LOSS OF SUITABLE HABITAT AND PHENOLOGICAL SHIFTS OF GROUPER AND SNAPPER SPAWNING AGGREGATIONS IN THE GREATER CARIBBEAN UNDER CLIMATE CHANGE

By

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With the effects of climate change already observed in both terrestrial and marine ecosystems, an understanding of the resulting changes to the environment is necessary to assess fish population status and form appropriate fishery management plans that can be adjusted and adapted to remain effective under changing conditions. This study focused on modelling the effects of climate change on the distribution and phenology of spawning aggregations of reef fishes in the Greater Caribbean region, examining four snapper and four grouper species to compare families (Lutjanidae and Serranidae, respectively). A series of ecological niche models were developed to project how the distribution and seasonal timing of fish spawning aggregation sites will change under projections from the NOAA GFDL Earth System Model and the RCP 8.5 climate scenario. The Non-Parametric Probabilistic Ecological Niche (NPPEN) Model was used to model data on fish spawning aggregations linked with information on environmental conditions from satellite data. Findings suggest that there are significant differences between groupers and snappers in their response to warming temperatures. While there was some variation among species, groupers were seen to experience slight delays and contraction of spawning season, with a greater loss of suitable FSA habitat and poleward shifts in distribution.

Snappers had larger earlier shifts in phenology of spawning season, with a lower loss of suitable habitat and variable shifts in distribution. Snappers appeared to be more resilient under the effects of climate change and able to occupy a wider and warmer range of temperatures, contrasting with groupers that prefer cooler periods. As a result, groupers may lose preferred spawning conditions sooner due to climate change. Modeling shifts in fish spawning aggregation locations under climate change can be a useful tool for adaptive management because it provides information that could allow fisheries managers to adjust marine protected areas and fishing restrictions to be flexible with the impacts of climate change.

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1.1 Species Distribution and Phenology

For many species, life history events, such as migration, metamorphosis, and reproduction, are signaled by environmental cues (Visser and Both, 2005). The seasonal timing of these events in an organism's life is referred to as phenology. As a result of climate change and altered environmental and habitat conditions, evidence of earlier arrivals of spring conditions in many ecosystems has been noted in both marine and terrestrial environments (Parmesan and Yohe, 2003; Parmesan, 2007; Cook et al., 2012; Poloczanska et al., 2013; Cohen et al., 2018).

Temperature variations on annual-to-decadal scales can be associated with shifts in fish spawning site locations (Sims et al., 2004; Bellier et al., 2007; Asch and Checkley, 2013; Asch and Erisman, 2018). Additionally, changes in environmental characteristics, such as currents, water temperature and coastal upwelling associated with climate change, are leading to shifts in both spawning phenology and the geographical range of spawning locations (Ciannelli et al., 2007; Cheung et al., 2010; Asch, 2015; Asch and Erisman, 2018). These findings imply that population level or species level patterns in reproduction and distribution are likely to change substantially. This can be in the form of changes in the length of spawning periods, use of new spawning sites and abandonment of historical sites, and shifts in frequency and intensity of spawning (Munday et al., 2007; Sundby and Nakken, 2008; Asch and Erisman, 2018). Consequently, these changes could affect overall fecundity, survival, fisheries recruitment, and productivity.

Similar to changes in phenology, species distribution shifts resulting from environmental change can be particularly rapid in marine systems (Thorson, 2018). Understanding how species distributions will shift is important in fisheries management, fishing access rights, and estimating the economic potential of fisheries (Cheung et al., 2010; Pinsky and Fogarty, 2012; Thorson, 2018). Species distributions shifts can be a potential indicator of the intensity of environmental impacts as a result of direct changes in ecological community stability, reflecting the fact that species distribution is an integrated measure of changing demographic rates (Theobald et al., 2017; Thorson, 2018). This is not always the case as species that do not respond by shifting their distribution may also experience physiological impacts and stressors, but are constrained in their ability to disperse to avoid those impacts (Pörtner and Farrell, 2008; Cheung et al., 2009; Cheung et al., 2010). Historical and potential future shifts in distribution of marine species has been modeled as a result of climate change impacts (Cheung et al., 2009; Cheung et al., 2010; Pinsky et al., 2013; Morley et al., 2018). Generally poleward shifts have been observed; however, these shifts are not uniform and distribution shifts occur at various rates and in several directions (Pinsky et al., 2013). These shifts can vary based on species characteristics, habitat requirements, climate velocity and other environmental changes caused by climate change (Cheung et al. 2010; Pinsky et al. 2013).

Ecological niche models (ENMs) elucidate the statistical relationship between the current species distributions and environmental conditions. They have been used to support estimates of extinction risks resulting from climate change. These models combine current species distributions with environmental variables to generate future projections (Araujo et al., 2005). Fitting ecological niche models to historical distributions and projecting changes in future environmental conditions is a tool that can also be used examine potential changes in species interactions (Selden et al., 2017; Thorson, 2018; Schliep et al., 2018). In addition to projecting species response to climate change, these models can be used to estimate potential invasions of nonnative species.

1.2 Reef Fish Spawning Aggregations

Certain species of marine fishes reproduce *en masse*, with this behavior referred to as a spawning aggregation. Reproduction via spawning aggregation formation is a key life history event for many tropical fishes and occurs among groups of dozens to thousands of individuals spawning at predictable times and locations (Boomhower et al., 2010). While not all fish species reproduce in this manner, previous research suggests that fishes involved in these spawning aggregations gain fitness benefits from mating at high densities, which provides opportunities for greater mate selection and mate quality, increased fertilization success, and decreased predation risk per capita on gametes and larvae (Donahue et al., 2015).

Confirming the occurrence and location of spawning aggregation sites can involve both direct and indirect evidence. Direct evidence includes observation of the aggregations or the presence of hydrated oocytes within gonads of females collected from sites (Heyman, 2004; Boomhower et al., 2010). Indirect evidence can include increases in fish density, large and predictable catch increases, observations of courtship behaviors, fish with swollen abdomens, or increased gonado-somatic index (Boomhower et al., 2010). Historically, transient spawning aggregation sites are typically first identified by local fishermen (Sadovy de Mitcheson, 2008). Many spawning aggregations are not well studied by scientists and occur in countries with scarce resources available for management and conservation of marine fisheries (Sadovy de Mitcheson, 2008; Heyman et al., 2013). Due to this trend, there is a knowledge gap in locating spawning sites, with data availability varying between regions. Knowledge gaps also exist in terms of how to best implement management plans for spawning aggregations (Lowerre-Barbieri et al., 2016).

Among fish species that form spawning aggregations, reproductive traits and strategies can vary among species and across regions, with behaviors including migration, pre-spawning assembly, the act of spawning, and dispersal of adults from the sites (Nemeth et al., 2004). Species that spawn in large aggregations can be classified as transient or resident spawners based on the allocation of reproductive effort. While transient species migrate to specific locations outside of their home range to spawn, resident spawners in contrast migrate short distances within their home range and spawn for a period of minutes each day, with a spawning period that can last between 6-12 months every year (Heyman et al., 2013). There appears to be tradeoffs between allocating resources for reproductive effort and minimizing travel and energy expenditures associated with moving to suitable sites for spawning among species in these two groups (Karnauskas et al., 2011; Heyman et al., 2013). Due to the different energetic demands associated with transient and resident spawning behavior, understanding the life history characteristics of the different species can provide insight on spawning site selection and habitat suitability in the Greater Caribbean.

There are many potential reasons proposed as to why fish species select spawning aggregation sites, and why transient spawners allocate more time and energy for migrations sites with specific environmental variables. These fish species aggregate based on environmental cues including seasonal, lunar and diel cycles, as well as certain social cues (Mann et al., 2010; Heyman et al., 2013). If preferred spawning sites have been overfished or become unsuitable due to habitat degradation or changing conditions, populations may be forced to move to less suitable sites that are not optimal for population sustainability and will likely result in lowered reproductive success or the species will experience declines in abundance (Donahue et al., 2015).

The health status of fish spawning aggregations (FSAs) are good indicators of the health of the entire population. A prominent example of a species that has declined due to the overfishing of FSAs is the Nassau grouper (*Epinephelus striatus*) (Egerton et al., 2017; Sadovy de Mitcheson et al., 2008).It is estimated that 75% of all known Nassau grouper spawning aggregations have been eradicated or reduced to negligible numbers, and FSAs often fail to recover after overexploitation (Egerton et al., 2017). Many fishes in the family Sciaenidae that form spawning aggregations have also experienced severe declines from overfishing of aggregations. For example, the world's largest croaker, totoaba (*Totoaba macdonaldi*), was nearly driven to extinction as a result of overexploited spawning aggregations during the 1950s and continues to be overexploited and classified as critically endangered. (Cisneros-Mata et al., 1995; Erisman et al., 2017). Other species, such as the giant yellow croaker (*Bahaba taipingensis*) in China, white sea bass (*Atractoscion nobilis*) in the United States, and the black spotted croaker (*Protonibea dicanthus)* in Australia, have experienced substantial extirpations of spawning aggregations, demonstrating this issue is occurring on a global scale (Sadovy and Cheung, 2003; Pondella and Allen, 2008; Phelan, 2008; Erisman et al. 2017). Groupers (family Serranidae) are historically one of the most heavily harvested reef fishes in tropical and sub-tropical oceans. Most large grouper stocks are now at record low abundance (Nemeth et al., 2004). Fishing exploitation at spawning aggregation sites has impacted populations through reduced genetic diversity, changes in sex ratios, declines in reproductive output, and at times aggregation extirpation (Heyman et al., 2005). If spawning populations are fully or partially self-recruiting, meaning their population size is significantly influenced by recruitment of their own offspring, overfishing at aggregation sites can quickly remove a significant portion of local species biomass, as well as damage the population sustainability in the long term (Nemeth et al., 2004). Monitoring, managing, and conserving FSAs requires an understanding of the location, extent, and dynamics of these aggregations and characteristics of fish populations that use them as a method of reproduction (Egerton et al., 2017).

In fishery management, understanding the regulation of regional population dynamics can be important (Lindeman et al., 2000; Bryan et al., 2015). Factors negatively affecting spawning aggregations can have substantial, negative impacts on populations across a large spatial scale due to the high concentration of individuals spawning during a small window of time and space (Claro and Lindeman, 2003). When spawning aggregations decline, population sustainability is at-risk at the regional scale, with potential impacts on both local and distant populations that are connected through migration patterns and larval dispersal. Since species that reproduce through spawning aggregations risk population declines and are subject to heavier fishing pressures and potentially increased vulnerability to climate change, it is important to understand how these aggregations will be impacted so that they can be effectively managed (Claro and Lindeman, 2003; Hare et al., 2016).

Multiple strategies have been used in the past for management of transient FSAs. These included fishery, seasonal, and species-specific closures, as well as restrictions on gear, size weight, marketing restrictions and quotas (Sadovy de Mitcheson et al., 2008; Claro et al., 2009; Kobara et al., 2013). Different management techniques have been implemented from all levels of management, from local to international initiatives (Kobara et al., 2013). Marine protected areas (MPAs) and reserves have historically been used to allow the recovery of overexploited fisheries, protect critical life-history stages, and protect habitat from destructive fishing practices (Grober-

Dunsmore & Keller, 2008; Kobara et al., 2013). When determining the location of marine reserves, whether the area is used as a spawning ground is a factor often taken into consideration (Locascio and Burton, 2016). With climate change causing species distributions to shift, spawning aggregations may shift their distribution as well, making it important to monitor the effectiveness of marine reserves and adjust reserve locations so that they incorporate climate refuges. Similarly, the timing of seasonal sales bans intended to protect spawning aggregations may need to be adjusted accordingly to track changing climatic conditions (Asch and Erisman, 2018).

1.3 Habitat and Oceanographic Conditions that Influence FSAs

A majority of the spawning aggregation sites studied have been observed to host multispecies spawning aggregations, which suggests there is a commonality in suitable habitat (e.g., both geomorphological characteristics and oceanographic conditions) occurring at those locations (Kobara et al., 2013). There is a knowledge gap on the physical and biological interactions at these sites and how certain physical characteristics influence and attract aggregations, but research has been done examining some of these processes and their effect on fish species. Previous research examining spawning aggregations suggests that fitness benefits may be related to increased survival of fish eggs and larvae associated with the geomorphological features and oceanographic processes at the location where spawning occurs. For example, more rapid offshore movement of larval fish that occurs at spawning aggregation sites may lower predation risk, while the presence of eddies can retain larvae closer to suitable habitat (Heppell et al., 2008; Karnauskas et al., 2011; Donahue et al., 2015).

Reef fishes in particular have been observed to aggregate near certain geomorphological features, such as submerged capes or promontories (Kobara et al., 2013). Many snapper and grouper spawning aggregation sites are located near outer edges of reef passes (Claro and Lindeman, 2003). This pattern has been examined across the Caribbean, with studies suggesting a relationship between reef promontories and location of spawning aggregation sites. For example, in Belize, most documented spawning aggregation sites occur at shelf-edge reef promontories, with a similar pattern in the Cayman Islands (Kobara and Heyman, 2008; Boomhower et al., 2010). Transient spawning species that migrate large distances to specific sites suggest that there is an evolutionary advantage to spawning near these geomorphological features (Karnauskas et al., 2011). Previous research found that using capes with these "desirable" geological features provides optimal current conditions for larval dispersal, while other sites with eddies can provide conditions for larval retention (Karnauskas et al., 2011). This suggests that sites may be selected based on the highest probability of egg and larval survival.

The interaction of ocean currents with habitat features, such as promontories, seamounts and channels, can lead to upwelling and localized gyres that retain high volumes of nutrients, fish eggs, and larvae (Karnauskas et al., 2011; Erisman et al. 2017). Some research has hypothesized that primary and secondary productivity is a contributing factor in selection of spawning aggregation sites and plays a role in species distribution (Stock et al. 2011; Karnauskas et al. 2011; Kobara et al., 2013; Erisman et al., 2017). Upwelling and vertical mixing influences phytoplankton abundance, chlorophyll concentration and productivity in an area (Karnauskas et al., 2011). Mesoscale eddies and local gyre formation have been observed to facilitate egg and larval retention in nearshore habitats, which allows them to be returned to their natal habitat (Nishimoto and Washburn, 2002; Karnauskas et al., 2011; Kobara et al., 2013).

With regard to the timing when spawning aggregations form in selected locations, previous studies indicate that the main cues for spawning are ocean temperature, lunar cycle, and tides (Sale et al., 2010). Photoperiod and water temperature are believed to be particularly important cues for certain snapper species that form spawning aggregations (Pankhurst and Munday, 2011; Heyman et al., 2013). If these observations are an accurate reflection of spawning cues, changing temperature and oceanographic patterns from the El Niño Southern Oscillation and other sources of climate variation could affect larval survival and recruitment (Heyman et al., 2005). Temperature can be a lethal, controlling, and directive factor in marine environments, through controlling internal processes within an individual and causing distributional responses in seasonal migrations (Hare et al., 2012). Seasonal changes in water temperature can alter the timing of fish reproduction, meaning temperature increases can cue earlier spring spawning activity while decreasing seasonal temperatures can stimulate autumn reproduction among other species (Pankhurst and Munday, 2011). Looking at the relationship between temperature, biological processes, and species distribution can provide insight into future species distribution and phenology shifts.

1.4 Life History Characteristics of Target Species

Below is a description of life history characteristics of the target species that I will be examining in my thesis, with key spawning information highlighted in Table 1.1. These species were selected for study because the locations and timing of their FSAs were among the best documented in the Caribbean (Kobara et al., 2013).

Cubera snapper (*Lutjanus cyanopterus)* inhabit coastal waters near rocky bottoms and reef structures and spawn during March through September off the coast of Florida, the Gulf of

Mexico, Cuba, Belize, Venezuela and the U.S. Virgin Islands. Also a few observations of spawning in January through February and October exist (Claro and Lindeman, 2003; Heyman et al., 2005; Whaylen et al., 2006; Kobara et al., 2013). During this time, they typically form aggregations 2 days before to 12 days after a full or third quarter moon in outer reef slopes, promontories, and artificial reef or wreck structures (Domeier and Colin, 1997; Claro and Lindeman, 2003; Heyman et al., 2005; Whaylen et al., 2006; Kobara et al., 2013; SCRFA, 2014). Research has shown cubera snapper spawn in relation to location, photoperiod, water temperature, and the lunar cycle. Spawning is cued by time of day rather than tides (Heyman et al., 2005). They travel large distances to spawn at certain aggregation sites and are thus categorized as transient spawners. Cubera snapper are currently listed as a vulnerable species on the IUCN Red List (Claro and Lindeman, 2003; Heyman et al., 2005; Whaylen et al., 2006; IUCN 2018).

Lane snapper (*Lutjanus synagris*) have well documented spawning aggregations throughout Cuba, as well as the Dry Tortugas area of Florida in the United States. These aggregations have declined as a result of targeted fisheries (Lindeman et al., 2000; Donahue et al., 2015). In this region, they are primarily found in shallow reef lagoons and migrate to the shelf break during their reproduction period, which occurs between the third quarter and full moon in May and June. It is suggested that portions of lane snapper spawning aggregations may alternate days to spawn around the full moon (Donahue et al., 2015). Their observed spawning habitat is the closest reef edge to their primary habitat, indicating they are minimizing energy expenses and predation risk (Donahue et al., 2015). Lane snapper primarily utilize reef slopes, as well as hard rocky bottoms with coral cover during spawning events (Lindeman et al. 2000; Donahue et al., 2015; Kobara et al., 2013; SCRFA, 2014). They are listed as near threatened on the IUCN Red List (IUCN 2018). Based off their spawning behavior and relatively short distance travelled to spawning grounds they are considered resident spawners, which contrasts with the other study species classified as transient spawners (Donahue et al., 2015).

Mutton snapper (*Lutjanus analis*) migrate to specific spawning aggregation sites and typically spawn in late spring to early summer but have documented spawning between March and August around the full moon (Claro and Lindeman, 2003; Feely et al., 2018). They are considered transient spawners and all documented aggregations occur on or near reef structures and promontories, indicating that they are a reef-dependent species (Claro and Lindeman, 2003; Graham et al., 2008, Heyman and Kjerfve, 2008). Aggregation sites have been observed in Belize, Cuba, Venezuela, Bahamas, the Cayman and Virgin Islands, as well as off the Florida coast in the United States (Rielinger, 1999; Claro and Lindeman, 2003; Burton et al., 2005; Graham et al., 2008, Boomhower et al., 2010; Heyman and Kjerfve, 2008; Kobara et al., 2013). Mutton snapper are not currently considered to be overfished at this time, however they are historically one of the most target species by commercial and recreational fishermen off of Cuba (SEDAR, 2007; IUCN; 2018). They are listed as a near threatened species on the IUCN Red List with populations declining (IUCN, 2018).

Gray snapper (*Lutjanus griseus*) is a reef-associated species, occurring in the central Western Atlantic from Florida through the Gulf of Mexico and along the northern/central coast of Brazil. Spawning aggregations have been documented off the coast of Florida, as well as Cuba, in June through September around the full moon on reef slopes and hard bottoms with high coral cover (Lindeman et al, 2000; Claro and Lindeman 2003; Kobara et al. 2013). They have been observed to move between habitats seasonally and make onshore-offshore movements in relation to spawning, in which they migrate from inshore habitats to offshore reefs to spawn

(Luo et al., 2009; Hare et al., 2012). Previous studies examining distributions of gray snapper project that this species will shift northward as a result of climate change (Hare et al., 2012). However, changes in their spawning aggregation sites under climate change have not yet been studied.

Yellowfin grouper (*Mycteroperca venenosa*) form spawning aggregations in the Caribbean and Western Atlantic from January through May each year (Nemeth et al., 2004; Cushion et al., 2008). Spawning aggregation sites have been documented off Belize, Mexico, Cuba, the U.S. Virgin Islands, Cayman Islands, and Bahamas during full and third quarter moons primarily on reef slopes and promontories. (Claro and Lindeman, 2003; Nemeth et al., 2004; Whaylen et al., 2004; Cushion et al., 2008; Heyman and Kjerfve, 2008; Kobara et al., 2013; SCRFA, 2014). Due to variation in temperature ranges across aggregation sites, moon phase and month of year have been shown to play a larger role in seasonality of spawning rather than temperature (Nemeth et al., 2004). The distance travelled for spawning classifies yellowfin grouper as a transient spawner, and they are currently listed as near threatened under the IUCN Red List (Nemeth et al. 2004; Kobara et al., 2013; IUCN, 2018).

Black grouper (*Mycteroperca bonaci*) form multiple medium-sized aggregations at locations along offshore atolls. Spawning aggregation sites for black grouper have been documented in Belize, Honduras, Cuba, Bermuda and the Cayman Islands. This species has historically been exploited during its spawning season and is considered to be near threatened based on the IUCN Red List (Reilinger, 1999; Claro and Lindeman 2003; Heyman and Kjerfve, 2008; Paz and Sedberry, 2008; Locascio and Burton, 2016; IUCN 2018). They are transient, reef-dependent spawners that reproduce during third quarter and full moons (Claro and Lindeman 2003; Heyman and Kjerfve, 2008; Paz and Sedberry, 2008; Luckhurst, 2010; Locascio and Burton, 2016). The spawning period is believed to occur between December and March. However, there is evidence based on gonad condition suggesting spawning may occur year round (Locascio and Burton, 2016).

Red hind (*Epinephelus guttatus*) are protogynous hermaphroditic groupers forming yearly spawning aggregations, which have been observed typically during full moons in Belize, Bermuda, Netherland Antilles, Puerto Rico, Bahamas, the U.S. and British Virgin Islands, and Cayman Islands (Luckhurst, 2004; Nemeth, 2005, 2006, 2007; Cushion et al., 2008; Mann et al., 2010; Kobara et al., 2013). Spawning has been documented from December through February, as well as in May through August at higher latitudes in Bermuda, throughout red hind aggregation sites (Domeier et al., 1997; Nemeth, 2005, Cushion et al., 2008; Kobara et al., 2013). They are transient spawners and use reef slopes and shelf edges with high coral cover and promontories. This species forms a few large aggregations, which increases vulnerability to overfishing (Luckhurst, 2004; Whaylan et al., 2006; Nemeth, 2005; Cushion et al., 2008; Mann et al., 2010; Kobara et al., 2013; Locascio and Burton, 2016).

Similar to red hind, Nassau grouper also form a small number of large FSAs, acting as transient spawners. They are currently listed as critically endangered (IUCN, 2018). Nassau grouper generally spawn between December and April, with additional spawning in Bermuda occurring in June and July (Asch and Erisman, 2018). Previous research on Nassau grouper species distribution impacts due to climate change from Asch and Erisman (2018) will be used for comparison to other grouper and snapper species in this study.

1.5. Overview of research objectives

This study aimed to explore the phenological and distributional changes to fish spawning aggregations of selected grouper and snapper transient FSAs in the Greater Caribbean. After identifying spawning observations for each study species, an ecological niche model was used to link up FSA sites with the climatological environmental conditions to select a model including the variables that influence species distribution. The model of best fit was used with a climate model to project the shift in FSA distribution and seasonality under the representative concentration pathways (RCP) 8.5 climate scenario. RCP refers to a climate scenario categorized by the projected change in radiative forcing from greenhouse gases by 2100 (Bopp et al., 2013). For statistical analyses, phenological shifts will be measured through changes in seasonal central tendency, and habitat sites and distributional shifts will be measured through an integrated habitat suitability score and change in mean latitude of FSA occurrence.

In chapter 2 of this thesis, trends between groupers and snappers were compared to test the hypothesis that there would be differences between groups in their response to climate change due to their varying spawning preferences. It was further hypothesized that spring spawners may shift spawning to earlier in the season as a result of warming temperatures, while fall and winter spawners may shift to later in the year. Species that have a lower range of preferred temperatures for spawning may be more intensely impacted by climate change in timing, loss of habitat, and distributional shifts. In chapter 3, these results were used to draw conclusions about the effects of climate change on reef fish FSAs and discuss how fisheries management strategies could be adapted to respond to changing environmental conditions. Steps for future research are also discussed in chapter 3.

Table 1.1. List of study species and FSA characteristics, including spawning months, duration, depth, transient or FSA type, and conservation status. References for information on individual species are included in chapter 1.

Scientific Name	Common Name	Spawning Months	Duration of Spawning (Days)	Spawning Depth (Meters)	FSA Type	IUCN Status
Lutjanus cyanopterus	Cubera snapper	March-September	15	9 to 30	transient	vulnerable
Lutjanus analis	Mutton snapper	March–September	8 to 10	0 to 40	transient	near threatened
Lutjanus synagris	Lane snapper	May–October	8 to 10	0 to 50	resident	near threatened
Lutjanus griseus	Gray snapper	June–September	unknown	10 to 85	transient	least concern
Epinephelus striatus	Nassau Grouper	December–April, June-July (Bermuda)	1 to 12	0 to 120	transient	critically endangered
Mycteroperca venenosa	Yellowfin grouper	January–May	3 to 10	0 to 120	transient	near threatened
Mycteroperca bonaci	Black grouper	December–March, May–August (Bermuda)	8 to 10	0 to 90	transient	near threatened
Epinephelus guttatus	Red hind	December–February, May–August (Bermuda)	5 to 7	0 to 45	transient	least concern

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CHAPTER 2. SHIFTS IN SPECIES DSITRIBUTION AND PHENOLOGY OF GROUPER AND SANPPER FISH SPAWNING AGGREGATIONS

2.1. Introduction

Climate change has altered environmental conditions on a global scale and prompted changes in latitudinal distribution, depth range, and phenology of fish species in marine environments (Beaugrand et al., 2003; Edwards and Richardson 2004; Beaugrand et al., 2011; Poloczanska et al., 2013). In marine systems, climate change has affected the abundance, spatial distribution, and phenology of species from the base of the food web up to higher trophic level predators (Beaugrand et al., 2011). Impacts on tropical fish species are of particular concern as warming temperatures may result in unprecedented conditions for fishes not experienced anywhere in the world over recent geological conditions (Asch et al., 2018).

The impacts from climate change affect a range of environmental conditions in the oceans, including but not limited to temperature, salinity, currents, dissolved oxygen concentration, pH, and ice coverage (Fernandes et al., 2013). Ocean temperature has shown to be a driving factor in distribution for many fishes as different species have specific thermal tolerance ranges which they can occupy (Pörtner and Peck, 2010; Hare et al., 2012). Climatic events can alter water mass distribution, water column structure, current patterns, and upwelling across a variety of spatial and temporal scales (McGowan et al., 1998; Nishimoto and Washburn, 2002). These factors can cause changes in movement patterns, spawning, and recruitment patterns of fish populations (Nishimoto and Washburn, 2002). Consequently, these factors can lead to changes in size, growth, mortality, abundance, distribution, and productivity of marine species (Cheung et al., 2009).

Fish spawning aggregations (FSAs) are considered a phenological event where populations of fish species aggregate at the same time and location each year to reproduce on a seasonally recurring basis (Donahue et al., 2015). Transient FSAs are a life history phenomenon in which fish migrate to specific locations at predictable times of year to reproduce. In the Greater Caribbean, approximately 37 species from 10 fish families are known to form transient FSAs (Kobara et al., 2013). FSAs formed through spawning migrations can be particularly vulnerable to the effects of climate change, since they have adapted to certain annual climatic patterns and typically have fewer spawning sites compared to other species (Hare et al., 2016). Also spawning fishes exhibit a narrower thermal tolerance range than other fish life history stages (Dahlke et al., 2020). Warming conditions could alter the timing of migrations and spawning events or the thermal habitat quality at the FSA site (Mellin et al., 2016; Asch and Erisman, 2018). Additionally, fish populations that spawn in large aggregations are vulnerable to overexploitation due to the ability of fisheries to predict and intensively target seasonal spawning locations (Sadovy de Mitcheson, 2012).

Many snapper and groupers (families Lutjanidae and Serranidae) are important species in the Greater Caribbean in terms of both their ecosystem role and as fishery resources. They are managed and harvested as a multi-species complex in the United States, because these families share similarities in life history and ecological characteristics (Heyman et al., 2013). Species in this snapper-grouper complex are typically long-lived, have late reproductive maturity, and spawn together in transient aggregations. These common characteristics make snapper and grouper species vulnerable to overfishing and slow to recover if aggregation sites are overfished or extirpated (Heyman et al., 2013). There have been substantial fishing impacts to snapper and grouper aggregations documented in the northern Caribbean, including Puerto Rico, the US

Virgin Islands, Mexico, Belize and the Florida Keys, with overall population declines (Claro and Lindeman, 2003). The size and structure of aggregations varies among snapper and grouper species, and the characteristics of these aggregations directly influences vulnerability to fishing pressures (Locascio and Burton, 2016). For example, a few large aggregations are more susceptible to exploitation pressure compared to numerous small groups (Locascio and Burton, 2016).

Grouper species tend to spawn earlier in the year during cooler, winter months, while snappers typically spawn during warmer spring and summer periods (Kobara et al., 2013; SCRFA, 2014). I hypothesized that the differences in spawning seasonality and their thermal spawning preferences may result in grouper species experiencing greater changes to their distribution and timing of spawning as a result of climate change compared to snappers. A multivariate approach was also taken to determine the influences of additional environmental factors on FSAs beyond temperature.

The goal of this study was to model potential shifts in spawning aggregation distribution as a result of climate change examining eight Caribbean reef fish species from the Lutjanidae and Serranidae families. Since temperature is a driving factor in species distribution and is directly affected by climate change, a question that this research aimed to explore was how habitat preferences and spawning locations may change with species that spawn across varying temperature ranges during spawning. Temperature has been shown to be the predominant effect driving projected distribution changes in Nassau grouper (Asch and Erisman, 2018), so my research investigated whether or not this was the case for other reef fishes that form spawning aggregations in the Caribbean. Species with lower thermal spawning preferences will likely be more sensitive to climate change and will exhibit larger changes in their distribution, greater declines in habitat suitability and phenological shifts. Species with preferred spawning requirements may need to adjust their seasonality of spawning to a greater extent in order to stay within the preferred temperature range. With spring spawners, warming temperatures may cause species to spawn earlier in the year. Species spawning in the winter or fall may experience larger phenological shifts later in the year as a result of waiting for seasonal temperatures to cool down. Additionally, the seasonality of spawning events may have relevance to the intensity and directionality of species distribution shifts under climate change impacts.

2.2. Methods

To obtain records of spawning aggregation sites for all of the study species, a database developed through collaboration with specialists containing a comprehensive list of known FSA sites was referenced (Kobara et al. 2013; W. Heyman and B. Erisman, pers. comm.). The database includes observations and records of FSAs that have been verified by direct observation or published account (Heyman et al., 2013, Kobara et al. 2013). This database was used as a reference for this research to identify spawning aggregation sites in the Greater Caribbean within the latitudes of 11.7° to 32.2° N and longitudes of 61.6° to 92.4° W for each of the study species, along with literature review and consultation from experts in the field with research experience on the target species. The spawning locations were additionally modified from the publicly available version of Science and Conservation of Spawning Aggregations (SCRFA), a global database containing observations and available data on spawning aggregations (SCRFA, 2014). Geographic descriptions of spawning locations from the database were used to make minor adjustments to coordinates of FSA sites, since data on spawning aggregation locations is frequently rounded for security purposes to prevent exploitation of spawning aggregations. These adjustments included moving coordinates off land to the nearest stretch of the coastline and looking at location descriptions contained in both the database and the original literature referenced. Any gaps in the data and missing information on spawning months from the database were filled and cross checked with the scientific literature to confirm the final list of spawning sites. The families Lutjanidae and Serranidae include the most commonly listed species in the reference database and literature review, making these two groups ideal study species for this project. The study species in Lutjanidae include cubera snapper (*Lutjanus cyanopterus*), mutton snapper (*Lutjanus analis*), lane snapper (*Lutjanus synagris*), and gray snapper (*Lutjanus griseus*), while Serranidae includes yellowfin grouper (*Mycteroperca veneosa*), black grouper (*Mycteroperca bonaci*), Nassau grouper (*Epinephelus striatus*) and red hind grouper (*Epinephelus guttatus*). Species were selected based on data availability and number of observations within the Kobara et al. (2013) data base. Lane and gray snapper had fewer FSA sites compared to other species. However, they were included in the list of study species so there could be an even comparison between the number of species in both families. Based on data availability, sample size varied between species and among grouper and snapper FSAs. Grouper sample size overall had an average of 113.5 observations, while snappers had 58.75 (Table 2.1). Sample size was defined based on the number of FSA site observations and the number of months that spawning occurred. Nassau grouper FSAs have been previously examined by Asch and Erisman (2018) to develop a prototype species distribution model to examine climate change impacts. Data on this species was included herein for comparative purposes to assess more completely how thermal spawning preferences compared across these families of fishes.

Satellite data on several environmental variables was used to assess the conditions at different spawning sites. Seven different oceanographic variables were examined to determine their effect on the probability of occurrence at spawning aggregation sites. Factors that were examined included sea surface temperature (SST) and seasonal SST gradients (SSTG), geostrophic currents in both the east/west and the north/south direction, eddy kinetic energy (EKE), chlorophyll concentration, and vertical velocity of seawater (i.e., upwelling and downwelling). SST was selected as it influences the distribution of many fish species, and previous research showed it to be a driving factor affecting Nassau grouper distribution (Asch and Erisman, 2018). Seasonal SST gradients will be examined to determine temperature differences between months and seasons since some species may be triggered to spawn by directional increases or decreases in temperature rather than by an absolute temperature (Wooton and Smith, 2015; Asch and Erisman, 2018). Chlorophyll concentration is a proxy for biological productivity at spawning aggregation sites, while EKE, vertical velocity and geostrophic currents are connected to currents that can influence larval fish retention and dispersal, which can be all indicators of habitat suitability of a potential spawning site (Karnauskas et al., 2011; Donahue et al., 2015; Asch and Erisman, 2018).

The Reefs at Risk database was used to obtain information on coral reef distribution to constrain projections of spawning occurrence to areas containing reefs (Burke et al. 2011; Asch and Erisman, 2018). The monthly climatology of SST sensed remotely throughout the Caribbean was obtained through the Advanced Very High Resolution Radiometer (AVHRR) Pathfinder, version 5.0 from March 2014 (https://www.nodc.noaa.gov/SatelliteData/ pathfinder4km). Chlorophyll data were taken from the Hermes GlobColour dataset version 3.2 (https://hermes.acri.fr/index.php; data downloaded on October 2016), which was used to produce a monthly Chl climatology (Asch and Erisman, 2018). Vertical velocities were calculated based on data from the QuikScat SeaWinds scatterometer. This dataset was downloaded October 2016 from the National Oceanic and Atmospheric Administration's Environmental Research Division's Data Access Program (ERDDAP) archive (https://coastwatch.pfeg.noaa.gov/erddap/index.html). Geostrophic current anomalies and EKE data were calculated from mean sea level anomalies (MSLA) observed from AVISO satellite altimetry downloaded on September 2016 (www.avisio.altimetry.fr; Asch and Erisman, 2018).

The modelling and data analysis were conducted using Matlab software version R2018a. The Non-Parametric Probabilistic Ecological Niche Model (NPPEN) was used to model data on FSA location and timing that has been linked with information on environmental conditions from satellite data. The NPPEN model has been designed to work with presence-only data and is based on a modified version of the Multiple Response Permutation Procedure (MRPP) (Beaugrand et al., 2011). One of the benefits of presence-only models is that presence-only data is typically more widely available (Tsoar et al., 2007). Using a model that handles presence-only data was necessary for my study because there are no confirmed absences of spawning aggregations. A previous study comparing modelling methods of species distribution with presence-only data showed that a technique based on Mahalanobis distance had one of the best performances when predicting species distribution based on an independent dataset (Tsoar et al., 2007). Since NPPEN is also based on Mahalanobis distance, it is expected to produce high model skill compared to other methods (Tsoar et al., 2007; Asch and Erisman, 2018).

Included below is a summary of how the NPPEN model functions based on Beaugrand et al. (2011). NPPEN tested whether a particular observation belonged to a reference matrix that included observations of species occurrence to evaluate whether the particular observation occurred inside or outside of a species' ecological niche. Each row of the reference matrix represents the set of environmental conditions where a species has been detected. Collectively, all data in the reference matrix should cover the entire niche of a species to produce reliable projections of the probability of fish occurrence (Beaugrand et al., 2011). There are four steps undertaken by the NPPEN model. These steps include homogenization of the reference matrix, preparation of the data by creating matrices for each observation, calculation of the mean multivariate distance between observations to be tested and the reference matrix using Mahalanobis distance, and calculation of the probability that the observation belongs to the reference matrix based on permutation testing (Beaugrand et al., 2011). Homogenization of the reference matrix is undertaken to account for bias favoring areas that may have higher densities of data points, for example in areas with more frequent sampling, or potential inaccurate reporting of occurrence that could influence the model (Beaugrand et al., 2011). Preparation of data refers to construction of the matrix for each observation of environmental conditions that will be tested against the range of conditions where a species was detected (Beaugrand et al., 2011). The Mahalanobis distance is calculated to assess the multivariate, environmental distance between an observation where it is unknown whether spawning aggregations occur and the data in the reference matrix. Permutation testing is then done to calculate the Mahalanobis distance between each observation in the reference matrix and all other observations. The percentage of times that the first calculation results in smaller distances than the distances from permutation testing is used to calculate the probability of occurrence of spawning habitat at the test observation.

NPPEN models were used to evaluate habitat preferences for each species and see what conditions were best suited for their reproductive success. All possible combinations of environmental variables were used in the NPPEN model initially and the model with the set of environmental variables that minimized the corrected Akaike information criterion (AICc) was selected to use for developing future projections (Hurvich and Tsai, 1989; Asch and Erisman, 2018). For species that had AIC_c values in the top models of less than two, NPPEN results from each model were averaged and the results were used as input for future projections based on the GFDL climate model and subsequent statistical analysis (Burnham and Anderson, 2002). Running all combinations of the model with the seven environmental variables produces 128 model possibilities, including the null model. Akaike weights were calculated for each variable for all species to determine the weighted influence of environmental covariates on distribution of FSAs (Burnham and Anderson, 2002).

Future climate projections were based on the Intergovernmental Panel on Climate Change (IPCC) scenarios using Representative Concentration Pathways (RCPs). RCP refers to the potential greenhouse gas concentration trajectories projected for the year 2100, with varying levels of emissions used for modeling future impacts of climate change. RCP 8.5 is considered a high emissions climate scenario with an 8.5 W m^{-2} change in radiative forcing by 2100 resulting from anthropogenic impacts on climate (IPCC, 2013). An earth system model was used to examine how spawning aggregation sites for each species shift under the RCP 8.5 climate future scenario from 2081 to 2100 and compared against a historical scenario of 1981-2000. This analysis considered 20-year climatologies and conditions were analyzed under both the RCP 8.5 and the historical simulation. The model used for this study was developed by the NOAA Geophysical Fluid Dynamics Laboratory Earth System Model (GFDL ESM2M) (Dunne et al., 2012; Dunne et al., 2013). The GFDL ESM2M model was selected due to the moderate climate sensitivity compared to the other atmosphere-ocean circulation models included in the 2013 IPCC Assessment Report (Cheung et al., 2016).

GFDL ESM2M can be classified as a General Circulation Model (GCM) and Earth System Model (ESM) (Bopp et al., 2013; Dufresne et al. 2013). GCMs typically represent the physical processes that occur in the atmosphere, ocean, cryosphere and their interactions, while ESMs include biogeochemical cycling information for terrestrial and marine ecosystems (Asch et al., 2016). These models factor in latitude and longitude, as well as the altitude of atmosphere and ocean depth as a vertical component through a three-dimensional grid of the Earth (Asch et al., 2016). Initial conditions of environmental variables are based on global climatic and oceanic conditions, and each model simulates changes from these historical conditions based on the climate scenario to produce future projections. The model is parameterized to describe processes that cannot be fully represented, for example to include the effects of eddies, which cannot be fully resolved at the spatial resolution of most global models (Asch et al., 2016). Resolution of the GFDL ESM2M model is coarse and becomes finer in tropical region with a resolution of ~1° at high latitudes, gradually increasing latitudinally to 1/3 ° near the equator (Dunne et al., 2013; Cheung et al., 2016). The physical oceanography component of the GFDL ESM2M model is the Modular Ocean Model version 4.1 (Dunne et al., 2012; Dunne et al., 2013; Logan et al., 2014; Asch and Erisman, 2018). Marine biogeochemical components typically include nutrient-phytoplankton-zooplankton-detritus models with varying complexity with respect to the number of phytoplankton functional groups or limiting nutrients (Bopp et al., 2013). Biogeochemical changes are reflected in ESM2M as the sub-model Tracers of Ocean Phytoplankton with Allometric Zooplankton version 2.0 (TOPAZ2). TOPAZ2 includes 30 tracers for nutrient cycles, as well as three explicit phytoplankton groups (Dunne et al., 2013).

Model bias correction was used to optimize the comparability between the climate models and satellite observations. This bias correction was based on the monthly mean value of each individual environmental variable throughout the study area. Bias corrections have been shown to be useful in research studying climate change impacts on several tropical marine systems (Logan et al., 2014; Matear et al., 2015). This allows for comparisons with observational data and increased model accuracy as bias corrections create a statistical relationship between the original data and modeled values for each covariate and apply the resulting correction function to the modeled data (McHenry et al. 2019).

To further analyze the results from the climate model, statistical metrics were calculated for each species for comparison. Mean latitudinal shift shows the average degrees in kilometers per decade that species distribution moved. This was based on calculations with the area of each grid cell used as a weight. Phenological shifts in month of spawning from historical and future projections can indicate the extent to which spawning seasonality could be affected under the impacts of climate change. Central tendency was calculated as an indicator of phenological change that corresponded to the near center of a species' seasonal distribution and can be used to compare skewed seasonal distributions of spawning habitat (Edwards and Richardson, 2004). Central tendency was defined based on the following formula:

Eq. 1. $\sum(\textit{probability of spawning habitat*month of spawning})/(\sum \textit{probability of spawning habitat})$

These results were expressed as a phenological shift with units of days per decade. An integrated habitat suitability score (IHS) was calculated as a metric of future habitat loss under the selected climate scenario. This integral was calculated as a sum across months and locations for probability of spawning habitat to get the total habitat suitability across a species range. This was done for the historical and future scenarios. Change in IHS was measured as a percent change between the two scenarios and then converted to an odds ratio to perform a statistical test to assess the hypothesis that there were differences in IHS change across taxonomic groups. For the other two metrics measuring climate change impacts (i.e., central tendency and mean latitudinal shift), an independent, two-sample t-test was used to examine which metrics were more sensitive to climate change between groupers and snappers.

2.3 Results

2.3.1 Yellowfin grouper (Mycteroperca venenosa)

NPPEN selected a model of best fit for yellowfin grouper with three environmental variable including SST, seasonal SST gradients, and *u*-geostrophic current anomalies (Table 2.1). Those three variables had high Akaike weights between 0.99 and 1.00, suggesting high influence on distribution as well as a high AIC weight of the selected model (Table 2.2). Spawning occurs primarily between January and April each year based on observations, which was consistent with observations. Future projections indicated an overall decrease in spawning probability, with a peak during January through April (Figure 2.1c, deviance explained (D) = 63.5, d.f. = 36). Statistical analysis based on model results were consistent with trends seen among Nassau grouper. Central tendency calculations displayed change by 4.9 days decade^{-1} between the historical and future time periods, indicating a trend towards later spawning (Table 2.3, Figure 2.11). This was the largest shift in phenology seen among the other grouper species. There was a 71.1% projected loss in suitable habitat for spawning based on the IHS score (Table 2.4, Figure 2.12). Mean latitude of FSA sites shifted by 22.5 km decade^{-1} in the poleward direction (Table 2.5, Figure 2.13). Nassau and yellowfin grouper had greater poleward shifts than other species by 19.5 km decade^{-1}.

2.3.2. Black grouper (Mycteroperca bonaci)

Four variables were selected by NPPEN in the best fit model, including SST, seasonal SST gradients, *u*- and *v*-geostrophic current anomalies for black grouper. Akaike weights showed that these metrics had high influence between 0.98 and 1.0, while the remaining variables fell under 0.05 (Table 2.2). Black grouper spawn during winter months of December through March. However, in Bermuda spawning was observed to occur between May and November, which was similar to the projections from the historical period from the model. Future projections indicated spawning seasonality will continue to peak in those winter months but will be less seasonally variable and there will be a lower probability of suitable spawning habitat at those FSA sites (Figure 2.1b; D=10.3%, d.f.=98). Black grouper was projected to shift spawning to later in the season to 1.8 days decade^{-1} as a result of its flattened distribution curve for seasonal spawning (Table 2.3, Table 2.11). Based on the IHS scores from the model, black grouper experienced a 69.16% loss in spawning habitat (Table 2.4, Figure 2.12). FSA sites were projected to shift very slightly in the poleward direction by 0.15 km decade^{-1} (Table 2.5, Figure 2.3, Figure 2.13).

2.3.3. Red hind (Epinephelus guttatus)

The environmental variables selected in the model of best fit were SST, *v*- and *u*-geostrophic current anomalies, and $\log_{10}$ transformed Eddy Kinetic Energy ($\log_{10}$ EKE). Red hind was the only species in NPPEN to have $\log_{10}$ EKE selected as a variable influencing FSA distribution. Akaike weights were all above 0.99 for SST, *v*- and *u*-geostrophic current anomalies, with the Akaike weight for $\log_{10}$ EKE at 0.79. (Table 2.2). Spawning occurs in

Bermuda during summer months of May through August, while all other FSA sites are characterized by spawning between December and February. The historical model varied slightly from these observations for red hind with low probability likelihood of spawning (<0.2) during the months of September, October, March and April, as well. Future projections indicated seasonality may remain relatively consistent, but with reduced probability of spawning each month (Figure 2.1d; D=11.7%, df=26). Central tendency indicated a phenological change of 1.3 days decade^{-1} later in the season (Table 2.3, Figure 2.11). Shifts to spawn later in the season were consistent with results from the rest of the grouper species. IHS scores from the model projected a 66.8% loss in suitable habitat between historical and future periods (Table 2.4, Figure 2.13). Red hind had the smallest mean latitudinal shift of all species, with a shift of -0.01 km decade^{-1} equatorward (Table 2.5, Figure 2.13).

2.3.4 Nassau grouper (Epinephelus striatus)

A previous study analyzing spawning aggregation distribution shifts for Nassau grouper under climate change was replicated for spawning adults for comparison with other species (Asch and Erisman, 2018). My results were consistent with Asch and Erisman (2018), indicating that the primary oceanographic factors affecting Nassau grouper spawning distribution across large spatial scales were sea surface temperature, seasonal surface temperature gradients, and *v*-geostrophic current anomalies in the north-south direction. Akaike weights also matched the previous study of Nassau grouper indicating these top three variables exerted high influence on FSA distribution (Table 2.2).

Spawning for Nassau grouper typically occurs between December and April, with the exception of Bermuda where they spawn during June and July. Central tendency of spawning phenology suggested a shift of 3.1 days per decade^{-1} later in the season between historical and future scenarios (Table 2.3, Figure 2.11). The 2081-2100 projections showed spawning will primarily occur between January to March (Figure 2.1a). The integrated habitat suitability score indicated Nassau grouper may experience an 82% loss in suitable spawning habitat (Table 2.4, Figure 2.3; D=8.7%, df=280). Mean latitude of FSA occurrence projected a 39.8 km decade^{-1} poleward shift (Table 2.5, Figure 2.13). Of the eight study species examined, Nassau grouper experienced the greatest loss in suitable spawning habitat and the largest overall mean latitudinal shift.

2.3.5. Cubera snapper (Lutjanus cyanopterus)

Similar to the findings for Nassau grouper, the primary oceanographic factors affecting spawning for cubera snapper across a distribution-wide spatial scale were SST, seasonal SST gradients, and geostrophic current anomalies in the north-south direction (v) (Table 2.1). These three environmental variables had Akaike weights above 0.9 (Table 2.6). While the responses of Nassau grouper and cubera snapper to environmental variables are similar, cubera snapper were shown to have more variability in range of environmental variables associated with its FSAs. Cubera snapper tended to use warmer temperatures to spawn at an average of 29°C and exhibited higher variability in temperatures used (Figure 2.5e). Nassau grouper spawned during cooler periods at an average of 25.5°C with a narrower spawning preference (Figure 2.5a). With respect to geostrophic velocity, both species spawn in areas with little-to-no current velocity present (Figures 2.8).

Historical models and observations are consistent in indicating that spawning occurred primarily during April through October. Under RCP 8.5, future projections indicated spawning will shift earlier in the year to peak between February and June by the years 2081-2100 (Figure 2.2a). Central tendency results from the model displayed an earlier shift of spawning season by -5.2 days decade^{-1} (Table 2.3, Figure 2.11). This reflects approximately a six-week change in overall between the time periods. Cubera snapper experienced the greatest shift in spawning seasonality compared to other species that were modeled. The IHS score showed an 18.1% decline in spawning habitat, which was the smallest absolute change compared to all other species (Table 2.4, Figure 2.12). However, projections still showed a lowered probability of spawning between historical and future periods (Figure 2.4; D=3.9%, df=64). Of all the snapper species, cubera snapper also had the lowest mean latitudinal shift of 1.3 km decade^{-1} in the poleward direction (Table 2.5, Figure 2.13).

2.3.6. Mutton snapper (Lutjanus analis)

The four environmental variables selected in the model for mutton snapper spawning habitat were the same as for black grouper. These included SST, seasonal SST gradients, *v*- and *u*-geostrophic current anomalies. Akaike weights for all selected variables exerted high influence around 1.0 (Table 2.6). Historical spawning baselines show increases in spawning activity during May through October, although FSA observations do not include the month of October for mutton snapper spawning aggregation formation. Future projections indicated a decrease in spawning particularly during summer months June through October, with the maximal amount of spawning during December through March (Figure 2.2c; D=15.5%, df=88). This was supported by the central tendency results, which showed a shift to earlier spawning by -4.8 days decade^{-1} (Table 2.3, Figure 2.11). Overall seasonality for mutton snapper spawning still appeared to encompass a wide number of months (Figure 2.2c). IHS scores from the model indicated a

34.7% decline in overall habitat suitability under RCP 8.5, as well as a lowered spawning probability (Table 2.4, Figure 2.2, Figure 2.12). A poleward change in distribution of FSA sites was calculated at a rate of 3 km decade^{-1} (Table 2.5, Figure 2.13).

2.3.7. Lane snapper (Lutjanus synagris)

Lane snapper was the only study species considered to be a resident spawner rather than a transient spawner (Table 1.1). The model of best fit had three variables including SST, seasonal SST gradients, and *u*-geostrophic current anomalies (Table 2.1). SST, *u*- , and seasonal SST gradients had high Akaike weights around 1.0 (Table 2.6).

Comparison of historical to future time periods of spawning phenology show a shift in peak spawning from May through September to January through March, as well as a lowered probability of spawning (Figure 2.2b; D=22.8%, df=57). Observations of spawning from April to October were consistent with the historical spawning period from the model. Central tendency showed a phenological shift to earlier in the season at a rate of -5.8 days decade^{-1} (Table 2.3, Figure 2.11). The climate model calculated a 44.2% loss in suitable spawning habitat from the IHS scores between the historical and future periods (Figure 2.12). Lane snapper had the greatest equatorward change in mean latitude across all species at a rate of 10.7 km decade^{-1} (Table 2.5, Figure 2.13).

2.3.8. Gray snapper (Lutjanus griseus)

Gray snapper was the only study species to have a ΔAIC of less than 2 between the first six models of best fit, so steps were taken to average the NPPEN results of those top models. This higher level of uncertainty in the model selection for gray snapper could possibly be related to a smaller sample size for this species compared to others. The first model included SST and vertical velocity (*w*) as the two variables influencing distribution. Results from vertical velocity data indicate gray snapper occurred in areas with slight downwelling (Figure 2.10). The remaining models with a ΔAIC<2 included a combination of five variables. The variables included were not only SST and *w*, but also seasonal SST gradients, *u* and *v*-geostrophic current anomalies (Table 2.1). Akaike weights for environmental covariates were more variable for gray snapper compared to other species. SST was the primary influence at 1.0, while the remaining significant variables ranged from approximately 0.4 to 0.6 (Table 2.6).

Consistent with the historical model, gray snapper were observed to spawn primarily between June through September. The future scenario from the model suggested spawning will become more variable, decreasing during summer months and spiking during November and December and during April and May (Figure 2.8d). Essentially, this species was projected to develop a bimodal spawning season under the RCP 8.5 climate change scenario. Spawning seasonality was projected to shift by -2.9 days decade^{-1} earlier in the season based on central tendency scores (Table 2.2, Figure 2.11). IHS for gray snapper varied differently compared to other species. While all other species in both the grouper and snapper FSAs experienced 18-82% loss of spawning habitat, gray snapper showed a 104.7% increase of suitable habitat (Table 2.3; D=17.5%, df=11). An equatorward shift was seen from the model by 8.5 km decade^{-1} (Table 2.4, Figure 2.13).

2.3.9. Comparison between grouper and snapper FSAs (Families Serranidae vs. Lutjanidae)

Data presented herein showed that groupers tended to prefer cooler winter months and historically have spawned between December-April throughout most of their range, with the exception of Bermuda. The selected snappers typically spawned later in the spring and summer between March and September, preferring warmer temperatures (Figure 2.1). Modelled spawning probability was maximized for groupers was between 24 and 28°C (Figure 2.1). For seasonal SST gradients, the maxima modelled probability of encountering FSAs falls between -1.5 and 1°C for groupers, with the exception of red hind in which the model of best fit did not include seasonal SST gradients (Figure 2.2). The modelled probability of spawning for the snapper group was maximized at SSTs of 26.5-31°C and at between -1 and 2°C for seasonal SST gradients (Fig. 2.1-2.2).

Significant differences between taxonomic groups were seen in central tendency of phenological shifts and integrated habitat suitability, while the results of mean latitudinal shift were not significant (Table 2.5). However, there was a significant difference in central tendency for shifts of spawning seasonality between grouper and snapper FSAs ($P<0.05$, $t=4.6$, $df=6$) . Groupers had a mean shift of 2.8 days decade^{-1} between historical and future scenarios, while snappers had a shift of -4.7 days decade^{-1} (Table 2.5). A positive mean value suggested groupers will shift to spawn later in the season, while a negative value signified spawning season for snappers will move to earlier in the year. In Figures 2.3 and 2.4, peak habitat use for historical areas was not always equal to areas with observed aggregations which could imply a level of uncertainty with species distribution.

Differences in IHS scores between historical and future periods were measured as an odds ratio for statistical analysis. The results of the statistical analysis indicated a difference between snappers and groupers in terms of changes in the probability of suitable spawning habitat ($P<0.05$, $t=3.8$, $df=6$).

On average, groupers had a poleward shift in distribution of 15.6 km decade^{-1} compared to a -3.7 km decade^{-1} equatorward shift among the snapper group (Table 2.5). There was not a statistically significant difference between snapper and grouper FSAs in the latitudinal shift of spawning sites ($P>0.05$, $t=1.9$, $df=6$). The mean latitudinal shift was highly variable among species.

2.4. Discussion

2.4.1. Variables influencing FSAs

For all species, spawning habitat was modeled by a combination of SST and a hydrographic variable, including *u* or *v* geostrophic current anomalies, EKE and vertical velocity. The most frequent metric selected in the models as influencing species distribution was SST. Results from all of the study species are consistent with previous research on Nassau grouper indicating the importance of temperature in habitat selection and influence on distribution changes (Asch and Erisman, 2018). Findings from this study are also consistent with previous work showing that seasonal deviations in monthly SST were among the most important influences on the distribution on large-bodied fish species (Mellin et al., 2016). In this study, I found that grouper species spawned at similar temperatures (24-28°C). However, Nassau grouper were the most selective in their range with regards to temperature, while red hind was the most variable (Figure 2.5). Snappers spawned within similar geographic ranges, but at warmer temperatures (26.5-31°C) compared to groupers (Figure 2.1).

Seasonal SST gradients was an important metric in all species except for red hind, indicating that the change in temperature across seasons was a factor influencing spawning habitat in addition to the absolute temperature. Certain reef fish species spawn during warming and cooling periods rather than at a specific temperature (Wooton & Smith, 2015). Snappers tended to favor warming temperatures within -1 to 2°C compared to groupers, which overall had gradient results at -1.5 to 1°C but varied more between species (Figure 2.2).

Four snapper and three grouper species had *v* geostrophic current anomalies as a metric selected in the model, while three grouper and two snapper species had *u* geostrophic current anomalies selected. For both variables, the data are centered around zero, suggesting spawning occurs in areas with slow currents in those directions. However, this may be due to the fact that this study looked at climatologies of geostrophic currents anomalies averaged over a 20-year period, which resulted in the majority of values for geostrophic currents being close to zero. Using climatologies, it is more appropriate to interpret that the results indicated deviations from typical conditions in currents are not conducive to spawning.

EKE was selected as a metric in the model of best fit for both red hind and gray snapper (Figure 2.5), while vertical velocity was only detected as an important metric in gray snapper (Figure 2.6). EKE and vertical velocity may affect FSA distribution through creation of conditions that influence larval fish feeding, as well as the transfer of eggs and larvae. Drifters released during spawning periods were retained in eddies, indicating they may act to retain larvae closer to suitable habitat (Heppell et al., 2008; Donahue et al., 2015). Additionally, drifters released at FSA sites moved more quickly offshore than those released at adjacent sites, which suggested that rapid offshore movement lowered predation risk (Gladstone, 2007; Donahue et al., 2015).

However, both red hind and gray snapper had low Akaike weights, 0.29 and 0.14 in the top models, respectively (Table 2.1). This suggests lower confidence for these models, implying uncertainty in the importance of EKE and vertical velocity in influencing spawning habitat suitability. Compared to other species, gray snapper had a low number of spawning observations with a sample size of 16, while the sample size for red hind was 30. This may have impacted results. Lane snapper also had low Akaike weights compared to other study species (Table 2.1). Results may have also been variable due to the fact that lane snapper is classified as a resident spawner rather than a transient spawner, which could cause its distribution to be less tightly influenced by environmental conditions in the model. Rather than migrating to specific sites with certain environmental conditions, this species stays within its home range for spawning. Resident spawning sites may minimize costs of migration and time exposed to increased predation risk (Donahue et al., 2015). This may indicate that geomorphic or oceanographic conditions important to transient FSA species may not be applicable in the same manner to lane snapper.

Chlorophyll was not selected in any of the models of best fit, indicating that spawning habitat may either not be influenced by biological productivity or the measure alone is not enough to capture the influence of productivity in the system. Biological productivity is potentially important to FSA locations, but may not be adequately captured by chlorophyll at the spatial scale of this analysis. Studies have shown chlorophyll to be a useful indicator of primary production when expressed as a flux and phytoplankton biomass when expressed as a scalar, but this has limitations at larger scales (Friedland et al., 2012). Different measures of productivity may be more appropriate to include as a future variable, for example primary production, zooplankton productivity, or export of energy to the benthos (Stock et al., 2016). Friedland et al. (2012) explored primary production and fisheries yields in marine ecosystems and found metrics such as particle-export ratio and the ratio of secondary to primary production provided greater understanding to factors controlling fisheries production than only examining chlorophyll concentration.

2.4.2. Phenological shifts in FSA occurrence

There was a clear pattern in phenological shifts between groupers and snappers that fell in line with the original hypotheses that there would be differences in phenological change between taxonomic groups. Groupers shifted phenology slightly later in the season. Groupers spawn during colder months and consequently cannot shift the timing of spawning by very much in order to track seasonal climate velocity since they are spawning already in the coldest months of the year. This is consistent with previous research suggesting that climate change will cause marine organisms to track the velocity of climate change and shifts in seasonal timing of temperatures (Burrows et al., 2011). Since marine biodiversity is higher in the tropics, this is of particular conservation concern as these areas tend to have greater phenological velocities of climate change (Burrows et al., 2011). In contrast to the groupers, snappers were projected to shift spawning earlier in the year, with peak spawning months moving from summer to spring and even late winter, with some variability between species. Gray snapper was the only species to exhibit a bimodal response in phenology with climate velocities pointing in both directions, meaning shifts in spawning occurred both earlier and later in the year. As previously stated, gray snapper had a comparatively small sample size, the lowest Akaike weights and had six models with ΔAIC < 2, which were all averaged prior to running climate projections.

These phenological shifts have implications for predator-prey mismatch since certain fish species are known to match the seasonal timing of spawning to the food availability for larvae in the environment (Cushing, 1990; Neuheimer et al., 2018). Adult predators respond to environmental cues to match the timing of first feeding by larvae with the seasonally varying timing of prey availability (Neuheimer et al., 2018). Mismatches caused by phenological shifts of spawning events could increase vulnerability of predator and prey species (Kharouba et al., 2018). The environmental cues used by predators may lose predictive power under the effects of climate change, further increasing the mismatch in the future (Mackas and Trudel, 2007). Previous research has supported that adaptations to prey timing may drive life-history timing for many species (Reglero et al., 2018). For example, a study on Atlantic cod populations found that, in the absence of local adaption, fish populations produce larvae when concentrations of preferred prey were likely to affect the growth and survival of larvae (Neuheimer et al., 2018). If the timing of predator and prey groups both respond to environmental shifts in similar ways, the survival effects of life history phenology shifts could be minimized (Mackas and Trudel, 2007; Neuheimer et al. 2018). However, asynchronous responses among trophic levels to rapid climate change could have negative impacts on the fitness of organisms and lead to drastic declines in local populations and extinctions (Willis et al., 2008). Differences in temperature sensitivity across trophic levels can have a larger effect on abundance if this causes interacting trophic levels to become decoupled (Mackas and Trudel, 2007; Riche et al., 2014). This risk of decoupling can be especially important for lower trophic levels where some of the major environmental factors controlling their productivity shifts, while other factors are held constant, for example shifting temperature, but constant light (Neuheimer et al. 2018).

2.4.3. Latitudinal shifts in FSA sites

Compared to phenological changes where there were distinct differences among fish families, the results of this study are less clear cut when looking at projected latitudinal shifts in groupers and snappers. Groupers tended to have larger poleward shifts in distribution, but this varied from species to species. Similar to the pattern seen with phenological shifts, Nassau and yellowfin grouper had the greatest latitudinal distribution shifts within the groupers. However, there was no statistical significance in poleward distribution shifts between the two families studied here (Table 2.5). The results for latitudinal shifts differed among all species and ranged from approximately -11 km decade^{-1} to 40 km decade^{-1} (Table 2.4). Results for Nassau grouper were consistent with Asch and Erisman (2018), which reflected consistency in methodology between the two studies. Equatorward shifts were observed with lane and gray snapper, whereas red hind was projected to have an extremely small shift in distribution (0.01 km decade^{-1}) (Table 2.4). Models from five of the eight study species that all had high confidence based on Akaike weights showed a poleward shifts in distribution. This is consistent with the global trend towards poleward distribution shifts observed for many fish species despite variations among studies in climate models used, species examined, and regions investigated (Cheung et al., 2009; Morley et al., 2018).

Local extinctions and invasions can be caused by shifts in latitudinal ranges (Parmesan et al., 2006; Cheung et al., 2009). These shifts in distribution have generally extended in the poleward direction with increasing temperatures, with the potential for climate-induced invasions and higher invasion intensity at higher latitudes (Hiddink and Hofsede, 2008; Cheung et al., 2009; Fodrie et al., 2009). Conditions that exceed the temperature range of fish species may make reproduction at preferred FSA sites and seasons no longer possible, forcing them to adapt or shift spawning to cooler regions and seasons to avoid extinction (Dahlke et al., 2020).

While this was the first study to examine climate change impacts on the spawning aggregation locations of Greater Caribbean groupers and snappers, several previous studies have investigated distribution shifts among these species outside of their spawning season. The southward shift for gray snapper identified in this study contrasts with previous research indicating a poleward distribution shift (Hare et al., 2012). However, the magnitude of distribution shifts for FSAs in general and gray snapper in particular are dependent on the climate change scenarios examined in each study. Also, the smaller sample size for gray snapper spawning aggregations and low certainty in model selection may have influenced results. Additionally, this study limited spawning observations to sites with presence of reefs and only examined the spawning life history stage, which differed from Hare et al. (2012). Findings from Morley et al. (2018) showed less agreement in shift direction of species with low certainty in the models, which was the case for gray snapper, lane snapper, and red hind.

2.4.4. Loss in suitable FSA habitat

Our integrated habitat suitability metric explained gains and losses in spawning habitat independent of shifts in fish distribution and changes in phenology. Overall loss of suitable FSA habitat between historical and future periods under the RCP 8.5 scenario ranged between 68-82% for groupers (Table 2.3). This contrasts with the smaller 18-44% loss of habitat among lane snapper, mutton snapper, and cubera snapper, producing significant differences between these two groups of fishes (Table 2.5). Gray snapper differed from all other study species and showed a gain of suitable spawning habitat of nearly 105% by 2100 (Table 2.3). Previous work on gray snapper has also found that this species expands their range under the impacts of climate change as temperatures increase (Hare et al., 2012; Morley et al., 2018). For example, a study conducted on gray snapper in the Gulf of Mexico found a 71% increase in thermal habitat (Morley et al., 2018). Range expansions may increase local biodiversity on short-term timescales as poleward-retreating species are outpaced by poleward advancing species. However, in the long-term these expansions may result in nonnative species invasions, as well as modified local dynamics related to competition, predation, herbivory, and parasitism (Fodrie et al., 2009).

Some research has suggested that rather than range shifts, it may be possible for fish species to respond to climate change by adjusting thermal range through individual acclimatization or evolutionary adaptation across generations (Angilletta et al., 2009; Dahlke et al., 2020). This could be applicable to the study species in their ability to adapt to changing temperatures and spawn in warmer conditions rather than shifting their spawning habitat and range. The model fit for habitat use should also be considered when looking at suitable habitat in both skill and accuracy. The decline in habitats for FSAs may also tie into the ecological needs for spawning habitat in addition to temperature requirements. Spawning sites may provide necessary substrates for egg deposition or hydrographic features that assist with egg and larval dispersal, including currents speeds and flow direction (Heyman & Kjerfve, 2008; Wooton & Smith, 2014; Dahlke et al., 2020). As a result, even if a range shift would provide more suitable temperature conditions for species forming FSAs, additional requirements related to hydrographic conditions and reef geomorphology needed for reproduction may be missing. Studies with coupled physical-biological models suggested larval transport could influence the range of marine species irrespective of local environmental conditions like temperature (Gaylord & Gaines, 2000; Fodrie et al., 2009). Changes and shifts in spawning habitat has further ecological implications, as predation, competition, and prey availability can change in response to co-occurrence of temperate, subtropical and tropical species (Sax et al., 2007; Fodrie et al., 2009). These ecological interactions may influence whether it is possible to establish new FSAs in locations with suitable climatic conditions.

2.4.5. Conclusions

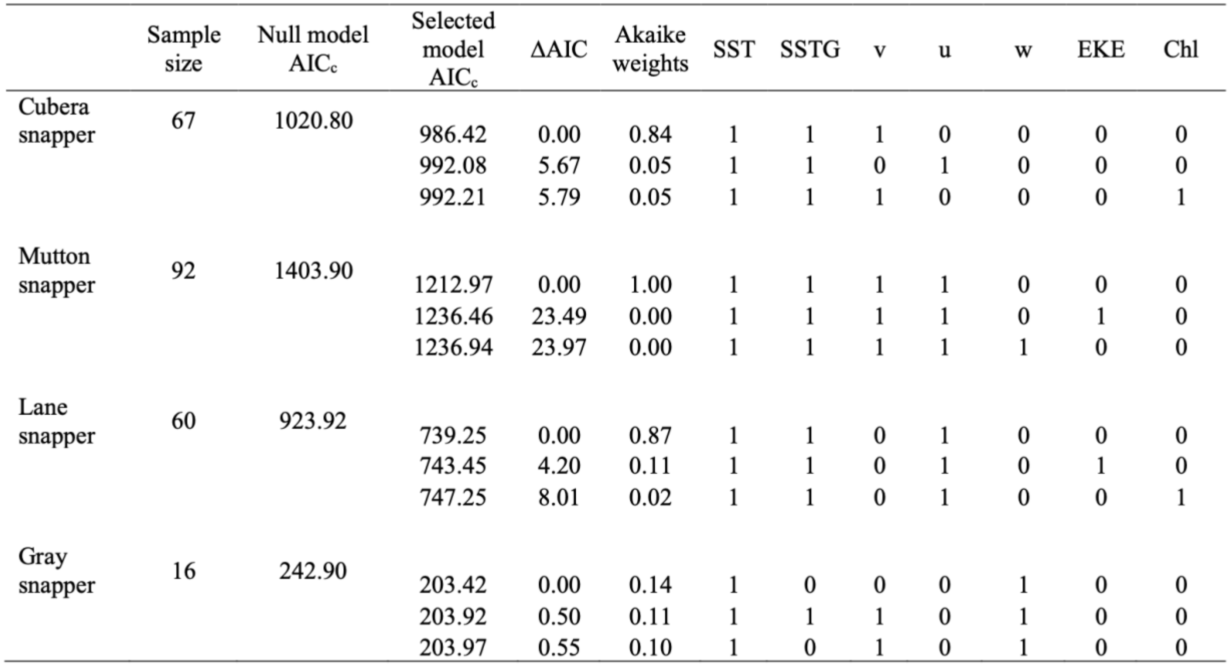
There appears to be tradeoffs between phenological shifts and geographic distributions shifts in how species respond to climate change. Groupers already spawn during the coldest periods, so rather than shifting the month of spawning, there is a small delay and a contraction of spawning season (i.e., few phenological changes). This was reflected in the significantly greater loss of overall suitable habitat of groupers compared to snapper species. The primary response to climate change of groupers was to shift the center of distribution poleward to more northerly waters. In contrast, snappers had larger changes in phenology, smaller changes in spatial distribution, and a lower percentage of suitable habitat loss. Snappers appear more resilient to climate change as evidenced by the lower loss of suitability habitat because these fishes are able to adjust their phenology to spawn earlier in the year when temperatures are cooler. Snappers were not seen to occupy a significantly higher variability of temperature but overall occurred at warmer temperatures compared to groupers during spawning.

The hypotheses of this study explored how suitable habitat, location and timing of FSAs may vary between reef fish groups with varying thermal preferences. These results are consistent with the hypothesis that spawning seasonality differences between groups and lower thermal spawning preferences have greater impacts to groupers in terms of distributional shifts and loss of FSA habitat. However, snappers were seen to have a greater change in the timing of spawning under the effects of the climate scenario. Groupers may experience the greatest shifts in distribution as the thermal spawning temperatures for those species will likely be exceeded before those of snappers under the effects of climate change. Results indicated that grouper spawning aggregations are more strongly affected by climate change for integrated habitat suitability, while snappers are more affected in phenological change. Overall, the findings from this study suggest that there are differences between groupers and snappers in the response of distribution and phenology of FSAs to climate change.

Table 2.1. Top three models for each species with the environmental variables selected from the NPPEN model. Results are based on minimization of the corrected Akaike Information Criterion (AIC).

	Sample size	Null model AIC_c	Selected model AIC_c	ΔAIC	Akaike weights	SST	SSTG	v	u	w	EKE	Chl
Nassau grouper	283	4368.80	4038.51	0.00	1.00	1	1	1	0	0	0	0
			4053.08	14.57	0.00	1	1	1	0	0	1	0
			4053.48	14.97	0.00	1	0	1	0	0	0	0
Yellowfin grouper	39	593.10	529.65	0.00	0.98	1	1	0	1	0	0	0
			538.93	9.27	0.01	1	1	0	1	0	0	1
			540.49	10.84	0.00	1	0	0	1	0	0	1
Black grouper	103	1557.50	1417.80	0.00	0.93	1	1	1	1	0	0	0
			1423.76	5.96	0.05	1	1	0	1	0	1	1
			1426.59	8.79	0.01	1	0	0	0	0	1	1
Red hind	30	445.90	395.27	0.00	0.29	1	0	1	1	0	1	0
			397.85	2.58	0.08	1	1	1	0	0	1	1
			398.18	2.91	0.07	1	0	1	1	0	1	1

Table 2. (cont.)1. Top three models for each species with the environmental variables selected from the NPPEN model. Results are based on minimization of the corrected Akaike Information Criterion (AIC).



	Sample size	Null model AIC_c	Selected model AIC_c	ΔAIC	Akaike weights	SST	SSTG	v	u	w	EKE	Chl
Cubera snapper	67	1020.80	986.42	0.00	0.84	1	1	1	0	0	0	0
			992.08	5.67	0.05	1	1	0	1	0	0	0
			992.21	5.79	0.05	1	1	1	0	0	0	1
Mutton snapper	92	1403.90	1212.97	0.00	1.00	1	1	1	1	0	0	0
			1236.46	23.49	0.00	1	1	1	1	0	1	0
			1236.94	23.97	0.00	1	1	1	1	1	0	0
Lane snapper	60	923.92	739.25	0.00	0.87	1	1	0	1	0	0	0
			743.45	4.20	0.11	1	1	0	1	0	1	0
			747.25	8.01	0.02	1	1	0	1	0	0	1
Gray snapper	16	242.90	203.42	0.00	0.14	1	0	0	0	1	0	0
			203.92	0.50	0.11	1	1	1	0	1	0	0
			203.97	0.55	0.10	1	0	1	0	1	0	0

Table 2.2. Relative importance of environmental covariates influencing the distribution of grouper FSA sites. Variables with a greater effect on habitat suitability can be identified by larger summed Akaike weights ($\sum w_i$) (Burnham and Anderson, 2002). Scores range from 0-1, with 1 having the greatest influence on distribution.

	Nassau grouper $\sum w_i$	Yellowfin grouper $\sum w_i$	Black grouper $\sum w_i$	Red Hind $\sum w_i$
SST	1.0000	1.0000	1.0000	0.9968
Seasonal SST Gradients	0.9994	0.9945	1.0000	0.3488
u	<0.0001	0.9999	0.9885	0.9999
v	1.0000	0.0005	1.0000	0.9945
w	<0.0001	<0.0001	<0.0001	<0.0001
EKE	<0.0001	0.0019	0.0115	0.7872
Chl	<0.0001	0.0150	0.0481	0.2995

Table 2.3. Central Tendency (CT) of seasonal spawning time for each species from the model for historical and future scenarios. CT corresponds to the weighted average month of spawning, so that a value of 1 indicates spawning in January, a value of 2 indicates spawning in February, etc. Differences between climate scenarios are expressed as changes in days decade^{-1}. Positive values represent a shift to later in the season and negative values are a shift to earlier in the spawning season.

	Historical 1981-2000 CT	Future 2081-2100 CT	Days decade^{-1}
Nassau grouper	0.82	1.84	3.10
Yellowfin grouper	0.53	2.15	4.92
Black grouper	0.57	1.16	1.80
Red hind	0.46	0.87	1.25
Cubera snapper	6.85	5.15	-5.16
Mutton snapper	7.37	5.80	-4.77
Lane snapper	7.16	5.26	-5.78
Gray snapper	7.76	6.80	-2.92

Table 2.4. Integrated Habitat Suitability (IHS) scores expressed in percent change for each species. Positive values indicate loss of suitable spawning habitat, while negative values indicate gain of habitat. Note that IHS scores are unitless and dependent on area of integration.

	Historical 1981-2000 IHS	Future 2081-2100 IHS	Percent Change (%)
Nassau grouper	516.08	92.82	82.01
Yellowfin grouper	501.20	145.07	71.06
Black grouper	599.25	184.80	69.16
Red hind	676.82	211.32	68.78
Cubera snapper	564.22	461.98	18.12
Mutton snapper	462.44	301.98	34.70
Lane snapper	264.02	147.30	44.21
Gray snapper	147.27	301.50	-104.73

Table 2.5. Mean Latitudinal Shift (MLS) for each species for historical and future scenarios. Historical and future values are in degrees of latitude, while differences between species are measured in km decade^{-1}. Positive values signify a poleward shift and negative values represent an equatorward shift.

	Historical 1981-2000 MLS	Future 2081-2100 MLS	Km decade^{-1}
Nassau grouper	17.42	21.02	39.82
Yellowfin grouper	17.09	19.13	22.49
Black grouper	20.26	20.31	0.15
Red hind	20.37	20.22	-0.01
Cubera snapper	16.62	16.74	1.33
Mutton snapper	18.84	19.11	3.00
Lane snapper	18.32	17.36	-10.65
Gray snapper	18.66	17.89	-8.54

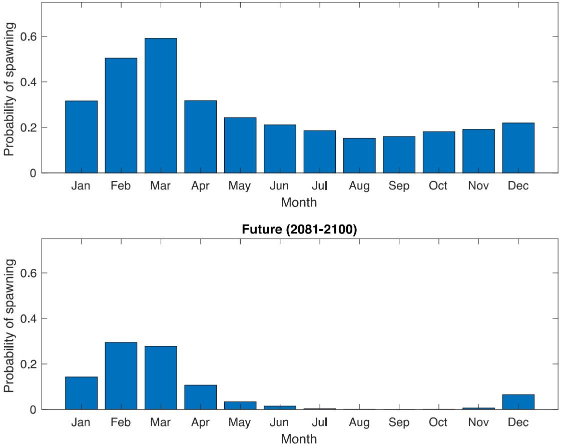
Table 2.6. Relative importance of environmental covariates influencing the distribution of snapper FSA sites. Variables with a greater effect on habitat suitability can be identified by larger summed Akaike weights ($\sum w_i$).

	Cubera snapper $\sum w_i$	Mutton snapper $\sum w_i$	Lane snapper $\sum w_i$	Gray snapper $\sum w_i$
SST	0.9970	1.0000	1.0000	1.0000
Seasonal SST Gradients	1.0000	1.0000	0.999300	0.4300
u	0.1088	0.9999	1.0000	0.5814
v	0.9453	1.0000	0.0013	0.4831
w	<0.0001	<0.0001	0.0041	0.4062
EKE	0.0013	0.0559	0.0873	0.0496
Chl	0.0658	0.0558	0.0168	0.2399

Table 2.7. Independent two-sample t-test comparing grouper and snapper metrics from historical to future periods under the RCP 8.5 climate scenario. Central tendency results show shifts in spawning seasonality by month. Integrated habitat suitability (IHS) was measured using an odds-ratio comparing change in suitable spawning habitat. Analysis of mean latitudinal shift of FSA sites was compared in days decade^{1}.

	Groupers	Snappers
Central tendency shift		
Mean	2.77	-4.66
Degrees of freedom	6	
Test Statistic (t)	7.27	
P(T<=t)	0.0003	
IHS odds ratio		
Mean	1.32	0.12
Degrees of freedom	6	
Test Statistic (t)	3.76	
P(T<=t)	0.0197	
Mean latitudinal shift		
Mean	15.61	-3.72
Degrees of freedom	6	
Test Statistic (*t*)	1.89	
P(T<=t)	0.1322	

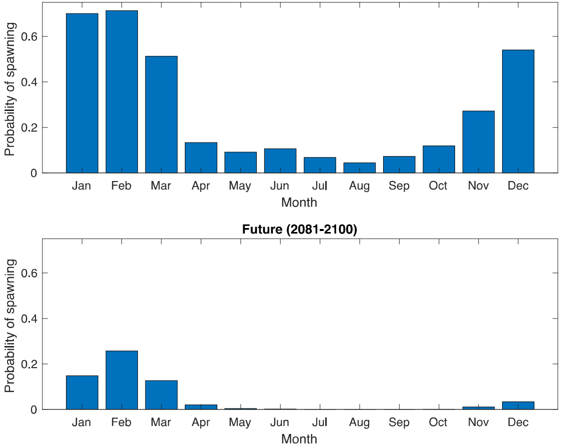
(a) Nassau grouper



Historical (1981-2000)

Future (2081-2100)

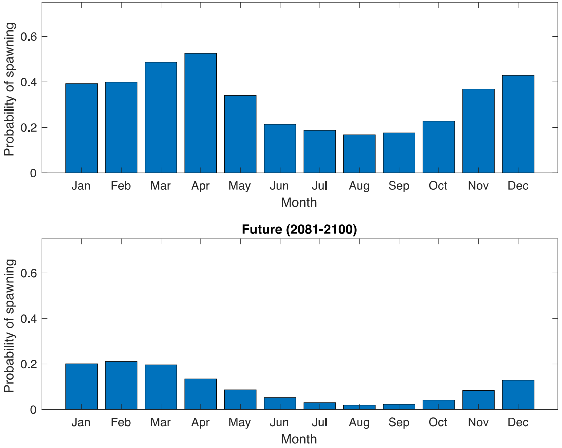
(c) yellowfin grouper



Historical (1981-2000)

Future (2081-2100)

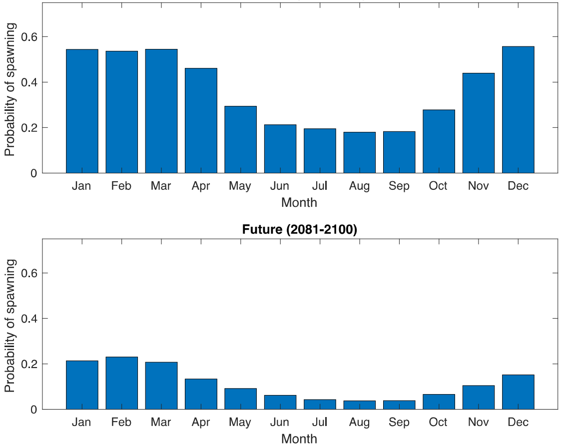
(b) black grouper



Historical (1981-2000)

Future (2081-2100)

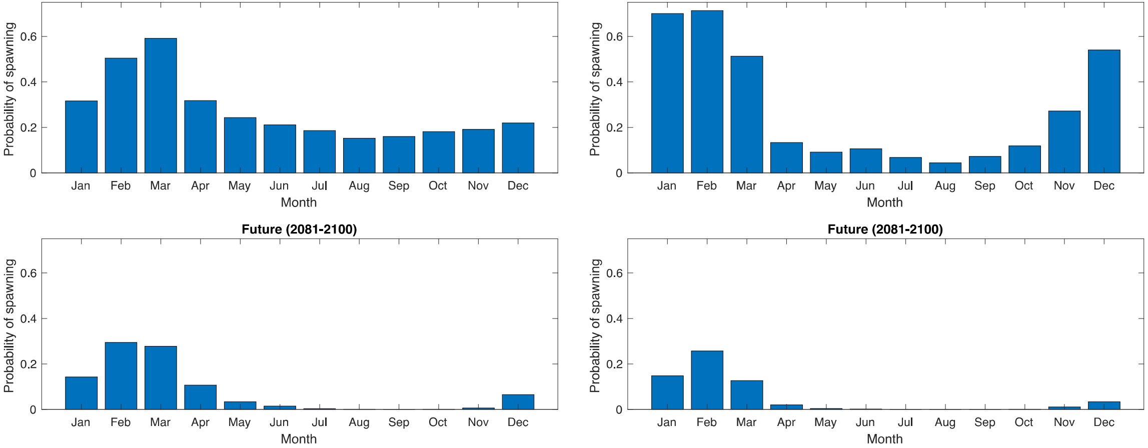
(d) red hind



Historical (1981-2000)

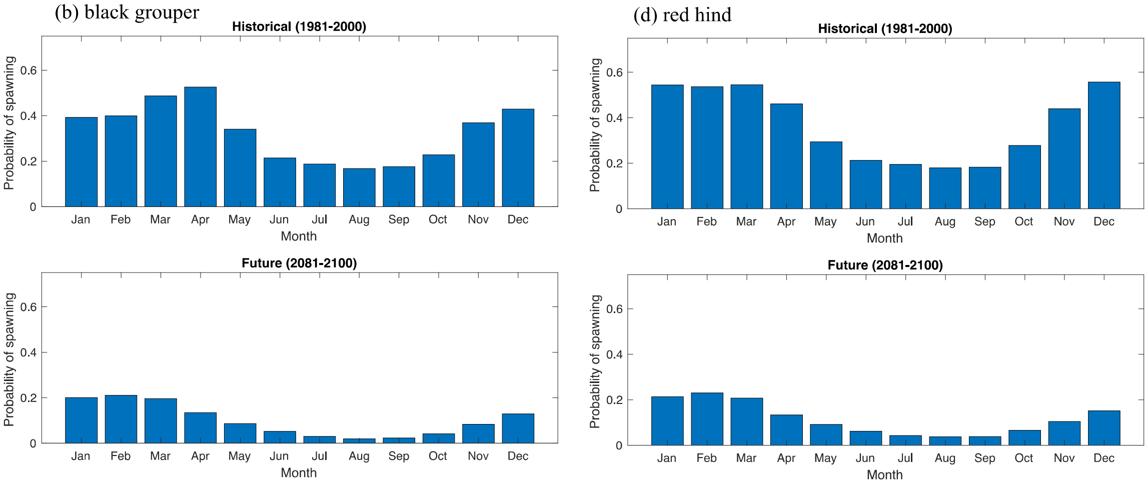
Future (2081-2100)

Figure 2.1. Phenological shifts in spawning seasonality for grouper species from the GFDL ESM2M model between historical and future periods. Species included on top of each subplot are Nassau grouper (a), yellowfin grouper (b), black grouper (c), and red hind (d).



(a) Nassau grouper

(c) yellowfin grouper



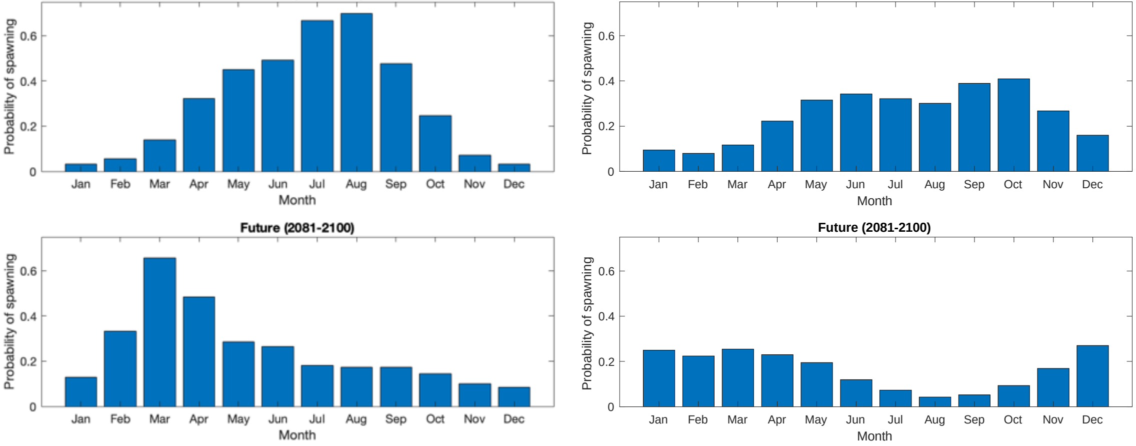
(b) black grouper

(d) red hind

Figure 2.1. Phenological shifts in spawning seasonality for grouper species from the GFDL ESM2M model between historical and future periods. Species included on top of each subplot are Nassau grouper (a), yellowfin grouper (b), black grouper (c), and red hind (d).

(a) cubera snapper

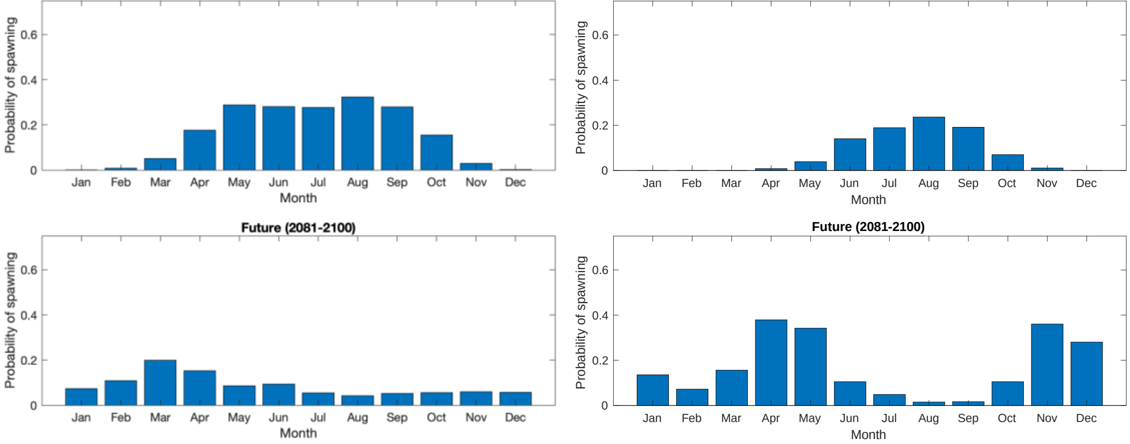
(c) mutton snapper


Historical (1981-2000)

Future (2081-2100)

(b) lane snapper

(d) gray snapper


Historical (1981-2000)

Future (2081-2100)

Figure 2.2. Phenological shifts in spawning seasonality for snapper species from the GFDL ESM2M model between historical and future periods. Species included on top of each subplot are cubera snapper (a), lane snapper (b), mutton snapper (c), and gray snapper (d).

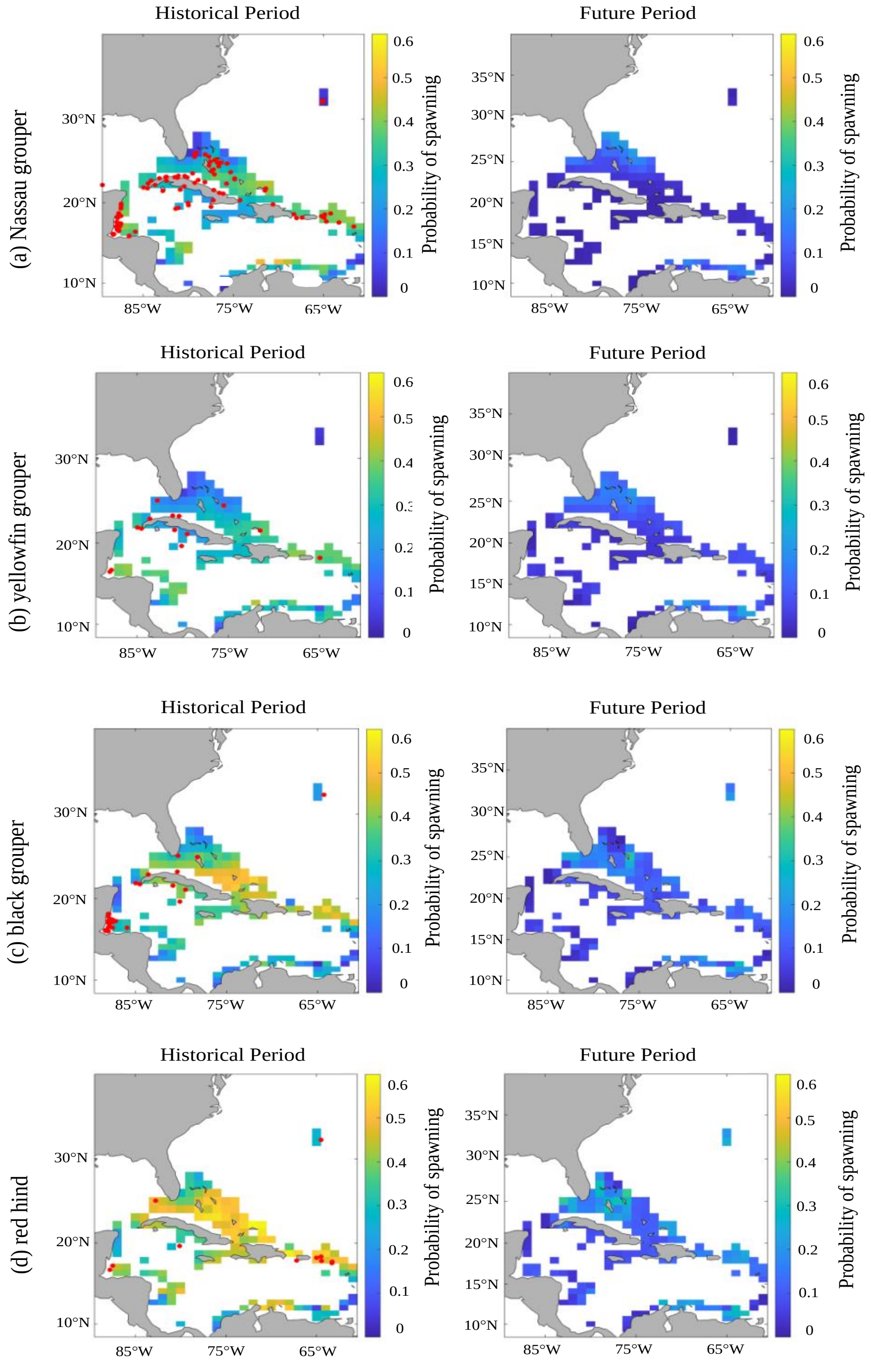


Figure 2.3. Historical and future projections based on annual averages of probability of spawning for grouper species FSAs using the GFDL climate model under the RCP 8.5 climate scenario.

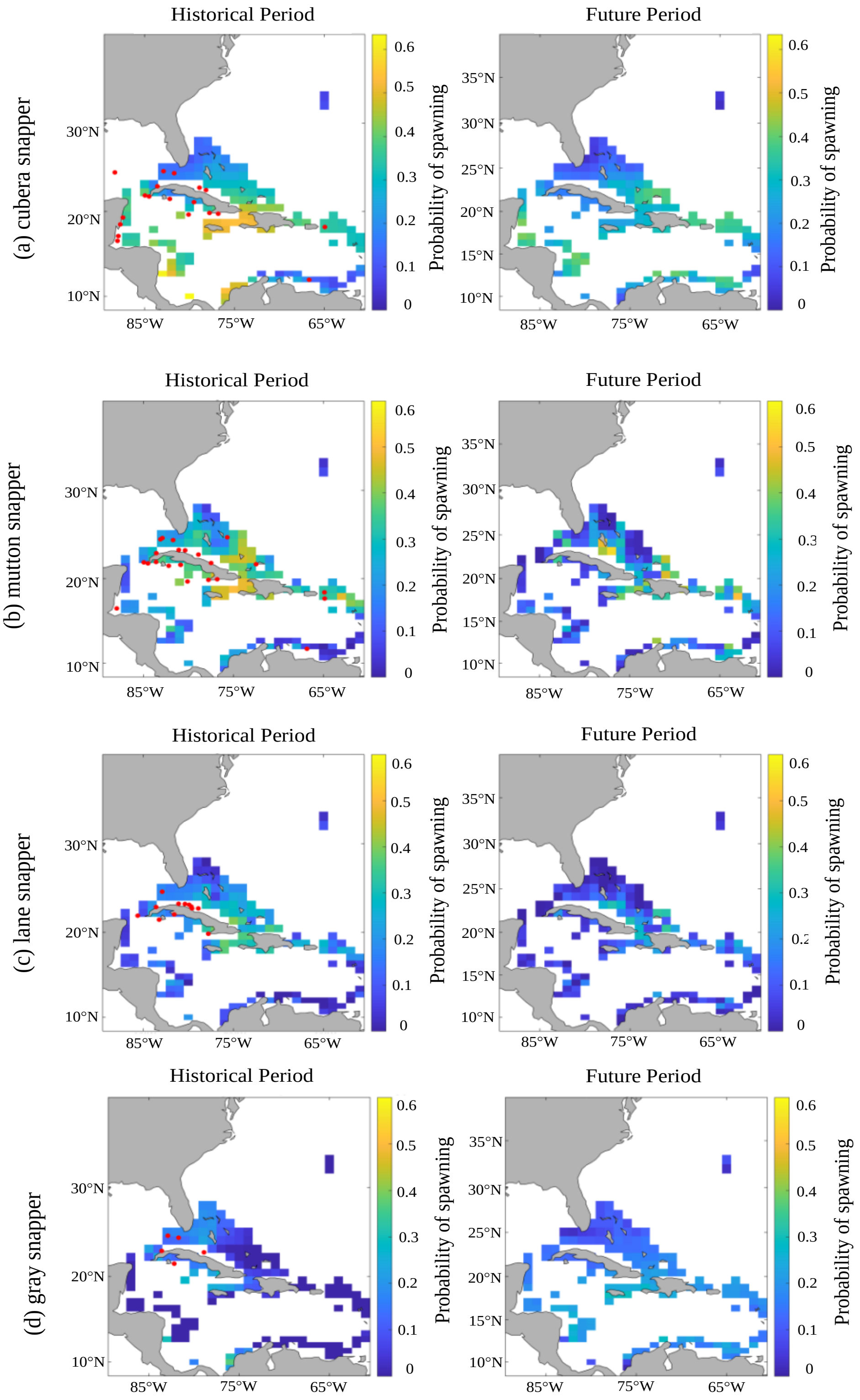
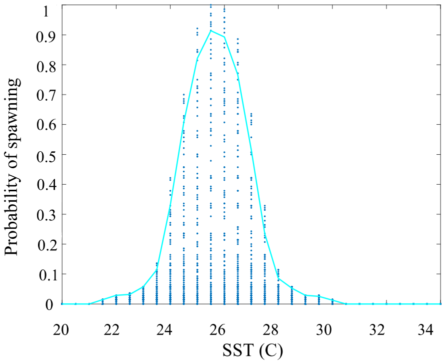
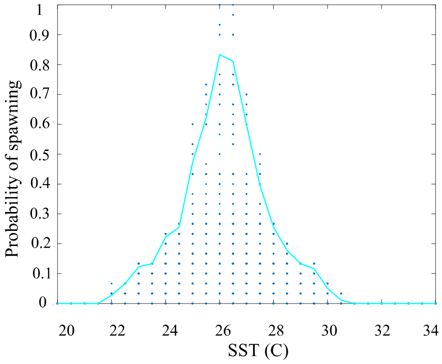


Figure 2.4. Historical and future projections with annual averages of probability of spawning for snapper species FSAs using the GFDL climate model under the RCP 8.5 climate scenario.

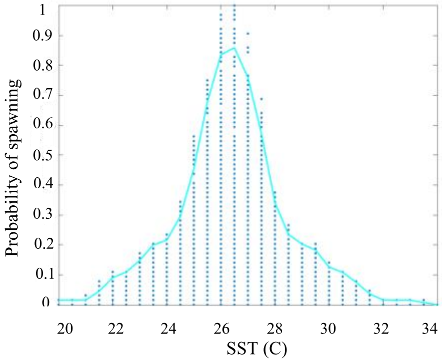
(a) Nassau grouper



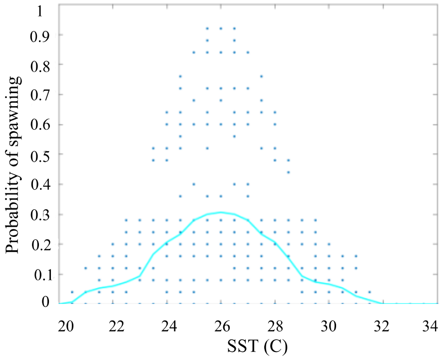
(b) yellowfin grouper



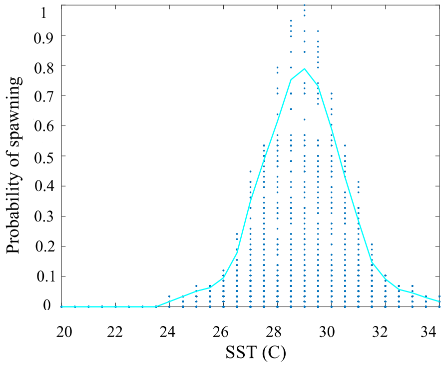
(c) black grouper



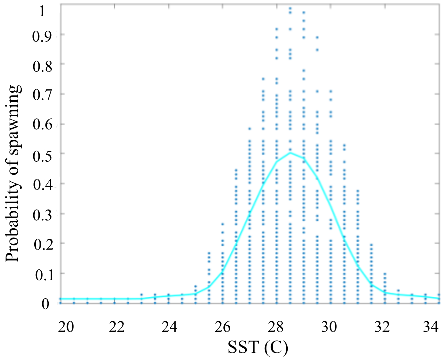
(d) red hind



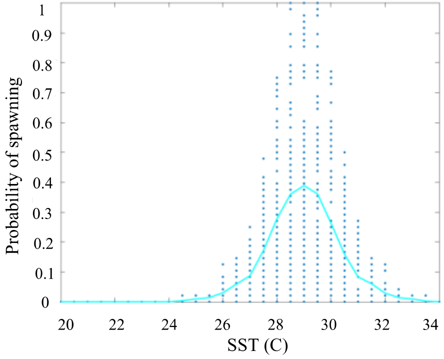
(e) cubera snapper



(f) mutton snapper



(g) lane snapper



(h) gray snapper

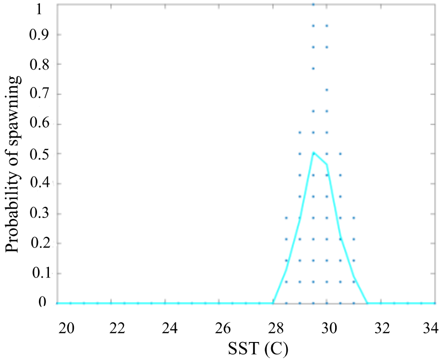
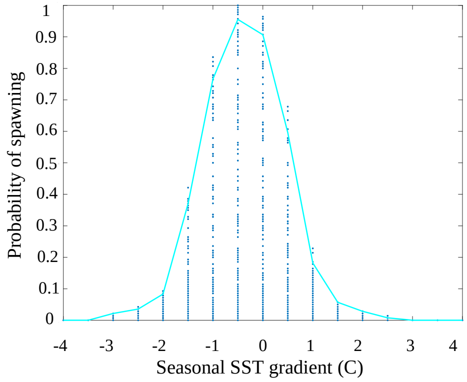
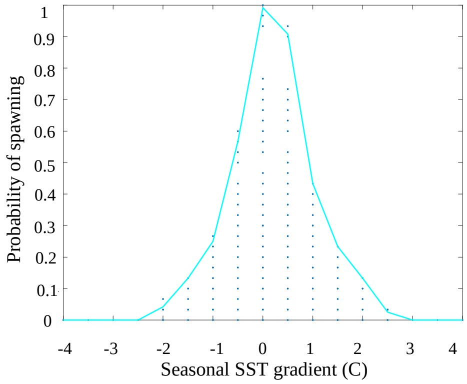


Figure 2.5. NPPEN results comparing seas surface temperature (SST) with PDF curves. All study species had SST selected in the model of best fit.

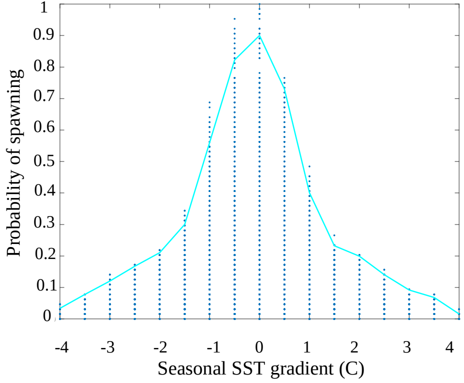
(a) Nassau grouper



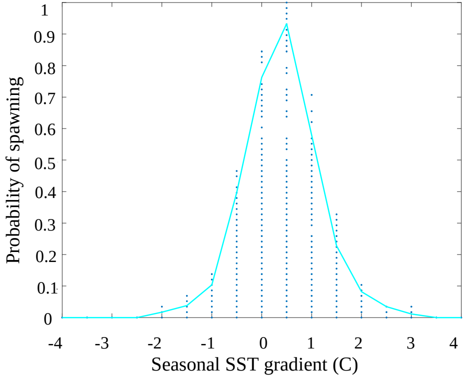
(b) yellowfin grouper



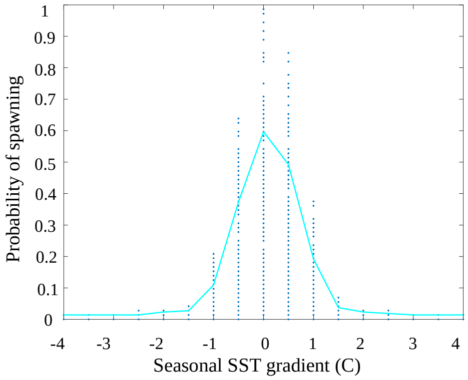
(c) black grouper



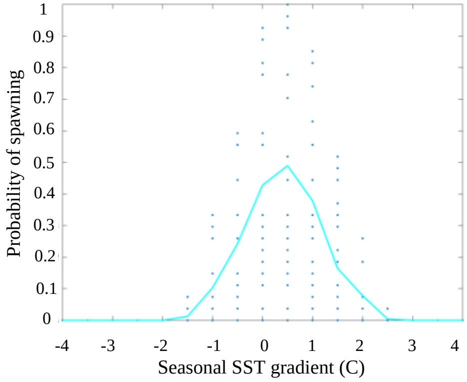
(d) cubera snapper



(e) mutton snapper



(f) lane snapper



(g) gray snapper

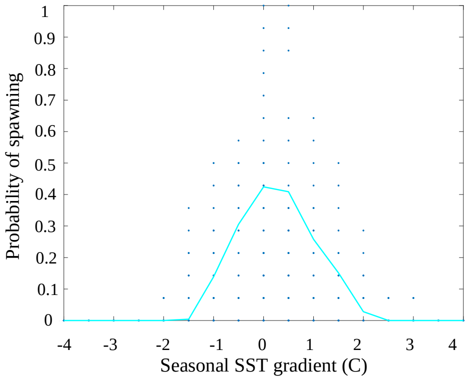
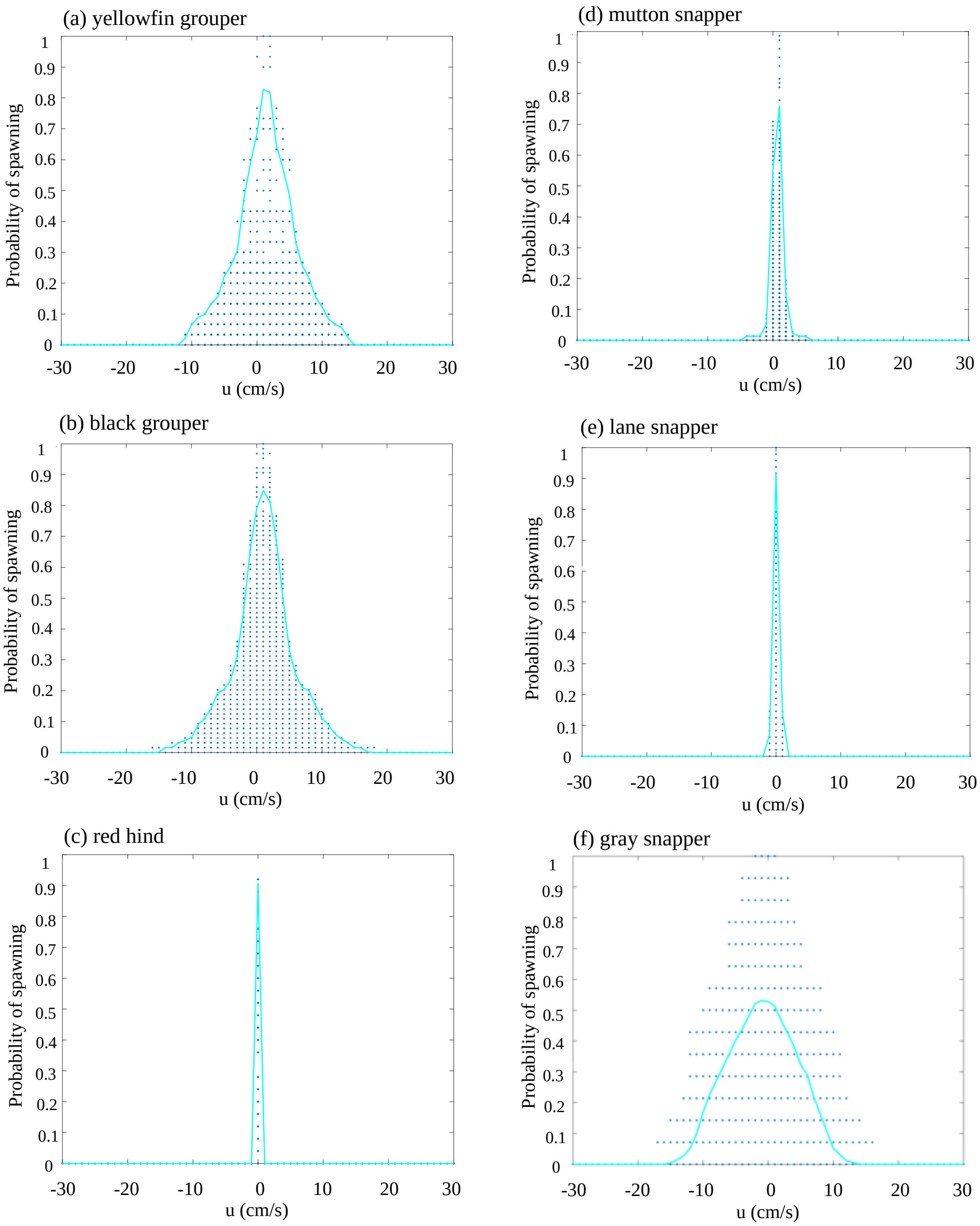


Figure 2.6 NPPEN results comparing seasonal SST gradients with PDF curves. With the exception of red hind, the species distribution model selected this variable in the model of best fit for all species. Negative seasonal SST gradients indicate spawning occurs as temperatures cool seasonally, while positive values show warming temperatures.


(a) yellowfin grouper

(b) black grouper

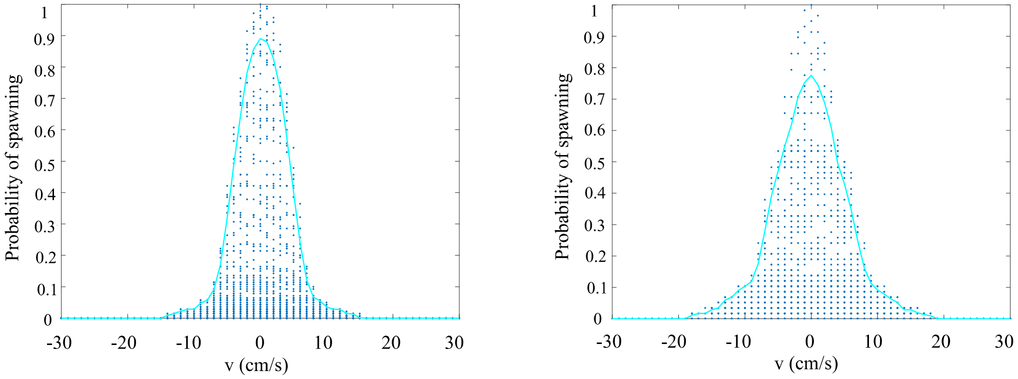
(c) red hind

(d) mutton snapper

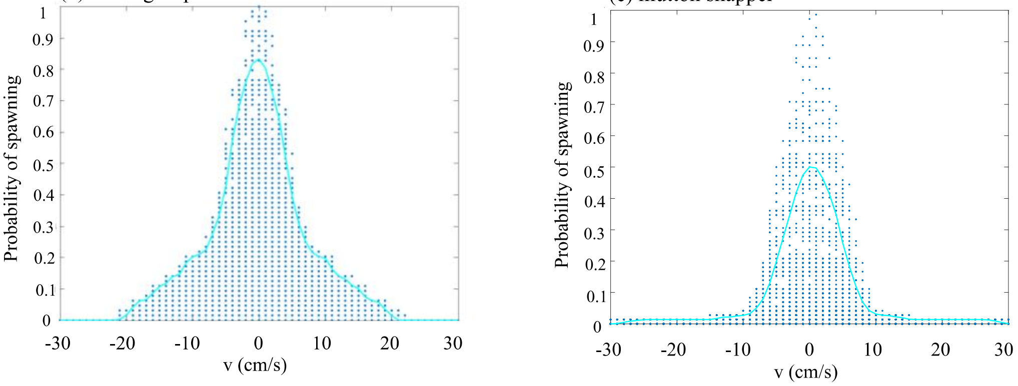
(e) lane snapper

(f) gray snapper

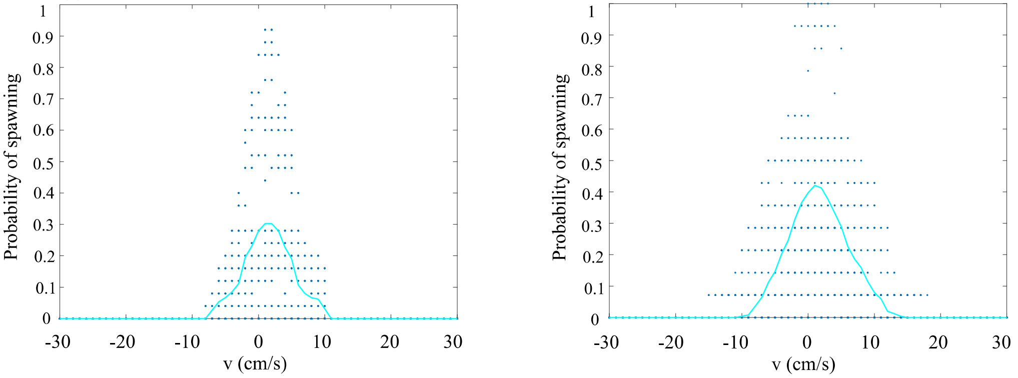
Figure 2.7. NPPEN results comparing seasonal geostrophic currents in the east-west direction (u) with PDF curves. Species with this variable in the model of best fit include above each subplot yellowfin grouper (a), black grouper (b), red hind (c), mutton snapper (d), lane snapper (e), and gray snapper (f).


(a) Nassau grouper

(d) cubera snapper


(b) black grouper

(e) mutton snapper


(c) red hind

(f) gray snapper

Figure 2.8. NPPEN results comparing seasonal geostrophic currents in the north-south direction (v) with PDF curves. The model selected this variable in the model of best fit for all species except for yellowfin grouper and lane snapper.

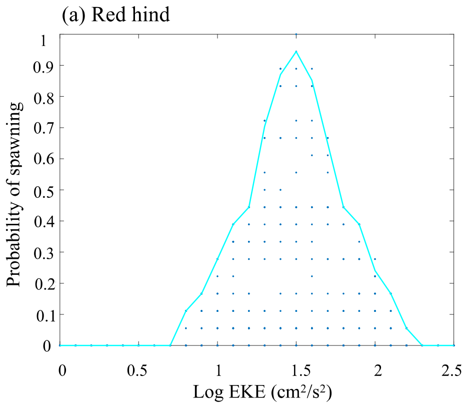


Figure 2.9. NPPEN results with PDF curves for eddy kinetic energy (EKE). Red hind had EKE selected in the model of best fit as a variable influencing FSA distribution.

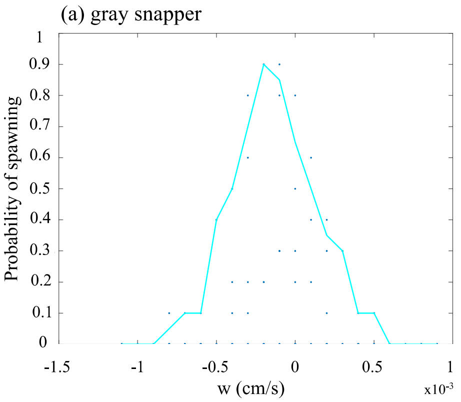


Figure 2.10. NPPEN results with PDF curves for vertical velocity (w). Gray snapper was the only species with vertical velocity selected as a variable influencing FSA distribution.

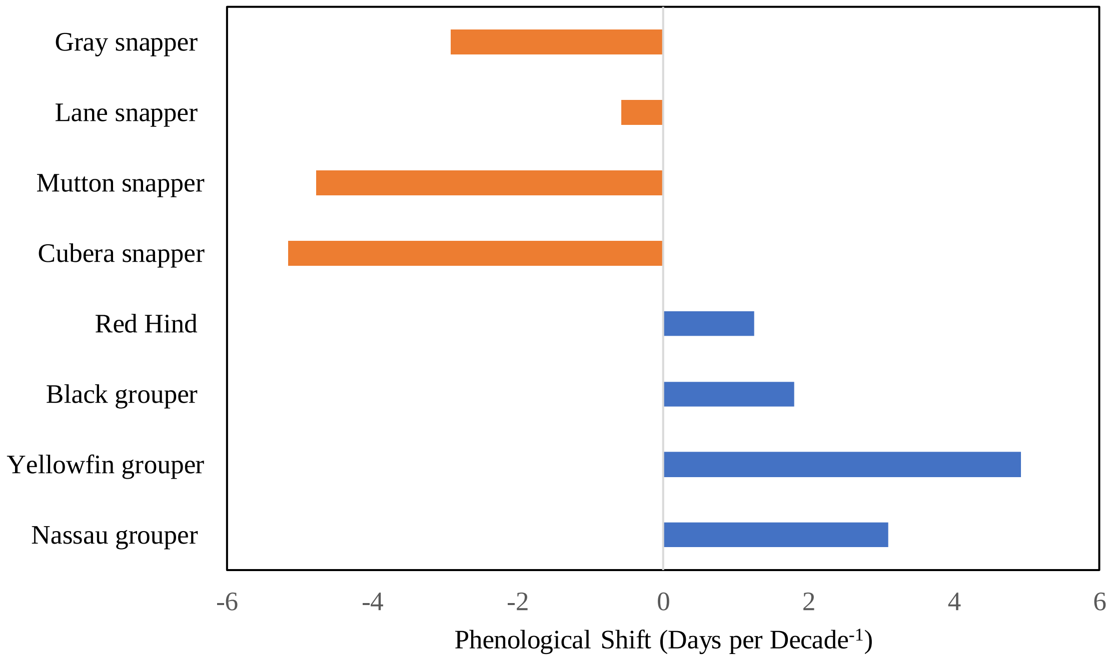


Figure 2.11. Phenological shift of study species from historical to future periods measured as central tendency and expressed in days per decade^{-1}.

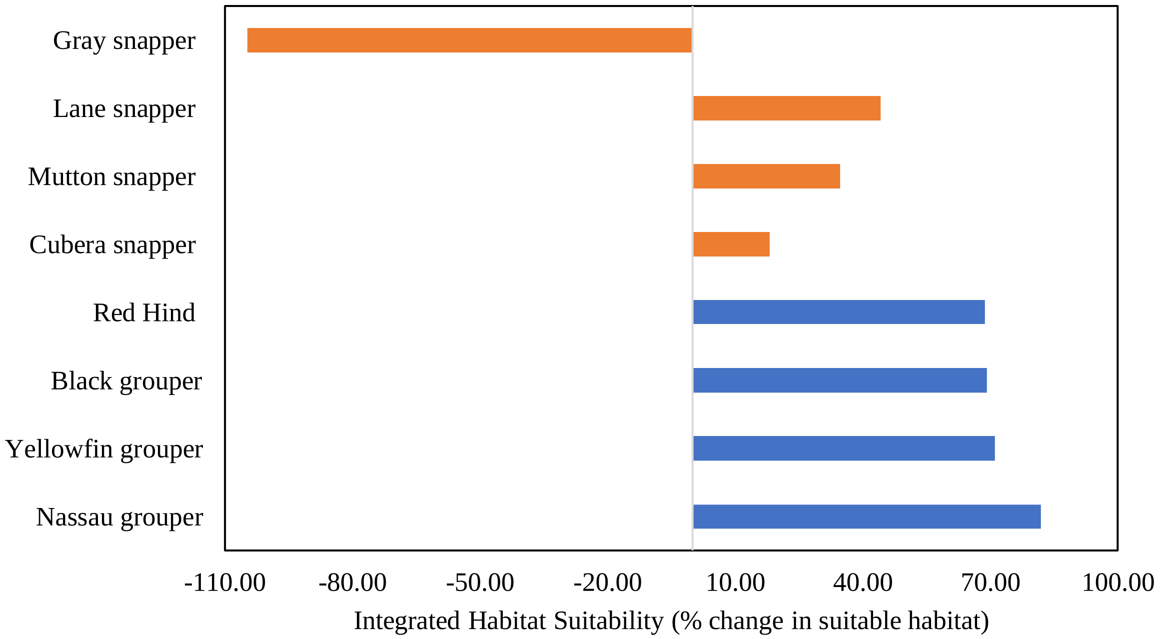


Figure 2.12. Integrated habitat suitability (IHS) of study species measured as loss of suitable habitat and expressed in percentage of suitable habitat lost from historical to future models.

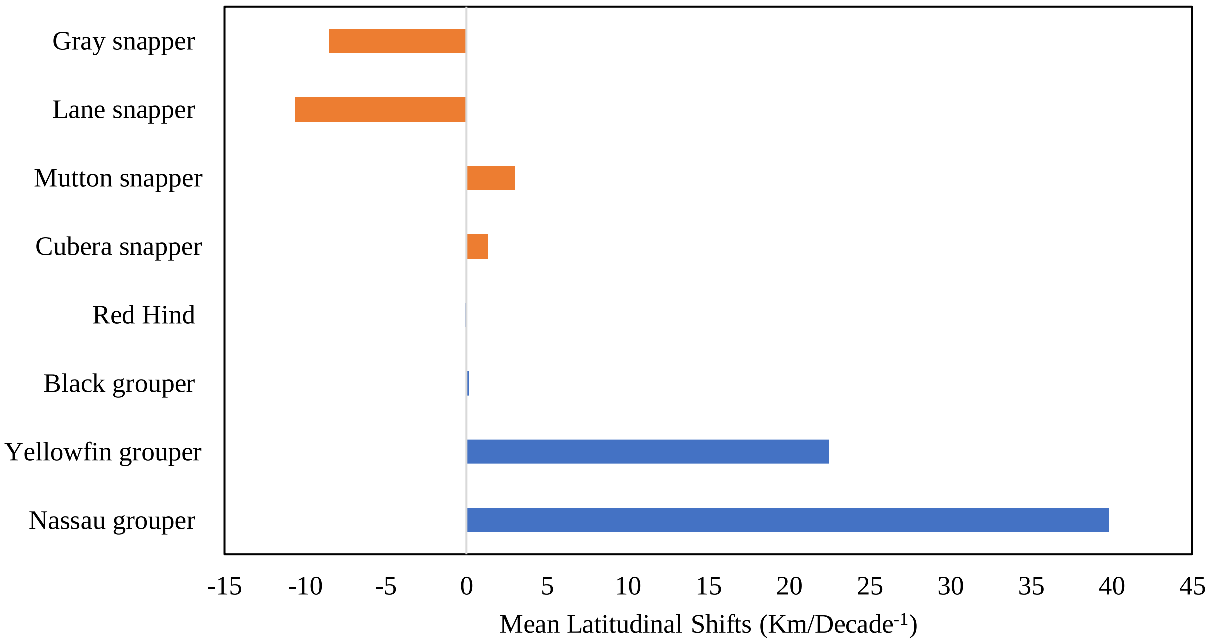


Figure 2.13. Distributional shifts of study species from historical to future periods measured as mean latitudinal shifts and expressed in km per decade^{-1}.

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CHAPTER 3. MANAGEMENT IMPLICATIONS, FUTURE RESEARCH AND CONCLUSIONS

3.1. Management Implications

Multiple management strategies have been used in the past for species that form FSAs, including seasonal fishing and gear restrictions, site closures, sales bans, establishment of marine reserves, as well as adjustment of boundaries for bans and restrictions (Kobara et al., 2013). The Southeast Data, Assessment, and Review (SEDAR) Stock Assessment Reports provide information on fisheries regulations in the United States implemented over time. For example, in 2002 legislation was passed to establish two marine reserves off of the Dry Tortugas where all fishing and anchoring is prohibited, which is a multi-species use FSA site for my study species (SEDAR, 2018). As of 2006, yellowfin grouper, black grouper, mutton snapper, and lane snapper all had closed seasons during spawning periods (SEDAR, 2007). Yellowfin grouper additionally had closures of spawning aggregation sites in 2005 (SEDAR, 2007). Fishing restrictions have previously been put in place on catch and size limits for harvest restrictions (SEDAR, 2018). Commercial permit moratoriums, as well as prohibition of fishing and anchoring, have been set in place in the Virgin Islands in the past to reduce fishing pressure on many reef fish species (SEDAR, 2007).

However, further research on transient FSAs are needed as there may be sites that are unmanaged or undiscovered currently (Kobara et al., 2013). Knowledge gaps on FSAs limit the effectiveness of management strategies meant to protect FSA habitat and productive fisheries, consequently hurting the performance or design of MPAs (Sale et al., 2005; Crowder & Norse, 2008; Kobara et al., 2013). Eklund et al. (2000) provides an example of this where a MPA developed in Florida to protect black grouper excluded an important FSA for the species in both latitude and depth due to a lack of geographic information on their spawning aggregations (Eklund et al., 2000; Kobara et al., 2013).

Management of marine fisheries in response to climate change is important in the tropics, as biodiversity in tropic regions is more likely to be impacted by local extinction and habitat loss (Cheung et al., 2009). Similar to other regions with transient FSAs, understanding the biology and spatial distribution of FSAs in the Greater Caribbean would aid all levels of management efforts through contributing to maintaining healthy and productive stocks (Gruss et al., 2018). From a research perspective, no-take marine reserves can provide a system for studying population movements across reserve boundaries, providing insight as to whether the size and location of the established reserved are being designated appropriately for the intended conservation measures (Feely et al., 2018). Fish populations can be sustained effectively through no-take reserves if spawning occurs within the boundaries or there is connectivity between FSA sites and marine reserves (Sale et al. 2010). Fisheries managers may also need to consider dynamic ocean management with species that are undergoing range and phenological shifts for FSAs. In this case dynamic ocean management refers to developing spatial management zones that are spatially and temporally flexible would allow management to adjust with changes in species distribution and FSA shifts (Maxwell et al., 2015; McHenry et al., 2019).

However, understanding the biology and life history of different species that form FSAs is critical in management as it may not always be practical to establish a single large marine reserve for multispecies movements across important habitats. In certain areas, such as South Florida, the families Lutjanidae and Serranidae are associated with deep offshore reefs, and spawning migrations may cover relatively long distances (Eklund et al., 2000; Gleason et al., 2011, Feely et al. 2018). MPAs could be designated as corridors for connecting current and future geographic distributions for species forming FSAs (McHenry et al. 2019). Corridors may not seem as practical with islands connected by open ocean in the Greater Caribbean Region. However, there are connections through different islands via larval dispersal.

Further research on defining habitats with multi-species use may need to be explored before moving forward with additional protection and establishment of movement corridors for FSAs (Feely et al., 2018).

Adjustment of fishing quotas is a strategy that could be considered based on findings for potential declines in FSA population size, as well as habitat loss and fragmentation. Quotas could help prevent further population declines and reduce fishing pressure on rebuilding fish stocks (McHenry et al. 2019). Past trends from studies have shown that unregulated fishing at transient FSA sites could have led to local extirpations and collapse of certain fisheries as seen with Nassau grouper (Sadovy & Domeier, 2005; Sadovy de Mitcheson et al., 2012; Kobara et al., 2013).

The effects of climate change on FSA populations phenology, distribution and habitat loss has management implications extending to the ecosystem-level. The loss and shift of FSA habitats has implications for organisms outside of the study species included in this analysis, so impacts to other fishes and species from warming temperatures in these regions should be considered in these habitats. Multiple species often share FSA sites, which act as productivity hotspots, attracting fishes to reproduce, apex predators to feed on spawners, and planktonic feeders to consume eggs (Nemeth, 2012; Gruss et al., 2018). I expect that phenological changes in spawning aggregations will impact other organisms in the ecosystem in terms of predator and prey interactions, potentially altering food web dynamics and leading to vulnerability of species with narrower thermal ranges in terms of both physiological impacts and population declines.

The information obtained from this study could be a useful tool in future management of both marine reserves and other types of protected areas as the timing and locations of spawning events could be altered as a result of climate change impacts. This has implications for harvest and fishing restrictions, as well as seasonal sales bans and site closures during spawning events, which may call for further exploration of species distribution shifts under climate impacts.

3.2. Model Uncertainty

Consistent with the methodology of this study, it is a common approach to project species range shifts by integrating geo-referenced spatial data, global climate model projections, and habitat suitability models (Elith & Leathwick, 2009; McHenry et al., 2019). There will always be some degree of uncertainty and limitations to the use of species distribution models, but different techniques and approaches can be used to increase the accuracy of model projections (Araujo et al., 2005). Ecological niche models assume an immediate response to climate change with no potential time lags; however biotic interactions, disturbances, dispersal ability, and rapid evolutionary adaptations may moderate the response of species to climate change (Araujo et al., 2005; Tsoar et al., 2007). By using a future projection period of 2080-2100, potential lagged responses to climate forcing due to time needed for dispersal are considered implicitly under my modeling approach. Since there is a level of uncertainty with these types of models, knowledge gaps can be reduced through the careful evaluation and validation of ecological niche models (Araujo et al., 2005). Increased model accuracy associated with model validation can be important in the decision-making process for fishery management. Establishing and maintaining FSA monitoring programs can help validate models, as well as improve understanding of the status of the fisheries. Since the topic of climate change is a relevant and controversial issue in our society, considering a broad range of models with varying techniques and specifications is essential so results may be used as management tools that consider a full range of possible ecological and fishery responses to the changing environment. Another aspect to consider is the higher level of uncertainty in projections of general circulation models (GCMs) at smaller spatial scales, which may result in large differences of species predictions when using varying GCMs (Neuheimer & Gronkjaer, 2012; Melle et al., 2014; Neuheimer et al., 2018). GCMs project temperature changes better than projections for other variables, such as currents or biological production, leading to a hierarchy of uncertainty between different variables with this modelling approach (Hare et el., 2012; Cheung et al., 2016; Frölicher et al., 2016; Morley et al., 2018).

3.3. Future directions

With the potential for model uncertainty and data limitations for certain species, running multiple climate models should be considered for future research. This method will produce more robust future projections of the geographic distribution of spawning aggregation sites under different levels of climate emissions scenarios (Hawkins and Sutton, 2009; Cheung et al., 2013). For example, the Institut Pierre Simon Laplace (IPSL CM5) model tends to have a higher equilibrium climate sensitivity while GFDL ESM2M has a moderate climate sensitivity. The higher climate sensitivity generates larger changes in temperature per a given change in greenhouse gas emissions, which affects the climate projections (IPCC, 2013; Bopp et al., 2013; Dufresne et al. 2013). Looking at various models can provide insight to how projections may change under with different scenarios. A multiple model approach with different climate models and scenarios could additionally quantify uncertainty ranges at smaller spatial scales and averaging the responses from multiple projections reduces bias from a single model and allows for variance calculations for projections (Melle et al., 2014; Asch, 2015; Neuheimer et al., 2018). Since there is uncertainty with projections of climate and ocean conditions, using more than one climate model allows for examining agreements and differences between models (Cheung et al., 2013). When combined with fishery models, climate projections can be important tools for designing management strategies for conserving and managing species experiencing range shifts (McHenry et al., 2019).

Continued observations of reef fish FSAs in the Greater Caribbean would be useful in increasing accuracy of future analyses. The lack of information on specific geographical locations of FSA sites and the optimal conditions of environmental variables required for spawning is considered a critical research gap preventing effective ecosystem-based fisheries management strategies (Sale et al., 2005; Crowder & Norse, 2008; Kobara et al., 2013).
b (Pecl et al., 2017; McHenry et al., 2019).

Future work exploring the life history characteristics of different species may provide key insights into responses under the impacts of climate change, and consequently managers may need to adapt management strategies. Different life stages of fish species are not equally sensitive to temperature and the effects of climate change. Studies have identified spawners and embryos as the most temperature sensitives stages in the life cycle of fishes (Asch & Erisman, 2018; Dahlke et al., 2020). These differences make it critical to develop modeling approaches that consider the interactions between multiple life history stages under the same framework.

Another aspect to consider for future research is change in depth of spawning since this study was limited to latitudinal shifts and phenology of FSA sites. Similar research conducted has projected species to become restricted to deeper habitats based on historic observations (Pinksy et al., 2013; Kleisner et al., 2016; Morley et al., 2018). This could be an important metric to consider for species that may adjust depth in response to warming temperatures rather than adjusting their phenology or latitudinal distribution. Observations of FSAs for the study species ranged from 0 to 120 meters, with grouper spawning a little deeper on average than snappers (Table 1.1). Establishment of MPAs and implementation of fishing restrictions can also be depth dependent, so this is an important factor to explore in further research.

The variation in my results between shifts in mean latitudinal shift, habitat suitability, and phenology highlights the importance of looking at multiple metrics when studying fisheries under climate change. While there are many studies exploring distributional changes, other metrics such as phenological shifts or habitat use patterns, may provide additional insight to movement patterns.

3.4 Conclusions

There was evidence from this study supporting that climate change will impact the phenology, distribution, and habitat suitability of reef fish transient FSAs. Within these effects, strong differences were seen between the two grouper and snapper families of study species with varying life history characteristics and thermal preferences for spawning. Sea surface temperature coupled with a hydrographic variable were found in each study species to influence distribution and probability of spawning. With cooler preferences for spawning habitat and an overall less change in spawning season, groupers were found to be more impacted by climate change under the RCP 8.5 scenario compared to snapper species, which was consistent with my hypotheses. While the directionality and average latitudinal shift was varied across species, there were significant differences between families in habitat loss and phenological shifts. Snappers are expected to shift spawning earlier in the season, while groupers' spawning season was projected to shift slightly later in the year and have a greater loss of suitable spawning habitat. Researchers should continue to identify and monitor transient FSA habitats for reef fish and expand the use of multiple climate models and scenarios to develop and refine projections of range and phenological shifts under changing future environmental conditions.

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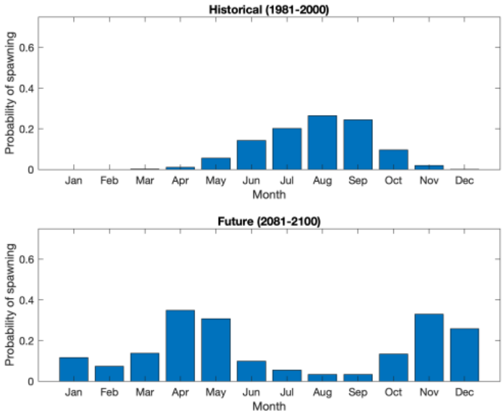
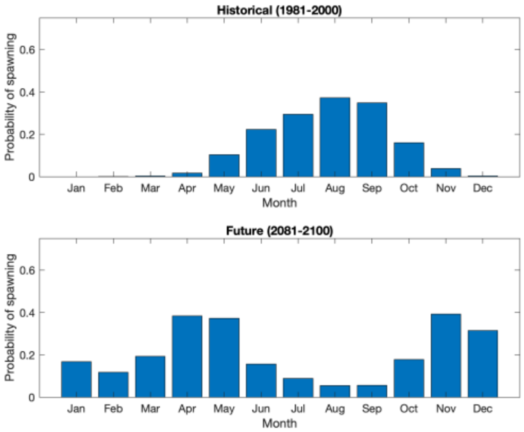
Appendix I. *Intermodel comparison for gray snapper with AIC<2.*

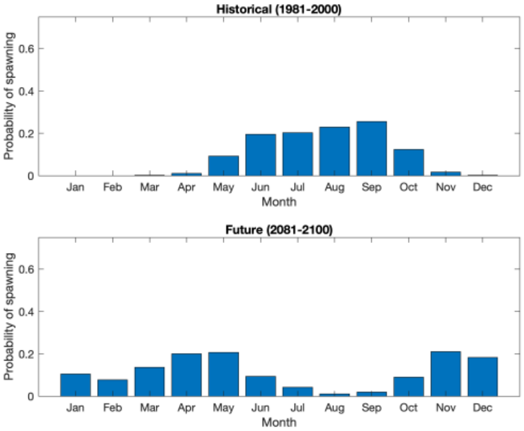
(a) SST, seasonal STG, v & w



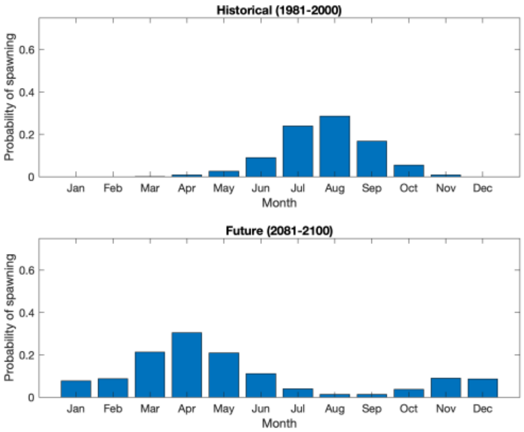
(b) SST, v & w



(c) SST seasonal STG, v & u



(d) SST & v



(e) SST & seasonal SST gradients

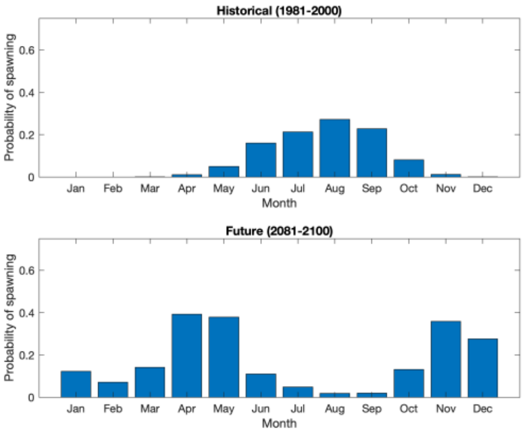


Figure A1. Phenological shifts in spawning seasonality for grouper species from the GFDI ESM2M model between historical and future periods for gray snappers. Models included all had AIC values of less than 2.

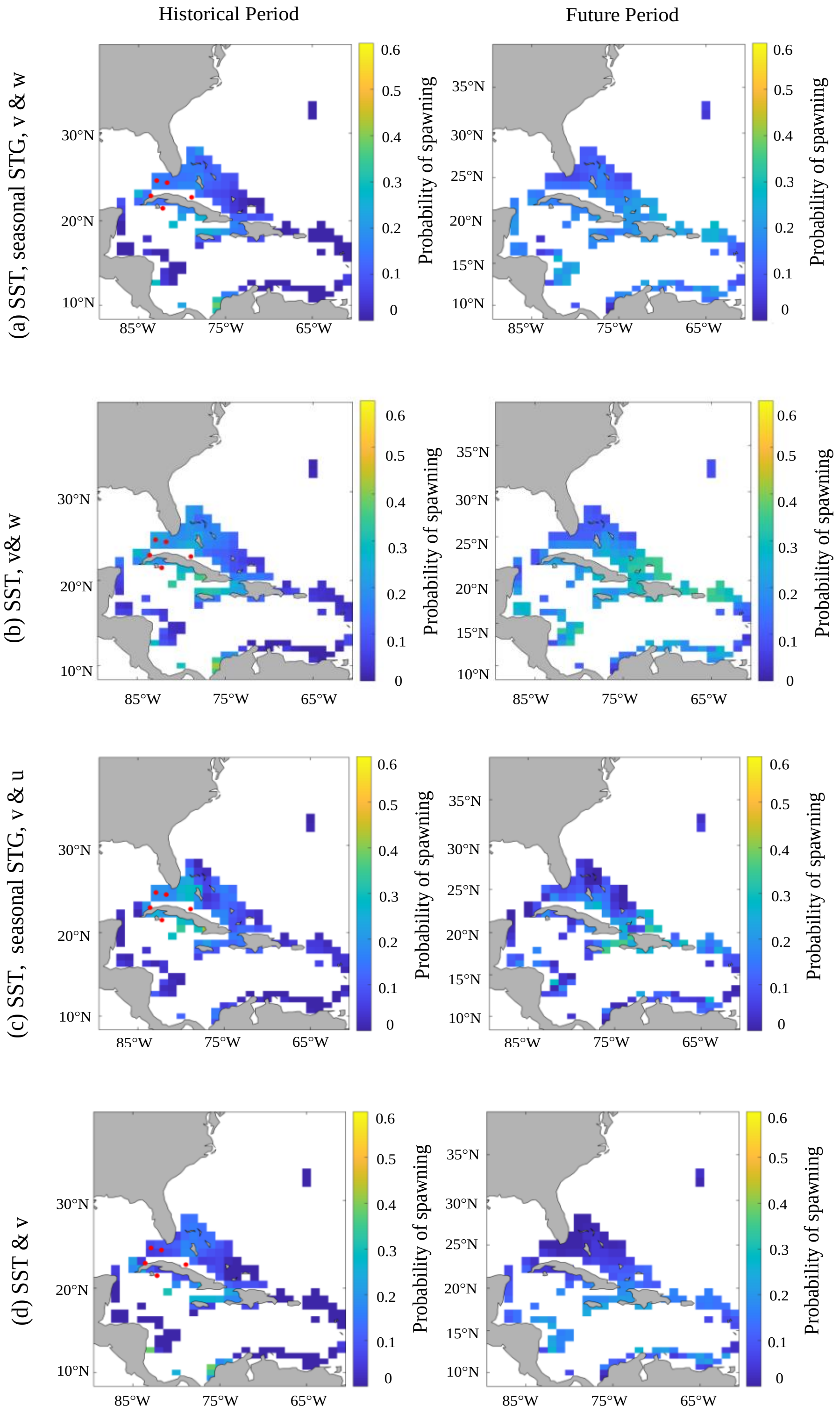


Figure A2. Historical and future projections with annual averages of probability of spawning for gray snapper species FSAs using the GFDL climate model under the RCP 8.5 climate scenario. All models included had an AIC score of less than two.

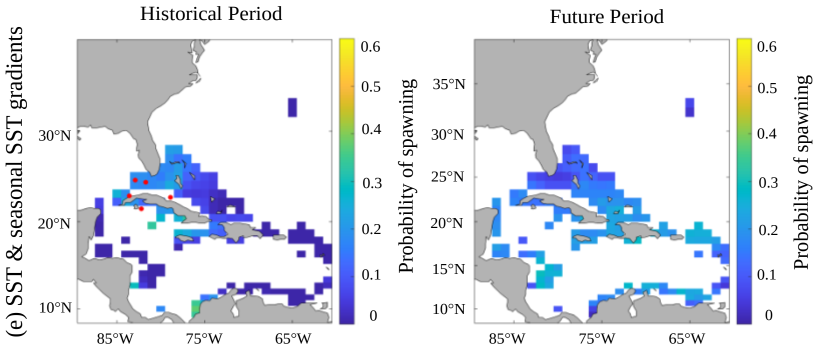


Figure A2 (cont.). Historical and future projections with annual averages of probability of spawning for gray snapper species FSAs using the GFDL climate model under the RCP 8.5 climate scenario. All models included had an AIC score of less than two.