many novel tools are available to facilitate the management and monitoring of grouper stocks. Management strategy evaluation could prove to be useful for identifying the most appropriate management procedures across the SEUS and beyond. The progression of FT-NIRS and epigenetic aging could facilitate cost-effective and timely mass aging of fishes. Larval transport simulations will continue to provide novel insights into the connectivity between grouper management units. Acoustic telemetry continues to provide novel insights into movement ecology and post-release behaviors of groupers. Autonomous systems and passive acoustics provide non-invasive methods of monitoring grouper spawning behavior and have been useful for identifying unprotected potential spawning areas. Lastly, video surveys have become one of the most effective ways of describing species composition, abundance, and size composition, and can easily be paired with other gears to simultaneously collect biological samples.

While this review focuses on synthesizing available information from the SEUS, the case studies and future directions covered can be applied beyond this region. In many countries, there are data-limited scenarios that make the use of many management and monitoring techniques covered here unlikely. However, several lessons can be applied almost universally, such as the protection of spawning aggregations and involving stakeholders in the management and monitoring process. Information provided on SEUS groupers can facilitate the production of hypotheses about groupers in other regions that are poorly understood. Given the relatively rich history of scientific studies and management of groupers in the SEUS, this synthesis can assist other jurisdictions in sustainably managing their valuable grouper fisheries for generations to come.

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Data Availability Statement

The stock assessments from which Figure 5 was derived are publicly available at https://sedarweb.org/sedar-assessments/. Recreational effort data are publicly available at https://www.fisheries.noaa.gov/data-tools/recreational-fisheries-statistics-queries. Commercial grouper landings are publicly available at https://noaa-sero.s3.amazonaws.com/drop-files/cs/2022_GT_AnnualReport_Final.pdf.

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