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Current Marine Protected Areas Conserve Fish Spawning Aggregations Under Climate Change due to Habitat Refugia

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ABSTRACT

In addition to overfishing threats, tropical reef fishes that form spawning aggregations are threatened by climate change, which can reduce management effectiveness. While management strategies such as marine protected areas (MPAs), seasonal sales bans, and seasonal fishing closures may be effective at reducing the impacts of fishing pressure, they may not be as effective in the future as climate change reduces suitable fish habitat. By examining oceanographic conditions at known spawning sites of critically endangered Nassau grouper (*Epinephelus striatus*), along with future climate conditions under multiple emissions scenarios (RCPs 4.5 and 8.5), projections were made of suitable spawning habitat throughout the species' range. Spawning habitat in no-take MPAs and protected under seasonal sales bans and fishing closures was compared to spawning habitat in unprotected regions and times of year to determine potential success in protecting Nassau grouper spawning under current and future conditions. By the end of the century, declines in suitable spawning habitat were projected throughout the region under both climate scenarios. Most countries showed declines in effectively protecting spawning habitat, but MPAs had 31% higher spawning suitability than surrounding areas due to the presence of refugia with persistently suitable temperatures at the end of the century. By the end of the century, only modest improvements ($\leq 10\%$) could be made by locating new MPAs to maximize protection of spawning sites. Additionally, spawning phenology shifts on average by 25 days under RCP 8.5, which can be mitigated in countries with seasonal bans by adjusting closures to match this change. Creating networks of smaller MPAs can maximize conservation of spawning habitat because they can incorporate climate refugia, are easier to enforce, and would protect a variety of habitats.

1 | Introduction

Many species of tropical reef fish form fish spawning aggregations (FSAs), which are temporary gatherings of large numbers of conspecific fish that form for the sole purpose of reproduction (Domeier 2012; Erisman et al. 2017). Due to the high abundance and density of fish present at specific areas during predictable periods, FSAs heighten the likelihood that fishers overexploit a species, which can result in rapidly dwindling numbers of fish at aggregation sites (Sadovy de Mitcheson and Erisman 2012). For many reef fishes, FSAs may be where all spawning occurs for a species. This implies that the continued presence of sizable aggregations may be an indication of a stable population, while absences of spawning at aggregation sites or decreases in aggregation size indicate declining or depleted fish populations (Erisman et al. 2017). Declines in these FSAs have been observed in many regions of the world since they are often highly lucrative to exploit and poorly managed—or not managed at all (Russell et al. 2014). For example, 55% of assessed spawning aggregations in the Mesoamerican Reef region are classified as declining, while 54% of known spawning aggregations have not been assessed (Fulton 2023). In addition, 8% of all FSAs are extirpated and no longer form at all.

Nassau grouper (*Epinephelus striatus*) are a slow-growing, long-lived species in the family Epinephelidae found throughout the Greater Caribbean (Sadovy and Eklund 1999). Nassau grouper FSAs occur at specific locations and times of year where thousands of fish convene to mate, around full moons during winter months at coral reefs (Kobara et al. 2013; Asch and Erisman 2018). Historically, Nassau grouper FSAs would be composed of as many as 30,000–100,000 individuals (Smith 1972), but as a result of widespread overfishing and large population declines throughout the Caribbean, Nassau grouper became the first reef fish species recognized by the Endangered Species Act (ESA) in 2016 (Sadovy de Mitcheson et al. 2008). Sala et al. (2001) indicated that in Belize only two of nine known FSA sites still had more than 150 Nassau groupers, while the other seven FSAs had been extirpated. Whaylen et al. (2007) described a more optimistic situation for an FSA on the west end of Little Cayman Island that appeared to have a stable population with over 2000 Nassau grouper during spawning. They also noted that there is very little fishing pressure at this site, which is likely why its population has remained stable, although at a density of fish substantially below what Smith (1972) described for historic FSAs. More recently, Waterhouse et al. (2020) demonstrated that, due to conservation and management efforts in the area, stocks at Little Cayman Island have recovered considerably, more than tripling over the past 15 years. These findings demonstrate the effectiveness of enforced management measures that reduce fishing effort for protecting and restoring Nassau grouper FSAs.

Coupled with overexploitation, climate change may pose a threat to Nassau grouper, since forming FSAs is a life history characteristic associated with vulnerability to climate change (Hare et al. 2016; Asch and Erisman 2018). Previous work has projected sizable decreases in suitable spawning habitat and northward shifts in FSA locations primarily as a result of sea surface temperature (SST) increases (Asch and Erisman 2018). Spawning Nassau grouper are more sensitive to temperature than other life stages (Asch and Erisman 2018). They also have more specific habitat requirements than other life stages since they utilize the outer edges of coral reefs near promontories to spawn (NOAA 2013). Asch and Erisman (2018) found SST to be a strong indicator of suitable spawning habitat since this species has a narrow thermal tolerance range during spawning (Nemeth 2009). Continual rises in SST may lead to declines in the spatial and temporal extent of potential spawning habitat through most of the Nassau grouper's range. However, Asch and Erisman (2018) utilized one Earth System Model (ESM) linked to one ecological model, while focusing on a limited number of climate change scenarios. As a result, the results of the initial study by Asch and Erisman (2018) may not have captured the full extent of possible variability in future climate and ecological projections, since the extent of model uncertainty can be better understood using multi-model approaches (Hawkins and Sutton 2009; Cheung, Frölicher, et al. 2016; Cheung, Jones, et al. 2016).

Multiple countries have management in place for Nassau grouper conservation (Sadovy and Eklund 1999; Sadovy De Mitcheson et al. 2021). In U.S. territories, Nassau grouper are a protected species (Federal Register 2024). For most other countries, there is little direct management of Nassau grouper outside of seasonal closures and sales bans (Table 1) and MPAs (Figure 1), although a 3-lb minimum bag size limit exists in The Bahamas (Sadovy De Mitcheson et al. 2021). Here we use the term seasonal closures to refer to both seasonal sales bans that prohibit the sale of captured Nassau grouper and temporal fishing closures that prohibit the landing of Nassau grouper, as their effects on fishing effort are similar. Sales bans behave similarly to seasonal closures, as they have been shown to reduce fishing pressure on the target species (Rhodes and Sadovy 2002; Rhodes and Tupper 2007).

TABLE 1 | Countries with seasonal management of Nassau grouper (NOAA 2013; SCRFA 2014).

Country	Start year	Fishing or sales ban	Months of closure	Notes
The Bahamas	1998	Both	December–February	Closure months as of 2003; prior, closure was only 2 months which varied based on full moon
Belize	1993	Both	December–March	
Bermuda	1974	Fishing	April–August	No-take closure for Red Hind, but this period aligns with Nassau grouper spawning in the region
Cayman Islands	2002	Fishing	December–April	Closed all fishing at spawning sites for a minimum of 8 years in 2011, renewed 2016[a]
Mexico	2003	Fishing	February–March	Part of multi-grouper fishery ban
Virgin Islands (USA)	2006	Fishing	February–April	In addition, U.S. Caribbean waters fully protect Nassau grouper year round
Virgin Islands (British)	Unknown	Fishing	March–May	

[a] Cayman Islands Department of Environment (2016).

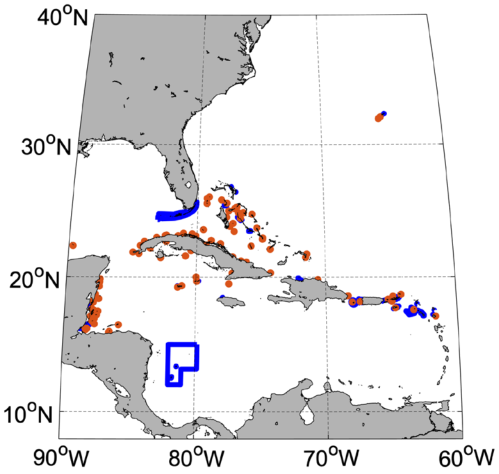

FIGURE 1 | Borders of no-take Marine Protected Areas (MPAs) shown in blue, with known spawning aggregations of Nassau grouper represented by orange dots.

Changes in the timing and location of spawning under climate change could influence the effectiveness of current area- and time-based management strategies if spawning fish no longer occur in the same places as in the past. MPAs that are sited without taking climate change into account could result in protections that may not be effective beyond a few decades. As water temperatures rise, previously hospitable waters may no longer be tolerable. For spawning Nassau grouper, warmer temperatures both at the ocean surface and depth may lead to current and historical spawning locations becoming intolerable (Asch and Erisman 2018). Therefore, it is necessary to build MPAs resilient to the effects of climate change (McLeod et al. 2009). Alternatively, existing MPAs may be valuable as protected regions for species whose distributions have shifted poleward due to climate change (Roberts et al. 2017). Therefore, having networks of MPAs at potential future FSA sites may be beneficial to protect species under climate change due to range shifts (McLeod et al. 2009; Roberts et al. 2017). MPA networks increase resiliency in the face of climate change by protecting metapopulation structure (Krueck et al. 2017), which helps to buffer populations against catastrophic events (Gleason et al. 2010). Therefore, for MPAs to remain effective in the future, climate change needs to be considered during planning and when defining an MPA's goals (Palacios-Abrantes et al. 2023).

Climate-induced changes in the timing of spawning are also likely to alter the effectiveness of static seasonal fishing closures and seasonal sales bans. As temperatures rise, changes in phenology occur in many marine species, often leading to earlier seasonal events in spring and summer, as well as either expanded or contracted spawning and migration seasons (Asch 2015; Rogers and Dougherty 2019; Langan et al. 2021). In particular, winter spawners often experience earlier and protracted spawning seasons under warming conditions (Rogers and Dougherty 2019; Langan et al. 2021). In fact, recent work suggests slight delays in phenology and a shorter spawning season for species including walleye pollock (*Gadus chalcogrammus*—Rogers and Dougherty 2019), longhorn sculpin (*Myoxocephalus octodecemspinosus*), Atlantic herring (*Clupea harengus*—Langan et al. 2021) and Nassau grouper (Asch and Erisman 2018; Gokturk et al. 2022). Therefore, adjusting the timing of these closures and possibly expanding them to include the historic and new spawning season may be necessary to protect FSAs in the future if their timing changes (Denny et al. 2014; Asch 2015; Rowell et al. 2015; Griffin et al. 2022; Nemeth et al. 2023). While it has been suggested that this type of adaptive management can promote resilience to climate change (Peer and Miller 2014; Melnychuk et al. 2014), the regulations that created seasonal closures and sales bans in the Caribbean often do not allow for such flexibility due to the extensive process necessary to modify them (NOAA 2013).

A better understanding of how spawning habitat (i.e., regions with both suitable substrate and environmental conditions for FSA formation) for Nassau grouper will change under global warming is important for effective management of this species. This research aims to investigate: (1) how suitable spawning habitat will vary under different climate change scenarios across two periods and three ESMs; (2) how changes in spawning habitat will alter the effectiveness of current management strategies for Nassau grouper, specifically focusing on current no-take MPAs, seasonal closures, and sales bans and (3) how new MPAs could potentially be sited to improve Nassau grouper conservation under climate change. Consideration of new MPA locations is especially timely given the 30 × 30 goal to conserve 30% of the world ocean by the year 2030 (Sullivan-Stack et al. 2022). We produce multi-model projections of the probability of suitable habitat for Nassau grouper FSAs at mid-century (2041–2060) and end-of-century (2081–2100) time scales under multiple climate change scenarios. Potential FSA locations are considered for all reef regions throughout the Greater Caribbean and Gulf of Mexico, including sites determined to presently or historically have contained Nassau grouper FSAs based on data in Asch and Erisman (2018). This will allow for recommendations to be made for how to better manage this species in the future under changing conditions.

2 | Materials and Methods

2.1 | Biological Datasets

We used FSA data for Nassau grouper compiled in Asch and Erisman (2018). This dataset includes data on months and locations of all known past and current FSAs. The geographic footprint of current-day coral reef habitat was obtained from the Reefs at Risk database (Burke et al. 2011; https://www.wri.org/our-work/project/reefs-risk) and the Global Distribution of Coral Reefs database from the United Nations Environment Programme-World Conservation Monitoring Centre (UNEP-WCMC; https://data.unep-wcmc.org/datasets/1). Bathymetry data were downloaded from the Smith and Sandwell SRTM30 dataset, which has global ocean bathymetry with a 30 arcsecond resolution (Becker et al. 2009).

2.2 | Climate Models and Scenarios

Climate change was simulated using three different earth system models (ESMs) from the Coupled Model Intercomparison Project—Phase 5 (CMIP5). These models were selected for their varying equilibrium climate sensitivities to greenhouse gas emissions (Andrews et al. 2012; Sabeerali et al. 2013). The models used were: (1) National Oceanic and Atmospheric Administration (NOAA) Geophysical Fluid Dynamics Laboratory Earth System Model 2M (GFDL ESM2M, or GFDL for short) model (Dunne, John, Adcroft, et al. 2012; Dunne, John, Shevliakova, et al. 2012), which has the lowest equilibrium climate sensitivity of the three models; (2) Max Planck Institute Earth System Model Mixed Resolution (MPI-ESM-MR or MPI for short) model (Ilyina et al. 2013), with moderate equilibrium climate sensitivity; and (3) Institut Pierre Simon Laplace Climate Model 5A Medium Resolution (IPSL-CM5A-MR, or IPSL for short) model (Dufresne et al. 2013), which has high equilibrium climate sensitivity (Table 2). Each model was bias corrected by subtracting observational data similarly to Asch and Erisman (2018). Models were averaged across historical model simulation years (1981–2000) for each month; then a weighted mean of each variable was calculated across all ESM grid cells. This method was then repeated using remotely sensed observational data (see details on datasets below), and monthly means were subtracted to calculate a model bias. This bias value was then subtracted from all modeled environmental variables for each month. Environmental data from models were linearly interpolated to fit on a 0.5°×0.5° latitude/longitude grid. This was done so that outputs from different ESMs on the same grid could be averaged.

Three 20-year time periods were analyzed: a historical period (1981–2000), a near future period (2041–2060), and an end-of-century period (2081–2100). Each of these periods was averaged as 20-year climatologies. This approach was used to better align the modeled historical period with the observational data on spawning aggregations since range-wide, in situ oceanographic observations coincident with spawning are unavailable, but observed monthly climatological conditions during spawning could be derived from remote sensing. For each future period, two different Representative Concentration Pathways (RCPs) from the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5) were utilized: RCP 4.5 and RCP 8.5. RCP 8.5 has radiative forcing that reaches 8.5 $\mathrm{W\,m^{-2}}$ relative to preindustrial forcing in 2100 and continues to increase after that period. It is a high greenhouse gas emissions pathway that includes no mitigation of emissions. RCP 4.5 displays an increase of 4.5 $\mathrm{W\,m^{-2}}$ in radiative forcing from preindustrial levels by the year 2100. The RCP 4.5 scenario is an intermediate climate change pathway where greenhouse gas emissions stabilize by 2100 due to mitigation efforts (IPCC 2014).

Across the spatial scale of this species' range, three variables were determined to best describe the spawning habitat of Nassau grouper based on the most parsimonious model out of 128 potential models evaluated in Asch and Erisman (2018). The three environmental variables that were selected in the best ecological niche model, utilizing remotely sensed data, were SST, seasonal temperature gradient (STG), and v geostrophic currents. SST was selected as opposed to temperature at depth, despite spawning aggregations forming at depth, due to the availability of empirical SST data for bias corrections of the modeled data, as well as the fact that Nassau grouper ascend partway to the surface to spawn (Starr et al. 2007). While SST may not be representative of the temperature that Nassau grouper spawn in, changes in water temperature at the surface will influence temperature at spawning depth, with results showing that heat transfers occur at the fastest rate in the first 700 m of ocean depth (Venegas et al. 2023), suggesting that warming SST will lead to warming temperatures at depth. STG refers to the rate of change in surface temperature from month to month, where positive values indicate seasonal temperature increases and negative values indicate declines. North/south geostrophic currents (v) were calculated using sea surface height (SSH) anomalies via the formula:

$$v = \left(\frac{g}{f}\right) * \mathrm{SSHa}$$

where g is gravitational force, f is the Coriolis force, and SSHa is spatial SSH anomalies. Additional oceanic variables, such as chlorophyll levels and eddy kinetic energy, were considered but were not selected in the evaluation of the most parsimonious, plausible model (Asch and Erisman 2018). Other variables, including interspecific interactions, variability in Nassau grouper abundance, depth, upwelling, and geomorphology, were not included due to either a lack of range-wide empirical data needed to parameterize the species distribution model, a lack of available output in the climate models, or a spatial scale mismatch between the ecological process and the scale of climate model projections. For producing future projections, our selected oceanic variables were obtained from ESMs to calculate probabilities of spawning habitat occurrence. For remotely sensed data, AVHRR satellite data (Saha et al. 2018) was used for SST, and

TABLE 2 | Metadata on earth system models used for analysis.

Model name (short name)	Institution	Ocean physics submodel	Ocean resolution	Number of depths	References
GFDL-ESM2M (GFDL)	NOAA-Geophysical Fluid Dynamics Laboratory	MOM v4	1°×1°[a]	50	Dunne, John, Adcroft, et al. (2012) and Dunne, John, Shevliakova, et al. (2012)
MPI-ESM-MR (MPI)	Max Planck Institute	MPIOM	1°×1°	41	Ilyina et al. (2013)
IPSL-CM5A-MR (IPSL)	Institute Pierre Simon Laplace	ORCA 2	1°×1°	31	Dufresne et al. (2013)

[a] This model has finer scale spatial resolution to resolve equatorial currents such that the native resolution is less than 1°×1° in tropical and subtropical regions.

AVISO (Hauser et al. 2020) data was obtained for geostrophic currents.

2.3 | Spawning Habitat Suitability Modeling

Suitable habitat for Nassau grouper spawning was modeled for the spawning months of December through April for the Greater Caribbean, and June through July for Bermuda (as described in Asch and Erisman 2018). These months were selected because the seasonality of Nassau grouper is different in Bermuda due to the colder waters compared to the Caribbean, leading to summer spawning in Bermuda (Sadovy and Eklund 1999). Our models projected potential spawning habitat, which differs from realized spawning habitat. Potential spawning habitat refers only to locations where conditions are suitable for spawning, but not necessarily to where spawning actually occurs (Planque et al. 2007). Model-based projections cannot identify actual spawning, which is dependent on Nassau grouper population size. However, for conciseness, potential spawning habitat (i.e., habitat with appropriate coral reef substrate, as well as SST, STG and *v* geostrophic currents conducive to spawning) will be referred to as "spawning habitat" hereafter. Observations of Nassau grouper FSAs are in presence-only format since some locations of fish spawning aggregations may remain unknown, making it difficult to determine where spawning may be absent. Consequently, a species distribution model equipped to handle presence-only data was utilized: the Non-Parametric Probabilistic Ecological Niche (NPPEN) model (Beaugrand et al. 2011). NPPEN was the model selected for this application because Mahalanobis distance-based species distribution models, such as NPPEN, fare well when compared against the accuracy of other presence-only species distribution models (Tsoar et al. 2007). NPPEN simulations were run in Matlab (Version R2020a). NPPEN utilized Mahalanobis distances to compare a test point where spawning habitat may or may not occur to a multivariate distribution of environmental conditions at known FSA sites (Beaugrand et al. 2011). If the test point (x) fell within the middle of this multivariate distribution, then the site was deemed to have potential spawning habitat (Beaugrand et al. 2011). For each test point, this calculation was compared to every point in the reference matrix (i.e., the conditions coincident with observed FSAs). The probability of spawning was based on the proportion of times the test point was classified as spawning habitat, divided by the total number of calculations (*n*) for that point.

The test points used in NPPEN were ESM grid cells with environmental conditions (SST, STG, and *v* geostrophic currents) from historical and future scenarios, which were used to determine the likelihood of spawning habitat occurrence. Habitat suitability for each ESM was considered individually, but probabilities of spawning habitat occurrence were averaged over all three ESMs for each scenario and model grid cell to assess overarching patterns in multi-model ensemble means. Since Nassau grouper FSAs only occur adjacent to reef substrate (Sadovy and Eklund 1999), NPPEN calculations were only performed in regions of the Greater Caribbean with current-day coral reefs. Additionally, some NPPEN figures were created depicting only regions with coral reefs along the continental shelf (i.e., depths shallower than 200 m, Wilson and Hayek 2019). Due to the resolution of climate models and narrow breadth of the continental shelf and insular platform across many parts of the Caribbean, it is not possible to run species distribution model projections for just the continental shelf. We addressed this issue by making projections at the GCMs' downscaled resolution and then only visualizing areas < 200 m post hoc based on the Smith and Sandwell SRTM30 bathymetry. Figure 2 (Figures S1 and S2) were made to depict results at shallow depths by including this depth limitation, but other figures are presented at the GCM resolution used for analysis.

2.4 | Analysis of FSA Conservation and Management Impacts

Two predominant management strategies for Nassau grouper FSAs were evaluated in terms of their resilience to climate change. These strategies included no-take MPAs (from here on, MPAs) and seasonal closures, which are the most common forms of conservation for Nassau grouper in the Caribbean (NOAA 2013; SCRFA 2014). MPA locations and sizes were obtained from the World Database on Protected Areas (WDPA, protectedplanet.net, Figure 1), while seasonal closures were obtained via the NOAA Biological Report on Nassau Grouper

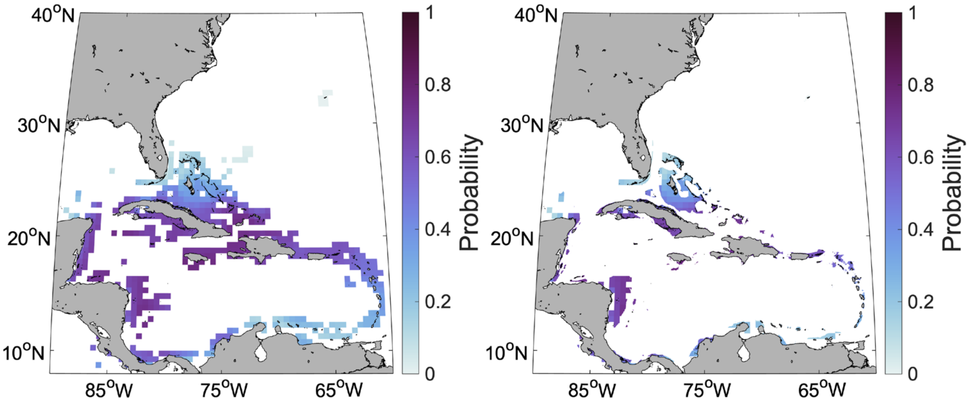

FIGURE 2 | Mean suitable spawning habitat probability for historical period (1981–2000) averaged across three earth system models for spawning months (Dec–Apr, except for Bermuda, which has a Jun–Jul spawning season). The model is shown for regions with reefs that show the range of data used for analysis (left) and regions with reefs at a depth of 200 m or less, which were assessed post hoc (right).

(NOAA 2013; Table 1). For seasonal closures, the U.S. Virgin Islands were included despite it being illegal to fish Nassau grouper in all U.S. waters, as a fishing seasonal closure was also implemented from February through April. MPAs were included in the analysis if they were listed as "no take" or if they contained no-take areas in the WDPA database. However, we recognize that many of these MPAs include multi-use protected areas where only a subset of the whole MPA is classified as a no-take zone. Due to the limited resolution of the climate models, full MPAs were included in the analysis even if only a portion of a protected area included no-take zones. Duplicate MPAs were removed from the WDPA database. Additionally, any MPAs whose calculated area (calculated from WDPA shapefiles in QGIS 3.24) had a discrepancy of $>10\%$ difference from the WDPA-reported area that also accounted for a difference of more than $50\,\mathrm{km}^2$ was investigated. These discrepancies usually reflected inclusion of land area in QGIS calculations. In such cases, areas of these MPAs were corrected by subtracting the area of islands that MPAs encircled. MPAs with discrepancies in area less than this were not corrected since these differences were unlikely to have any substantial effect on outcomes due to the comparatively low resolution of the ESM grids (i.e., discrepancies of $<50\,\mathrm{km}^2$ would be less than 1.6%–2.3% of the area of each $0.5° \times 0.5°$ latitude/longitude grid cell depending on latitude).

2.5 | Marine Protected Areas

First, to determine the resilience of MPAs to climate change, the change in habitat suitability of MPAs was determined across all months. Following Araújo et al. (2011), habitat suitability (*HS*) was calculated for each month, climate scenario, and MPA using environmental data averaged over each 20-year time frame as follows:

$$\mathrm{HS}(m,g) = \sum_{g=1}^{z} \sum_{m=1}^{12} \mathrm{SH}(m,g) * P(g)$$

where g is a grid cell, z is the total number of grid cells, m is a month, SH(m, g) was the probability of spawning habitat in a given month and grid cell, and P(g) was the proportion of the grid cell that contained MPAs.

Then, the habitat suitability for MPAs in each spawning month (December through April, except above 32° N latitude where spawning occurs during June through July) was summed to create a total score for the particular MPA. Here we assumed that the habitat suitability of each MPA was a proxy for the MPA's effectiveness at conserving habitat for Nassau grouper FSAs. Repeated measures analysis of variance (ANOVA) was used to determine the difference in habitat suitability between the historical and future periods for each RCP scenario. Each MPA was treated as a separate replicate in this study design. Additionally, the seasonal central tendency (CT)—the measure of the middle of the distribution—of monthly habitat suitability was calculated for MPAs to assess changes in spawning phenology (Reed et al. 1994; Edwards and Richardson 2004). This was calculated as:

$$\mathrm{CT} = \frac{\sum \mathrm{HSMPA} * M}{\sum \mathrm{HSMPA}}$$

where HSMPA is the habitat suitability score within the MPA, and M is monthly weight. For winter spawning regions, June was assigned '1' as a monthly weight, July was assigned '2', etc., while for summer spawning regions, January was assigned '1' and so forth to ensure that changes in month of spawning occurred across continuous values. These weights were used to avoid a discontinuity between the months of December and January in regions where Nassau grouper reproduce during winter. Differences in CT were evaluated with repeated measures ANOVA to examine differences in spawning phenology among time periods for each RCP scenario.

To determine the change in relative habitat suitability of MPAs compared to non-protected areas, grid cells that contain MPAs were compared to those without. Any grid cell which contained any portion of an MPA was classified as an MPA area. Next, the habitat suitability was summed across months and separated into MPA categories (i.e., protected vs. non-protected). MPA and non-protected grid cells were compared using a two-way ANOVA with RCP and period as independent variables.

Finally, model-based spawning habitat projections were used to identify regions for siting MPAs that may best protect spawning events both now and in the future. The current percentage of grid cells with MPAs in the Greater Caribbean (9.01% of analyzed pixels) was used as a baseline to maintain the same amount of area protected, but MPA locations were shifted to evaluate how to maximize the effectiveness of these areas for conserving Nassau grouper spawning habitat. We used a bootstrap approach (10,000 iterations, without replacement) to examine potential MPA network configurations with the same quantity of ESM grid cells as currently protected (Efron and Tibshirani 1994). Habitat suitability scores were calculated for each bootstrap iteration. Areas that maximized the cumulative habitat suitability score were considered regions that should be protected in the future under climate change. Annual mean habitat suitability scores were examined at the end of the century (2081–2100) for both RCP scenarios. The percentage of bootstrap iterations with habitat suitability scores that exceeded current protected area scores for each period and RCP was evaluated. To ensure that 10,000 iterations were sufficient to encapsulate potential variability in habitat selection, the analysis was performed five times and the similarity of results from each analysis was assessed. The percentages of potential MPA areas with habitat suitability scores exceeding those of current MPAs varied by 1% across five iterations of the bootstrap analysis. This showed that this analysis was robust to small variations in configurations of MPAs that may have been selected during different bootstrap trials.

2.6 | Seasonal Sales Bans and Seasonal Fishing Closures

To investigate the resilience of seasonal fishing closures and sales bans to climate change on a country-by-country basis, a similar set of analyses to those for MPAs was performed. These analyses also allowed us to project what months the closures could be moved to in the future to best protect FSAs in the face of climate-induced changes in spawning phenology. Seasonal closures and sales bans were treated as the same type of management measure since both of their goals were to prevent harvest of Nassau grouper during the months of the closure or sales ban. For each country that has seasonal closures, pixels within the country's exclusive economic zone (EEZ) were analyzed, and the habitat suitability during each month of the closure or sales ban was calculated. This was performed under all time frames and climate scenarios for peak spawning months within each EEZ. Results were compared to historical spawning habitat suitability in areas with seasonal closures and EEZs with sales bans. Central tendency was used to determine the magnitude of seasonal changes in spawning suitability and to determine whether changes in closure timing may improve resilience under future conditions. Once again, repeated measures ANOVAs were done to compare central tendency inside and outside of EEZ areas, with the independent variable of period for each RCP.

3 | Results

3.1 | Spawning Habitat Suitability and Model Variability

For the historical period, the cross-ESM annual average projected high spawning habitat suitability throughout most of the region since more than 75% of cells showed at least half the maximum suitability score (Figure 2). The historical period had a maximum spawning habitat suitability score of 0.49 and a mean of 0.26 ± 0.02 S.D. By mid-century, spawning habitat suitability declined in the southern region, while the northern Caribbean showed increases compared to the historical period (Figure 3a,b). Under RCP 4.5, the mean decline in habitat suitability was 7.1% by mid-century, while the mean decline was 11.7% under RCP 8.5. By the end of the century, large declines in habitat suitability occurred through much of the region under RCP 8.5 (Figure 3d). Under this scenario, mean spawning habitat suitability scores declined by 0.17 habitat suitability units (a 70% decrease) across the region, with a standard deviation of 0.02. A smaller decline in spawning habitat was projected under RCP 4.5, in which the mean spawning habitat suitability scores declined by 0.1 habitat suitability units (i.e., a 40% decline), with a standard deviation of 0.01.

End-of-century spawning suitability was heavily influenced by RCP in certain regions of the Caribbean. For example, in the northern part of the study area near The Bahamas, southern Florida, and northeastern Cuba, spawning habitat suitability showed a minor increase under RCP 4.5 but a decline under RCP 8.5 (Figure 4a,b, Figure S1). In other regions, minor spawning suitability declines under RCP 4.5 became more severe under RCP 8.5, such as near Hispaniola (Figure 4c,d), and northern Colombia (Figure 4e,f).

Despite some regional distinctions, different ESMs depicted agreement in the overall direction of change. Such agreements were observed among nearly 67% of grid cells for RCP 4.5 and over 76% of grid cells for RCP 8.5 (Figure 5). When comparing habitat suitability during the historical period compared to the end of the 21st century, the three models showed most variability north of Cuba and the northern coasts of Venezuela and Colombia, by

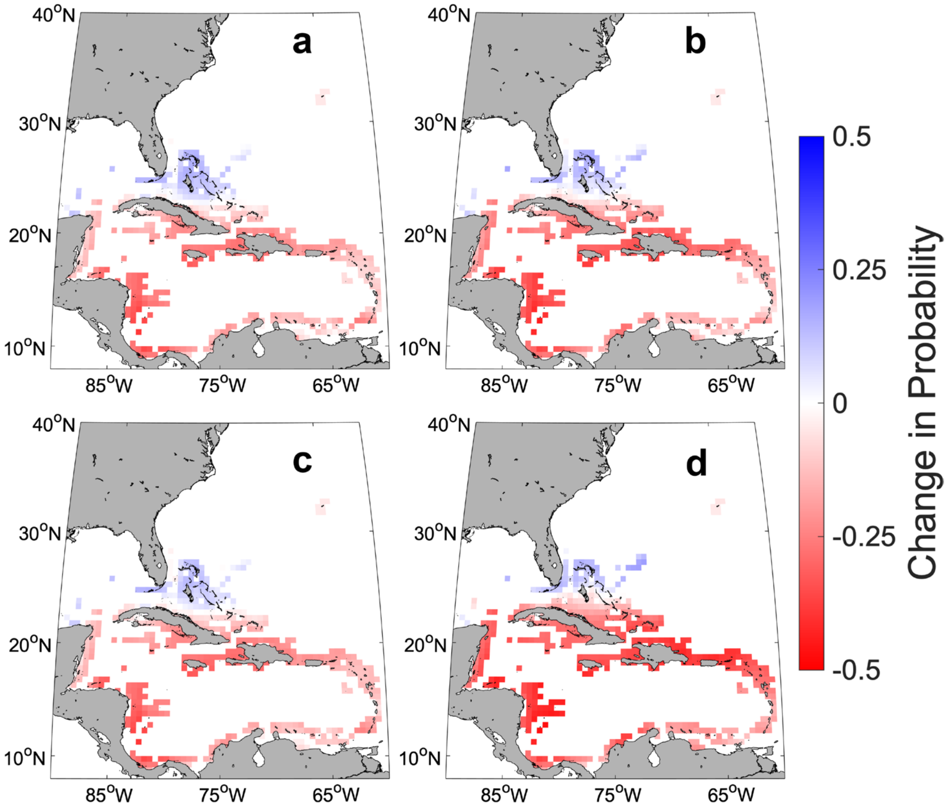

FIGURE 3 | Changes in cross-ESM mean suitable spawning habitat from historical (1981–2000) to near future (2041–2060, a and b) and end of century (2081–2100, c and d) for RCP 4.5 (a and c) and RCP 8.5 (b and d).

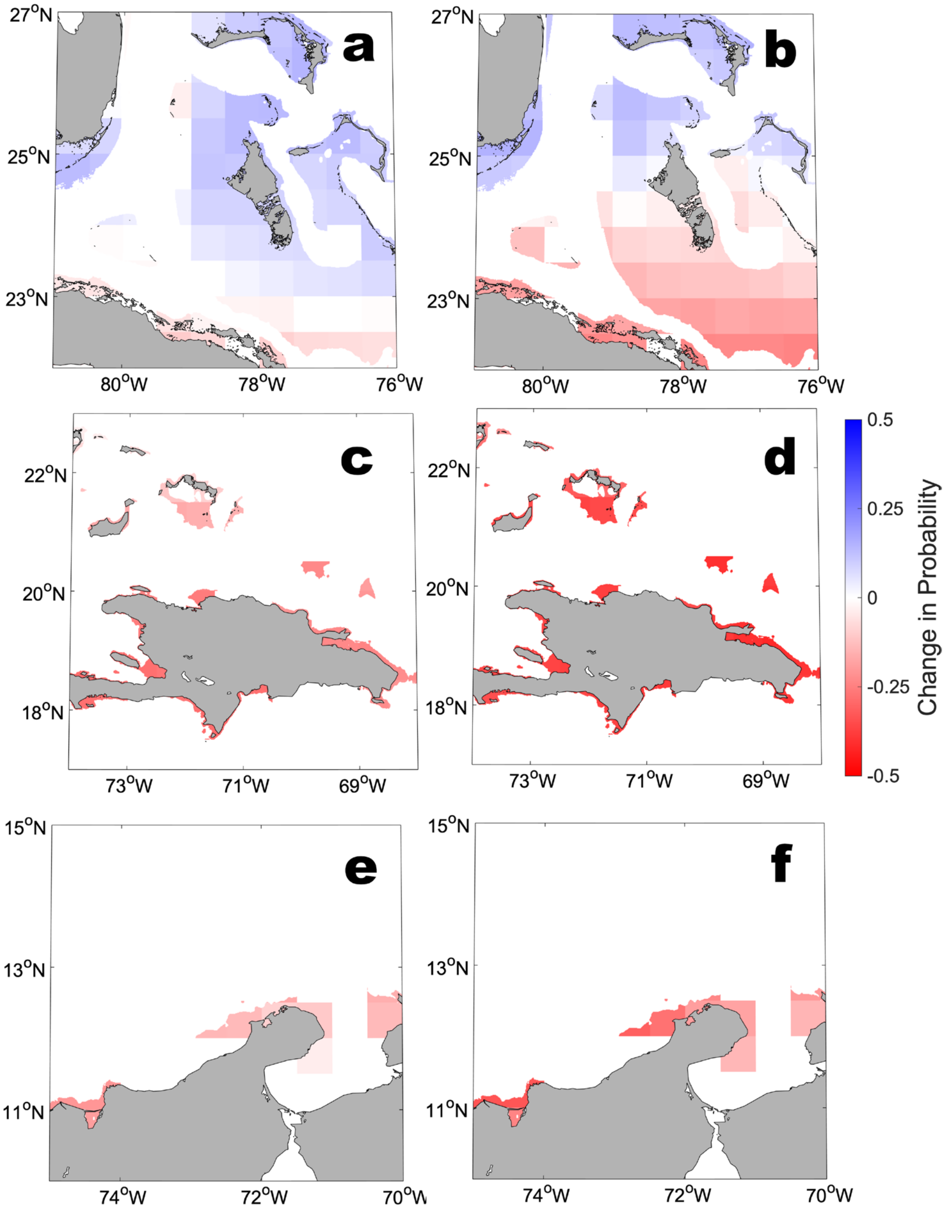

FIGURE 4 | Regional suitable spawning habitat changes from the historical to end-of-century periods under RCP 4.5 (a, c, e) and RCP 8.5 (b, d, f). Results have been masked to display only regions with a depth of 200 m or less. Highlighted regions include The Bahamas (a and b), Hispaniola (c and d), and north of Colombia (e and f).

Aruba and Curaçao (Figure 6, Figure S2). Under RCP 4.5, all three models projected increases in spawning habitat in the northern Caribbean off the coast of Florida and near The Bahamas. The IPSL model also indicated marked increases in spawning habitat east of Puerto Rico and the British Virgin Islands. Under RCP 8.5, the GFDL model projected the largest increase in habitat suitability of the three models, particularly off the coast of Florida and The Bahamas, while IPSL indicated declines in spawning habitat throughout nearly the entire region for the end of the century.

3.2 | Marine Protected Areas

MPAs and non-protected areas both exhibited declines in spawning habitat suitable for Nassau grouper across all RCPs and periods (Figure 7). For MPAs, a repeated measures ANOVA indicated changes in spawning suitability across all months were not significant across time periods for both RCPs (Table 3). Despite the similarity in the direction of change at mid-century and end-of-century, regions with MPAs showed lower magnitudes of decline than regions without MPAs (Table 4, Figure 7). MPA regions during the historical period had lower spawning suitability compared to non-MPA regions, although these differences were not statistically significant during the historical period. However, during both the mid-century and end-of-century projections, non-MPA regions experienced larger declines in habitat suitability than MPAs. By the end of the century, there was a significant difference in the amount of change for protected and non-protected regions under both RCPs from the historical period.

Additionally, due to changing oceanic conditions, the seasonality of spawning suitability as measured by central tendency

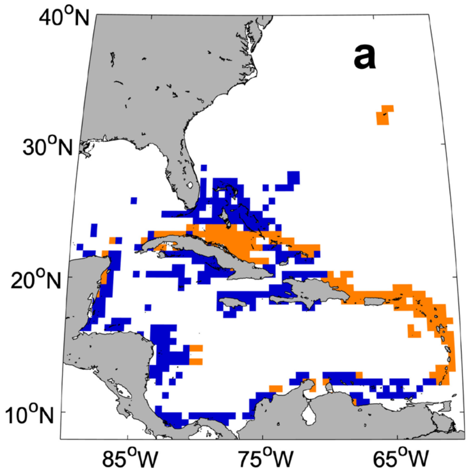

FIGURE 5 | Directional agreement in changes in suitable spawning habitat across different ESMs when comparing the historical period (1981–2000) to the end of the century (2081–2100) under RCP 4.5 (a) and RCP 8.5 (b). Model agreement is assessed across the average of all three ESMs. Blue grid cells represent directional agreement across all models (i.e., a grid cell showed suitable habitat increases or declines for all three models), while orange represents disagreement among models.

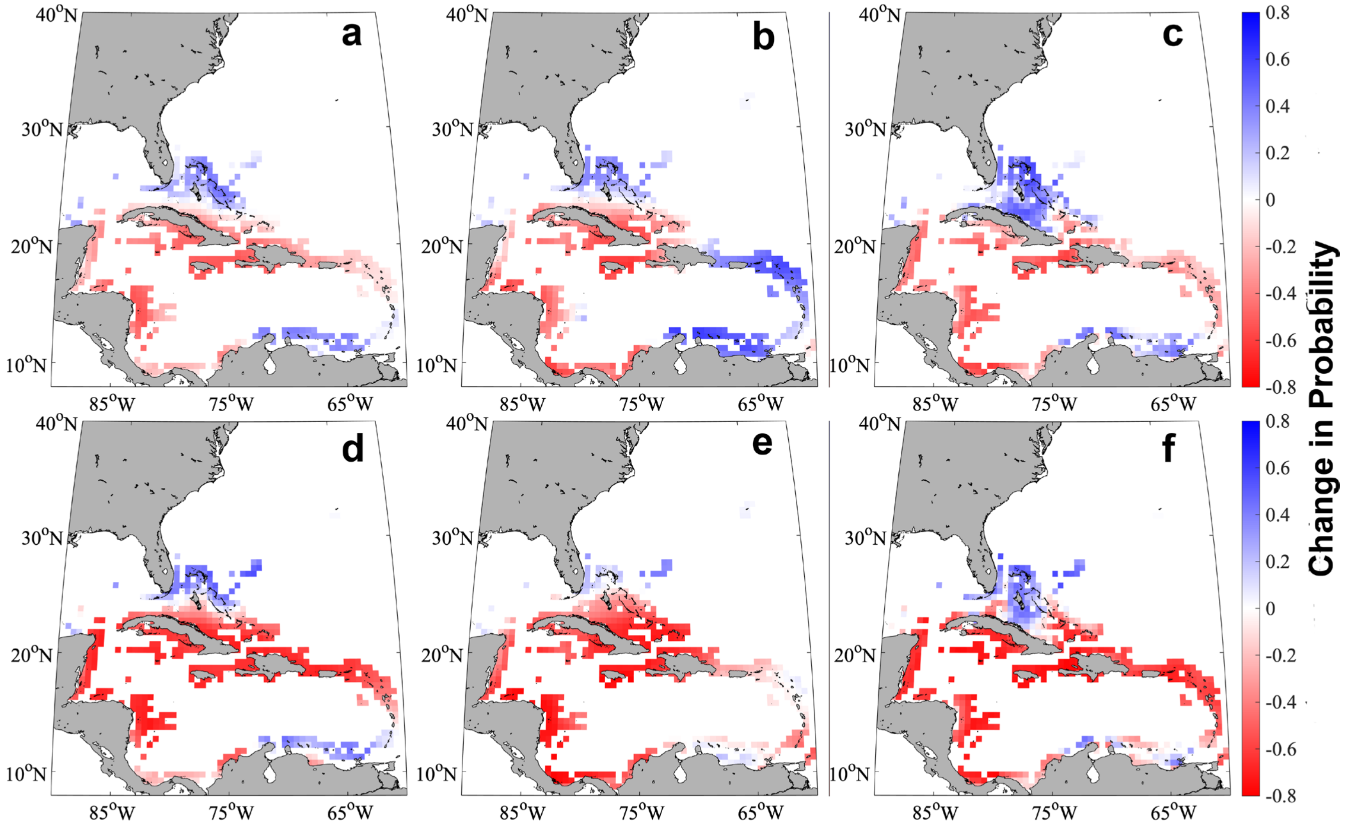

FIGURE 6 | Differences in suitable spawning habitat from the historical period (1981–2000) to the end-of-the-century (2081–2100) under RCP 4.5 (a–c) and RCP 8.5 (d–f) for the three models: GFDL (a and d), IPSL (b and e) and MPI (c and f). Blue colors indicate increases in spawning habitat from the historical period, while red colors reflect suitable spawning habitat declines.

shifted later within MPAs for all periods and RCPs (Figure 8). By mid-century, central tendency was delayed by almost 1 month under both RCPs. Throughout most of the Caribbean where Nassau grouper spawns in winter, this entailed a shift from peak spawning in December–January to January–February, an approximately 0.6°C decrease in SST under RCP 8.5 by the end of the century. In Bermuda where this species reproduces in the summer, NPPEN projected a shift in the central tendency from August–September to early August/late July, representing a nearly 1.5°C decrease in SST under RCP 8.5 by the end of the century. All time periods were different in terms of central tendency for both RCPs (Table 3), with RCP 4.5 indicating a delay of 4.8 weeks and RCP 8.5 exhibiting a delay in spawning of nearly 6.1 weeks by the end of century.

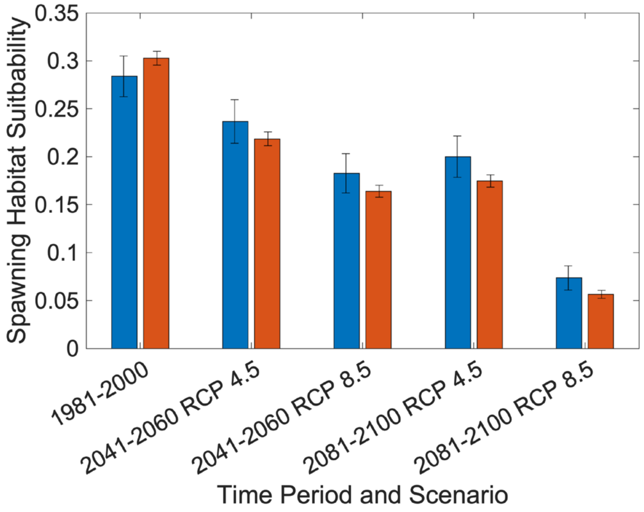

FIGURE 7 | Mean spawning habitat suitability integrated across grid cells and months for areas with MPAs (blue) and without MPAs (orange). Error bars represent 95th percentile confidence intervals.

TABLE 3 | Repeated measures ANOVA results examining Nassau grouper spawning habitat suitability and seasonality of spawning as measured by central tendency. Changes in seasonality and habitat suitability are compared across time periods in areas with MPAs and seasonal restrictions (i.e., fishing closures and sales bans).

		Test statistic		
	RCP	***F***	***p***	**df**
MPA spawning suitability	4.5	0.781	0.459	2150
	8.5	1.128	0.326	
MPA central tendency	4.5	253.95	< 0.0001	2120
	8.5	290.65	< 0.0001	
Seasonal restriction spawning suitability	4.5	0.352	0.709	2,12
	8.5	2.189	0.155	
Seasonal restriction central tendency	4.5	6.996	0.0097	2,12
	8.5	5.381	0.0215	

3.3 | Seasonal Sales Bans and Seasonal Fishing Closures

Under both RCPs and periods, the EEZs with seasonal sales bans and seasonal fishing closures saw declines in spawning habitat suitability as did areas outside these EEZs (Figure 9). Across EEZs with seasonal conservation measures, the change in spawning habitat was not significant for the time period in either RCP, likely due to small sample size (i.e., the number of EEZs with seasonal protection measures), averaging across months and high variability (Table 3). However, there was a difference in the amount of habitat lost dependent on the presence/absence of seasonal protection measures, with this effect seen across multiple time periods (Table 4). In this analysis, the RCP scenario also affected changes in suitable habitat, but the RCP did not interact with whether an area had seasonal protection measures. In the historical period, some of the larger EEZs with seasonal fishing restrictions had lower spawning probabilities than regions with non-seasonal fishing restrictions. Under RCP 4.5, both grid cells with and without EEZs with seasonal fishing restriction measures exhibited minimal declines in suitable spawning habitat under both future periods compared to RCP 8.5. Under RCP 8.5, both grid cells in areas with and without seasonal fishing restrictions showed larger declines in suitable spawning habitat than under RCP 4.5 (Figure 9).

TABLE 4 | Two-way ANOVA results examining whether changes in spawning habitat suitability differed based on protection status, RCP scenario, or an interaction between these factors. Separate ANOVAs examined near-future (2041–2060) and end-of-century (2081–2100) periods. Protection is characterized both in terms of MPA status and whether an economic exclusive zone (EEZ) contains seasonal fishing closures or seasonal sales bans.

			Test statistic		
	Time period	**Variable**	***F***	***p***	**df**
MPA status	Near-future	Present/ Absent	10.49	0.0012	3,75
		RCP	25.62	< 0.0001	3,75
		Interaction	0.01	0.91	3,75
	Future	Present/ Absent	8.63	0.0034	3,75
		RCP	81.23	< 0.0001	3,75
		Interaction	0.05	0.8186	3,75
Seasonal fishing protection	Near-future	Present/ Absent	20.18	< 0.0001	3,6
		RCP	35.87	< 0.0001	3,6
		Interaction	1.02	0.31	3,6
	Future	Present/ Absent	21.03	< 0.0001	3,6
		RCP	94.53	< 0.0001	3,6
		Interaction	1.09	0.3	3,6

In terms of changes in phenology, areas with seasonal fishing restrictions were projected to experience an approximately 0.6-month delay in phenology under RCP 4.5 by mid-century; while this change was projected to be 0.7 under RCP 8.5 (Figure 8). Additionally, by the end of the century for each RCP, this phenology shifted an additional 0.1 months later from mid-century. These results were significant across all time periods under both RCPs (Table 3).

3.4 | Siting of Future MPAs Under Climate Change

Given projected declines in spawning habitat suitability in MPAs, configurations of potential MPAs that may better protect Nassau grouper spawning areas in the future were investigated. Under historical conditions, existing MPA regions did not fare better at protecting FSAs than a randomly selected assortment of grid cells, with 51% of the 10,000 randomly selected MPA locations having better cumulative suitable spawning habitat scores than

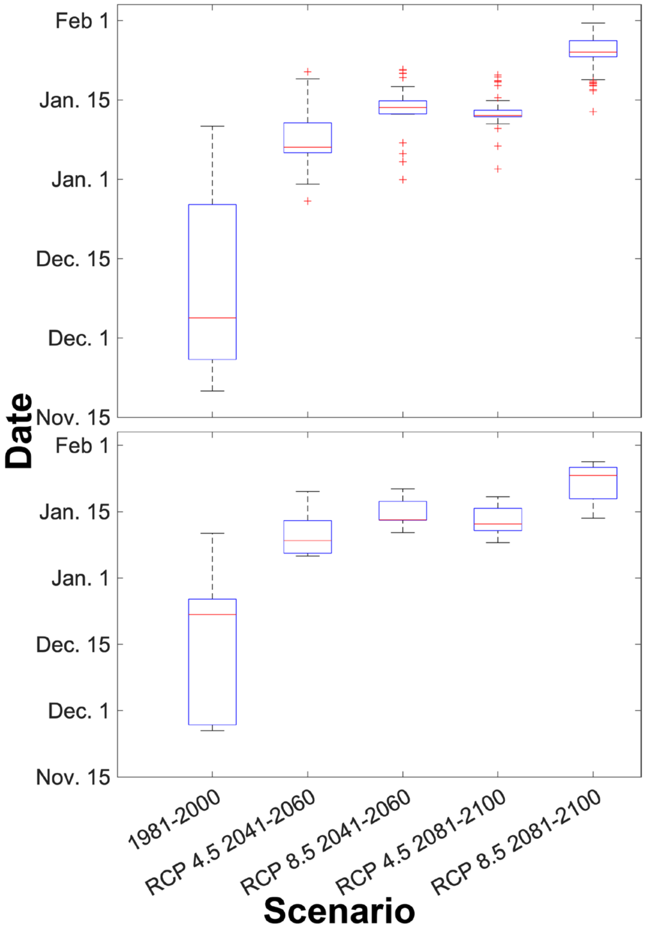

FIGURE 8 | Spawning date central tendency of spawning habitat occurrence in areas with MPAs (top) and seasonal closures (bottom). Bottom, middle (red) and top lines of box represent 25th, 50th and 75th percentiles, respectively. Whiskers are minimum and maximum points, excluding outliers (red '+' markers).

the current configuration of MPAs (Figure 10). Under future conditions, there were declines in suitable spawning habitat both inside and outside of current-day MPAs, but these declines were projected to be more severe outside current-day MPAs. Protected areas had suitability scores that were 15% higher under RCP 4.5 and 31% higher under RCP 8.5 than areas outside MPAs. This led to existing MPA configurations that fared better than randomly selected bootstrap iterations under both future climate change scenarios. For RCP 4.5, only 0.2% of random grid cell configurations contained more suitable spawning habitat than the current MPAs; while under RCP 8.5, 0.8% of randomly selected grid cells fared better than current MPA protections.

Looking at the top five configurations of potential no-take MPAs, 2.4% more spawning habitat was conserved under RCP 4.5 compared to the current-day configuration of MPAs. Similarly, under RCP 8.5, the top five configurations of potential no-take MPAs conserved 10.6% more spawning habitat than current MPAs. These optimal MPA configurations protected areas that were spread out as opposed to having multiple adjacent grid cells protected (Figure 11).

Current MPA placement contained regions of climate refugia, which explained why they fared better than other potential MPA configurations in regards to Nassau grouper spawning suitability (Figure 12). These climate refuges were associated with SSTs remaining within the thermal tolerances of spawning Nassau grouper (24°C–27.5°C, from Asch and Erisman 2018). In the historical period, 82.4% of current MPAs had temperatures within this range during spawning months compared to 92.3% of areas outside of MPAs. By the end of the century, under RCP 4.5, current MPAs with conditions in the optimal thermal range for Nassau grouper spawning increased to 84.1%; while unprotected areas that met this criterion decreased to 72.0%. Under RCP 8.5, protected and non-protected regions had large declines in regions with appropriate SSTs, but protected areas had a larger proportion within the optimal thermal range (31.4%) than unprotected areas (16.9%).

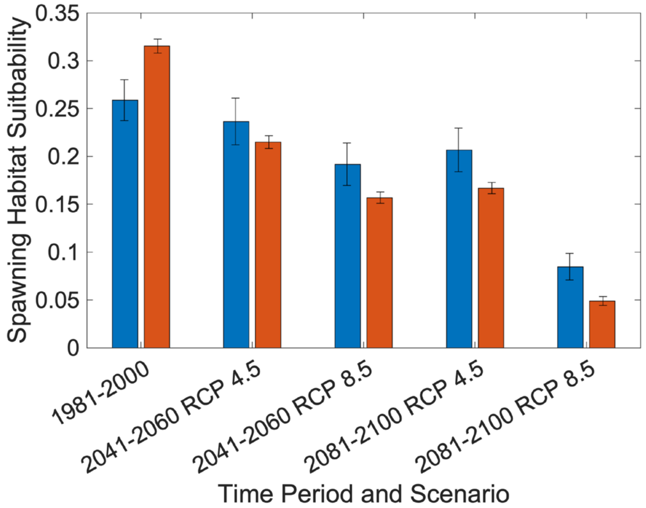

FIGURE 9 | Mean spawning habitat suitability integrated across grid cells and months for areas with (blue) and without (orange) seasonal fishing closures or sales bans in their EEZs. Means are presented with, error bars representing 95th percentile confidence intervals.

4 | Discussion

Under both RCPs, suitable spawning habitat for Nassau grouper declined from the historical period by mid-century, with larger declines by the end of the century. Historical model simulations across all ESMs coincided with observations of Nassau grouper spawning times, which occurred in winter months through most regions and June and July near Bermuda. Declines in Nassau grouper suitable spawning habitat were consistent with projected declines among other Caribbean reef fish species in response to climate change and fishing pressure (Cheung et al. 2009; Maharaj et al. 2018; Gokturk et al. 2022; Millington et al. 2022). Declines were projected to be more precipitous under the more extreme climate pathway (RCP 8.5), suggesting that Nassau grouper outcomes may be directly tied to how well climate change is mitigated. Moreover, declines in suitable spawning habitat were similar, although less severe, within management areas than outside. While these findings suggested that some MPAs may be more resilient to climate change than unprotected areas, they also showed that utilizing climate projections when determining what areas to protect can help identify additional climate refugia.

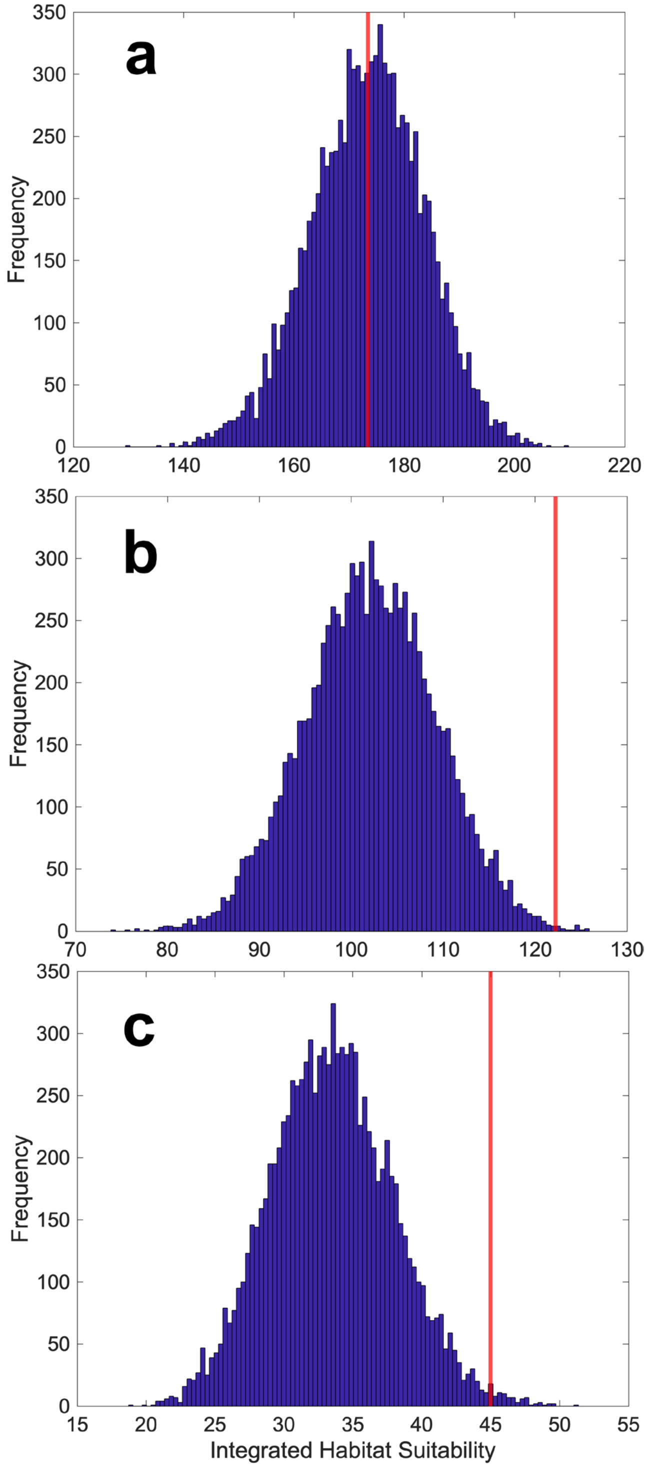

FIGURE 10 | Frequency of integrated suitable spawning habitat scores for 10,000 random selections of grid cells for historical period (a), and the end of century under RCP 4.5 (b) and RCP 8.5 (c). X axes have different score ranges based on time periods. Red lines represent the score of currently protected grid cells.

4.1 | Multi-Model Approach for Suitable Spawning Habitat

Utilizing a multi-model approach for this research improved confidence in results (as compared to Asch and Erisman 2018), since there was a high level of agreement in projected changes in oceanic conditions across models throughout the region. Agreement across models was most frequent in regions that appear to have substantial changes from the historical period, which suggests that the models depict large changes in habitat suitability similarly. While models agreed in the direction of change, they had variations in the severity of changes, reflective of their differences in climate sensitivity (Dunne, John, Adcroft, et al. 2012; Dunne, John, Shevliakova, et al. 2012; Ilyina et al. 2013; Dufresne et al. 2013). Utilizing projections across multiple models can produce more robust results, because this better quantifies model uncertainty (Hawkins and Sutton 2009; Deser et al. 2020; Lehner et al. 2020).

Quantifying and understanding model uncertainty is important, since it allows fisheries and marine ecosystem managers to focus on scenario uncertainty (e.g., uncertainty associated with not knowing which emission pathway we will follow). This can be addressed by considering several emissions scenarios, as well as assessing uncertainty due to changes in fishing pressures in the future. While managers generally cannot influence what climate change scenarios are most likely to occur due to their global scale, understanding scenario uncertainty can help managers determine what local actions would be most appropriate to employ under each of the potential emissions scenarios. In addition to utilizing multiple models to understand uncertainty, these findings can be compared to observations and other research.

4.2 | Climate Refugia and Management Implications

Within the historical period, Nassau grouper spawning suitability was fairly consistent within and outside of protected areas. This was likely reflective of the fact that MPAs are often not sited with specific species or climate change in consideration (Kelleher and Kenchington 1991; Hopkins et al. 2016). While suitable spawning habitat showed declines throughout much of the region by mid-century and end of century, areas within MPAs declined less than areas outside of MPAs. Although the analyses here included multi-use MPAs with no-take areas in addition to full no-take MPAs, these findings show that MPAs are providing suitable habitat for Nassau grouper. These results may suggest an overestimate of suitable spawning habitat found in solely no-take zones since multi-use MPAs were included in this analysis. However, regions with multi-use MPAs may still convey other benefits, such as cleaner waters and reduced disturbances from coastal development, dredging, and offshore energy development. These results suggested that by the end of the century, MPAs will provide protection for more suitable Nassau grouper spawning habitat than areas without MPAs. This pattern held true for seasonal fishing restrictions as well. Historically, EEZs with seasonal fishing restrictions contained less suitable spawning habitat than areas outside of these regions. By later in the century, this pattern reversed. In all cases, areas with seasonal fishing restrictions had suitability indices equal to or better than non-protected areas.

While our results indicate that MPAs will fare comparatively well under climate change conditions compared to non-protected areas, current seasonal fishing restrictions will likely not protect

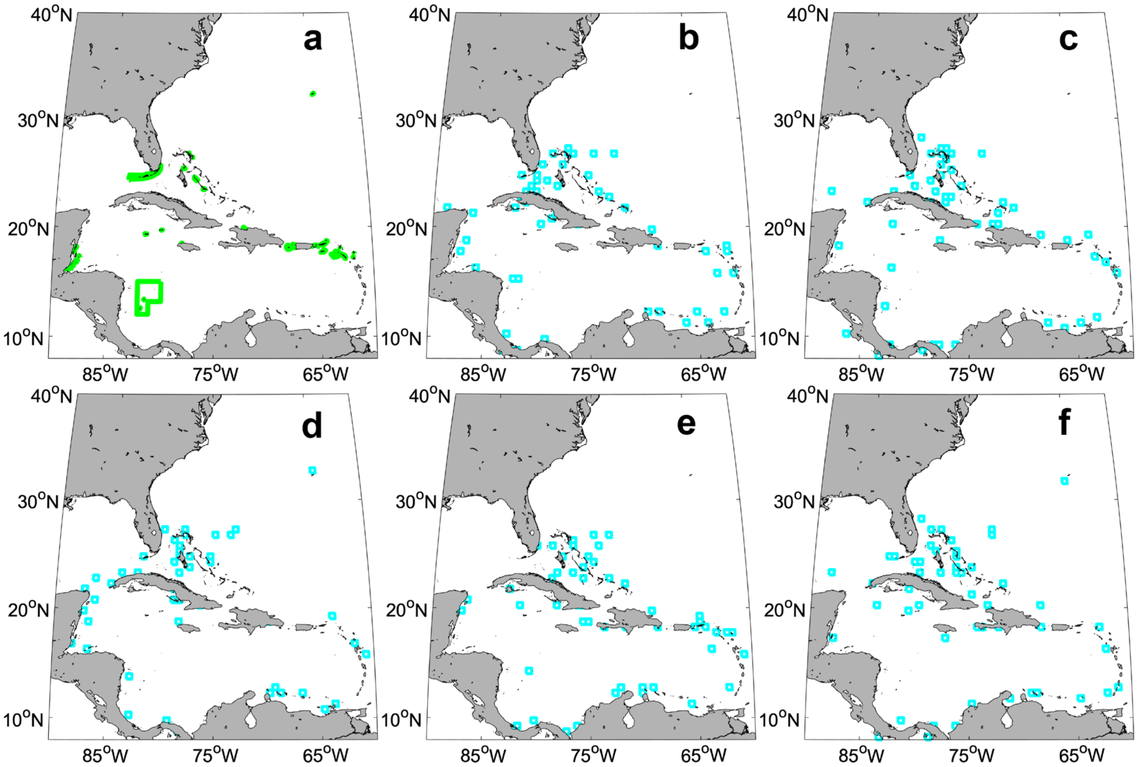

FIGURE 11 | Configuration of current protected grid cells (a, green) and top five grid cell configurations from bootstrap analysis (b–f, blue). These are based on maximum suitable spawning habitat scores at the end of the century under RCP 8.5 (b–f).

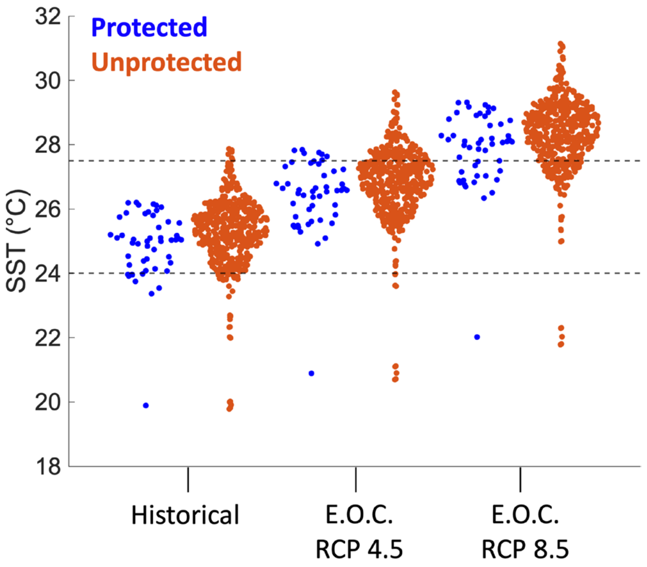

FIGURE 12 | Sea Surface Temperature (SST) within (blue) and outside (orange) protected area grid cells under historical (1981–2000) and end of century (2081–2100) periods. Dashed lines represent minimum (24°C) and maximum (27.5°C) range of thermal tolerance of spawning Nassau grouper (from Asch and Erisman 2018).

Nassau grouper FSAs as well as they could in the future. EEZs of countries with seasonal fishing restrictions saw declines in spawning habitat suitability that were statistically similar to the entire region, though lesser in magnitude. While Figure 9 shows seasonal restrictions faring better than non-protected areas, these restrictions could still be improved by shifting their timings to better match changes in spawning phenology. When looking at the central tendency of spawning suitability, The Bahamas, British and U.S. Virgin Islands all had shifts of over a month later, and projected phenology of spawning in Bermuda shifted over a month earlier. Mexico, the Cayman Islands, and Belize also exhibited shifts towards later spawning, although these changes were less than a month. These changes in central tendency do not depict individual spawning events, which are specifically tied to the lunar cycle (Sadovy and Eklund 1999; Whaylen et al. 2007). Instead, central tendency provides insight into broader changes in seasonality of spawning due to the monthly temporal resolution of ESM output. However, the association between Nassau grouper spawning and lunar phases is not expected to be affected by climate change. Instead, we anticipate that shifts in spawning phenology will occur such that there is a greater amount of spawning during the appropriate lunar phase, but potentially during a different month that better optimizes preferred spawning temperatures. This implied that seasonal fishing restrictions will need to be adapted in the future to continue to protect suitable spawning habitat. Adaptive management may become necessary, such as changing the months of restrictions (perhaps a decadal basis) as opposed to having static closed seasons. This can be better achieved by implementing an objective-driven framework to identify spawning timeframes, such as described in McDonald et al. (2017) or continual in situ monitoring of spawning phenology.

While much of the Nassau grouper's geographic range is expected to see declines in suitable spawning habitat, model results identified some regions that may serve as climate refuges. Under both RCPs, some areas of the northern Caribbean displayed increases in suitable spawning habitat at the end of the century. In these regions, increases in spawning suitability were due to the fact that historical conditions were colder than optimal for Nassau grouper spawning, while warming due to climate change brought these areas closer to the ideal range. Refuges may also arise depending on the level of climate mitigation achieved. In the area north of Colombia (Figure 4c,f) declines in spawning habitat suitability may be less severe under RCP 4.5. Climate refuges in this region may also benefit from upwelling, bringing deep, colder water to the surface (Correa-Ramirez et al. 2020). Under climate change, upwelling systems may provide refugia for fishes that are otherwise stressed by changing conditions (Lourenço et al. 2016).

4.3 | Identifying Future Protected Areas

The findings of this research suggest that when determining sites for MPAs, climate change considerations need to be taken into account. Currently, protected areas are sited either to meet specific conservation goals, protect certain regions or species, or create multi-use MPAs (Kelleher and Kenchington 1991). However, other considerations, such as politics, financial restrictions, geographic boundaries, enforcement limitations, and historical utilization of areas by stakeholders, often influence the siting of MPAs (Claudet et al. 2020). These considerations may lead to MPAs that do not necessarily protect ecologically important species, such as the Nassau grouper, or they may lead to MPAs that are not resilient to climate change. This work shows that for MPAs to meet future conservation goals, climate change needs to be considered, such as by seeking out potential future thermal refugia. Currently, the United States has a plan to protect 30% of US lands and waters by 2030 as part of the global 30 × 30 initiative under the Global Biodiversity Framework (Carroll et al. 2022). For this initiative to be better informed, climate change considerations should be taken into account to seek out locations resilient to climate change. These findings could also contribute to the United Nations Specially Protected Areas and Wildlife (UN SPAW) protocol. In 2017, the Nassau grouper was added to the SPAW Annex III, with an aim to focus protection on aggregation-forming species (Somma et al. 2021). Seeking out potential climate refuges to include in protected areas would align with the goals of the SPAW protocol since these areas are potential spawning sites for species such as the Nassau grouper. Using results from models such as those described herein to determine new protected area locations could help bolster regional resilience in the face of climate change.

Our bootstrap analysis to identify optimal future MPA configuration suggested that a series of smaller MPAs may be more effective at protecting Nassau grouper than fewer large-scale MPAs, which are not fully representative of marine geography (Agardy 1994; Roberts 1997; Sullivan-Stack et al. 2022). While the existing MPA configuration was shown to have a higher habitat suitability than most configurations of random areas, there were still some configurations that were slightly better than the existing configuration (at most 3% better under RCP 4.5 and 14% better under RCP 8.5). These configurations exhibited a series of smaller, spread-out MPAs. By spreading out smaller MPAs, management may better be able to provide safe, suitable habitat for Nassau grouper by protecting a broader range of locations, which may be more resilient to climate change. This would also potentially be of benefit during migrations to spawning sites, since Nassau grouper is known to travel hundreds of kilometers to spawn (Bolden 2000; Starr et al. 2007; Nemeth et al. 2023). If configured correctly, such MPAs could also serve as stepping stones allowing for poleward migration under climate change. These networks of MPAs could also enhance meta-population connectivity by protecting distant dispersal locations (Balbar and Metaxas 2019). However, on the other hand, larger MPAs may be able to cover a substantial portion of an individual's life history so that it is protected throughout its whole life cycle. Additionally, large MPAs can bring us closer to our 30 × 30 goal. Also, the cost for enforcement per unit area can be less for larger MPAs, so there are benefits to consider for both options (Wilhelm et al. 2014).

Considering climate change when siting MPAs and determining seasonal fishing restrictions has inherent challenges. For one, the spatial and temporal scales of management often do not align with the rates of change we may see under climate change (Wilson et al. 2020). For example, coastal zone governance may evaluate management strategies at timeframes (often 5–10 years) that do not match with climate change rates. Also, creating systems of MPAs or determining seasonal fishing restrictions can be a long process (Fox et al. 2013; Álvarez-Fernández et al. 2020) and, therefore, may be difficult to evaluate and adjust adaptively over time due to the time needed to formulate regulation. For both MPAs and seasonal fishing restrictions, it will be in the best interests of managers to set determinable goals and metrics of success and evaluate them frequently based on monitoring data. To properly monitor these sites, managers may need to keep better records of data to avoid shifting baselines (Fulton 2023).

4.4 | Caveats and Assumptions of Species Distribution Models

While the results of this study suggest significant declines in suitable spawning habitat for Nassau grouper, it is important to note that this NPPEN model only considers oceanographic conditions (specifically SST, STG, and v geostrophic currents). Other possible influences on suitable spawning habitat for Nassau grouper include interspecies interactions, such as predator and prey spatiotemporal variability in abundance (Peck et al. 2012; Petitgas et al. 2013). This work also assumed that appropriate substrate (in this case, coral reefs) will persist despite climate change and will remain suitable for spawning habitat. Other habitats were not considered, as there is little evidence of Nassau grouper utilizing artificial reefs or other substrates, and the evidence that does exist is anecdotal and identifies juvenile fish, not spawning populations (Beets and Hixon 1994; Colin et al. 1997). There are also other possible factors that may determine where Nassau grouper spawn, including spatial or temporal cues, such as photoperiod or lunar cycles (Nemeth et al. 2007), which were not considered in the NPPEN model. However, photoperiod and lunar periodicity will not change due to climate change. Other cues, including behavioral cues and migration routes, were not considered due to the inability to model their variation.

The use of SST as a variable for defining suitable spawning habitat is also a potential limitation of this work, which reflects the available empirical data and earth system models. Nassau grouper are typically found at spawning aggregations with depths of 30–60 m, but they rise to 20–25 m of the surface during spawning

(Olsen and LaPlace 1979; Carter 1986; Aguilar-Perera and Aguilar-Dávila 1996; Nemeth et al. 2023). This suggests the temperatures that FSA experience are not likely to be the same as at the surface. Using SST in our model was a decision based on available empirical data for bias correction, of which SST has more complete available data throughout the species' entire distribution range compared to data at depth, which is often limited to point sampling or transects by CTD or Argo profiles (such as the NOAA World Ocean Database, Mishonov et al. 2024). SST was also selected due to the fact that there is evidence that Nassau grouper rise in the water column at the actual time of spawning (Starr et al. 2007). Coupled with the fact that eggs are positively buoyant (Starr et al. 2007), this suggests that, while SST may not be the exact temperature for Nassau grouper spawning, it may still be a useful metric. These factors also make using temperature at depth difficult to use given that the depth of spawning likely varies. Lastly, this work builds off prior work from Asch and Erisman (2018) and Gokturk et al. (2022), which also used SST due to similar limitations. This allows us to make comparisons between these different bodies of work. That said, as datasets become more readily available, this could be a valuable area for future study, particularly to compare our results to those using SST.

In addition to the challenges presented by what variables could be included in spawning habitat models, large-scale analyses such as this often cannot represent interactions at the scale of individual fishes or populations (Rahbek 2005). These include factors, such as submesoscale circulation and reef geomorphology, which have been shown to influence FSAs (Karnauskas et al. 2011; Kobara et al. 2013). While this study focused on range-wide distribution patterns, it can be important to consider that there may be important smaller-scale relationships to consider that influence Nassau grouper spawning habitat because particular substrate types or bathymetric features (e.g., promontories at the edge of reefs) may influence where spawning occurs at a reef. Most species distribution models do not consider local adaptation or acclimation to changing climatic conditions (Robinson et al. 2011; Hällfors et al. 2016). On the other hand, fish will often seek out preferred habitat through movement as opposed to acclimating to novel conditions (Habary et al. 2017), which may bode well for the accuracy of projections from species distribution models. Other species of grouper and snapper have been observed utilizing artificial reef substrate (Overholtzer-McLeod 2004; Dance et al. 2011; Addis et al. 2013). It may be possible for artificial reefs at higher latitudes to support FSAs in the future. This would facilitate poleward changes in FSA distribution, while decreasing the extent of the decline in suitable spawning habitat projected by NPPEN. Alternatively, Nassau grouper may also seek out deeper, cooler waters at their current latitudes to escape changing conditions (Rutterford et al. 2015; Kitchel et al. 2022). Nassau grouper have been seen to dive to depths as great as 255 m at spawning aggregations (Starr et al. 2007), so seeking out cooler, deeper waters could be an alternative to migrating poleward. Future research is needed to address these alternate responses to climate change.

5 | Conclusions

The Nassau grouper is an economically, biologically, and culturally important species in the wider Caribbean region that has been heavily threatened by overfishing. Much work has been done on the species with a focus on non-spawning stage adult fish, which is when this species is more thermally tolerant than during other life stages (Asch and Erisman 2018). The findings of this work provide additional insight into how to best manage Nassau grouper given their reduced thermal tolerance as spawning adults. Specifically, this work suggests that adaptive management may become necessary to mitigate the effects of climate change, particularly by seeking out climate refugia for siting of future MPAs. For seasonal fishing closures and sales bans, being able to adjust the seasonal times of the management measure will also be important to effectively protect Nassau grouper spawning aggregations (Rowell et al. 2015; Nemeth et al. 2023). While there are other factors that may influence management strategies (including politics or cultural acceptance of management measures), where practical, these findings can help better manage the species.

While the scope of this work is species-specific, the results are transferable and can help assist managers in decision making when it comes to climate change resilience of other commercially, economically, and biologically important reef fish species. Many other Caribbean grouper species, including Yellowfin grouper and Black grouper, spawn in colder months (Heyman and Kjerfve 2008). Research has shown that these species will see declines similar to Nassau grouper (Gokturk et al. 2022). It is likely that these species may seek out similar refugia when forming spawning aggregations. Thus, this research can be applied to identifying potential habitats to protect for multi-species spawning aggregations. While information on thermal ranges and existing management of other species would be necessary, our approach may be used to identify where refugia will occur and aid in fisheries and marine ecosystem decision making throughout the region.

Author Contributions

Brian S. Bartlett: conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, validation, visualization, writing – original draft, writing – review and editing. **Brad Erisman:** methodology, resources, supervision, validation, writing – review and editing. **Rebecca G. Asch:** conceptualization, data curation, funding acquisition, methodology, project administration, resources, supervision, validation, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Coral reef data was obtained from Reefs at Risk and UNEP-WCMC at https://doi.org/10.1108/meq.2011.08322daa.003 and https://doi.org/10.34892/t2wk-5t34 respectively. The SRTM30_PLUS bathymetry data can be found at http://doi.org/10.1126/science.1258213. AVHRR and AVISO data for bias corrections can be found at https://doi.org/

10.3334/ORNLDAAC/77 and https://doi.org/10.5067/DYNTO-1D1M1 respectively. For climate data, NOAA GFDL ESM2M model runs (historical, RCP 4.5 and RCP 8.5) can be found at http://doi.org/10.1594/WDCC/CMIP5.NGEMeh, https://doi.org/10.1594/WDCC/CMIP5.NGEMr4, and https://doi.org/10.1594/WDCC/CMIP5.NGEMr8 respectively. MPI ESM-MR model runs (historical, RCP 4.5 and RCP 8.5) can be found at https://doi.org/10.1594/WDCC/RCM_CMIP5_historical-MR, https://doi.org/10.1594/WDCC/RCM_CMIP5_rcp45-MR and https://doi.org/10.1594/WDCC/RCM_CMIP5_rcp85-MR respectively. IPSL-CM5A-MR model runs (historical, RCP 4.5 and RCP 8.5) can be found at https://doi.org/10.1594/WDCC/CMIP5.IPIMhi, https://doi.org/10.1594/WDCC/CMIP5.IPIMr4 and https://doi.org/10.1594/WDCC/CMIP5.IPIMr8 respectively. Data and Code Associated with Publication "Current Marine Protected Areas conserve fish spawning aggregations under climate change due to habitat refugia" https://doi.org/10.5281/zenodo.16502562. This dataset includes all bias-corrected climatological data, Nassau grouper spawning aggregation data, reef shape data, and MPA border data used in "Current Marine Protected Areas conserve fish spawning aggregations under climate change due to habitat refugia". This repository also contains the species distribution model (NPPEN) code used to analyze this data in Matlab. These datasets were input for the NPPEN model, described in the paper, under various time periods and RCP scenarios. Climatological data is organized as MODEL_timeperiod_variable.csv. Each file consists of 14 columns, with columns 1 and 2 representing latitude and longitude respectively. Columns 3–14 represent the bias-corrected monthly value for that variable (3 = January, 4 = February… 14 = December) etc. Sea Surface Temperature (SST) variables are measured in °C; Seasonal Temperature Gradients (STG) are measured in change in °C/month. North/South geostrophic currents (v) are measured in cm/s. MPA_boundaries.csv lists the northernmost, southernmost, easternmost, and westernmost extents of individual MPAs. Pixels_with_reefs.csv provides a 0.5° × 0.5° grid with '1's representing pixels in our model region with reefs, and '0's representing the absence of reefs. NG_spawning_data.csv provides information on Nassau grouper spawning aggregations. Columns 1 and 2 provide latitude and longitude (respectively) data of spawning aggregations, truncated to the nearest 0.1°. Column 3 provides the month of the spawning aggregation. Column 4 provides SST in °C; column 5 provides STG in change °C/month; and column 6 provides north/south geostrophic currents in m/s. NPPEN_script_Matlab.rtf provides generalized NPPEN code for Matlab, using variables provided.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Regional suitable spawning habitat changes from the historical to end-of-century periods under RCP 4.5 (a, c, e) and RCP 8.5 (b, d, f). Highlighted regions include The Bahamas (a and b), Hispaniola (c and d), and north of Colombia (e and f). This figure depicts similar data as Figure 4, but includes all cells utilized in analyses. **Figure S2:** Differences in suitable spawning habitat from the historical period (1981–2000) to the end-of-the-century (2081–2100) under RCP 4.5 (a–c) and RCP 8.5 (d–f) for the three models: GFDL (a and d), IPSL (b and e) and MPI (c and f). Results have been masked to display only regions with depth of 200 m or less. An equivalent series of maps is shown in Figure 6, but without this depth mask since differences between ESMs are more evident when results are displayed at the model's native resolution. Blue colors indicate increases in spawning habitat from the historical period, while red colors reflect suitable spawning habitat declines.