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Spawning aggregations act as a bottleneck influencing climate change impacts on a critically endangered reef fish

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Abstract

Aim: Most projections of how climate change will affect species distributions and phenology are based on a species' most conspicuous life stage. However, not all life stages are equally sensitive to temperature. Among fishes, spawning adults often have narrower thermal tolerances than other life stages and may constrain population responses to climate change. We tested this hypothesis using data on Nassau Grouper (*Epinephelus striatus*), an endangered coral reef fish.

Location: Greater Caribbean.

Methods: Species distribution models of spawning and nonspawning adults were compared to determine which environmental variables exerted the greatest influence on grouper distribution. We calculated the thermal niche and ecological niche breadth of both life stages. An earth system model was applied to project how species distribution and phenology shift under two climate change scenarios.

Results: Sea surface temperature and seasonal temperature gradients affected the distribution of both spawning and nonspawning adults, but these life stages differed in their preferred temperatures and reaction to oceanic currents. While the two life stages exhibited similar ecological niche breadth, the thermal niche of spawners was narrower. By 2081–2100, potential spawning habitat was projected to decline under a business-as-usual scenario by 82% relative to 1981–2000, whereas suitable habitat for nonspawners decreased by 46%. Poleward shifts in latitude occurred 3.8–4.2 times faster for spawners than nonspawners. These changes were attributed to rising temperatures, whereas hydrographical changes did not have a substantial impact. Spawning phenology changed little, with a slight contraction in spawning season but a large reduction in spawning probability across all months.

Main Conclusions: A narrow thermal tolerance range among spawning fishes indicates that this life stage may be a bottleneck constraining responses to climate change. Future research should consider the reaction of each life stage to changing conditions. Conservation of *E. striatus* should take shifting distribution and phenology into account, as climate effects may exacerbate population declines due to fishing and reduce the efficacy of conservation measures.

KEYWORDS
climate change projections, coral reef fishes, fish spawning aggregations, greater Caribbean, Nassau Grouper, phenology, species distribution modelling

1 | INTRODUCTION

Water temperature sets the large-scale biogeographical distribution of most marine fishes, including the range where adults spawn, with smaller-scale dynamics of reproduction determined by life history strategies that evolved in response to habitat characteristics and biophysical processes that maximize fitness (Pörtner & Peck, 2010; Wooton & Smith, 2015). Similarly, seasonal changes in water temperatures affect the timing of reproduction in fishes such that increasing temperatures cue reproductive activity in spring-spawning species and falling temperatures stimulate reproduction in autumn spawners (Pankhurst & Munday, 2011). Changes in seasonal temperatures can significantly affect spawning phenology (Asch, 2015; Sims, Wearmouth, Genner, Southward, & Hawkins, 2004), while variations in temperatures on annual-to-decadal scales are associated with shifts in spawning ground locations (Asch & Checkley, 2013; Bellier, Planque, & Petitgas, 2007; Hutchings & Myers, 1994).

Given the relationship between temperature and the timing and distribution of spawning in fishes, it is not surprising that climate change is causing changes to fish reproductive and population dynamics. Changing water temperatures, currents and ecosystem characteristics associated with climate change and climate variability are triggering shifts in spawning phenology and the geographic range of spawning (Asch, 2015; Ciannelli, Bailey, Chan, & Stenseth, 2007). As fishes alter reproductive behaviour to avoid unfavourable conditions and move into suitable areas for spawning, population-scale or species-level changes in reproduction are likely, such as changes in spawning season length, shifts in spawning frequency and intensity, establishment of new spawning sites and abandonment of historical spawning grounds (Munday, Jones, Sheaves, Williams, & Goby, 2007; Sundby & Nakken, 2008). These changes in spawning behaviour affect reproductive output and recruitment success, which subsequently influence the growth rate, maintenance and distribution of populations and species (Cushing, 1990; MacKenzie, Hinrichsen, Plikshs, Wieland, & Zezera, 2000; Mertz & Myers, 1994).

The influence of climate change on specific life history stages has rarely been examined among marine organisms (Ong et al., 2015) but it may determine the overall response of species. Marine fishes experience ontogenetic changes in thermal habitat, with the temperature range of spawning often narrower than the temperature range where adults or juveniles can survive, feed and live (Brewer, 1976; Van Der Kraak & Pankhurst, 1997). The narrow thermal habitat of spawning fishes reflects physiological changes where spawners allocate more energy to reproduction and experience an increase in oxygen demand, which limits their ability to cope with temperature outside their optimal range (Pauly, 2010; Pörtner & Farrell, 2008; Pörtner & Peck, 2010). The thermal habitat for spawning is likely a "bottleneck," which may ultimately dictate how fish populations shift their distribution responding to climate change.

Transient fish spawning aggregations (FSAs) provide an ideal system to evaluate whether such "bottlenecks" in climate change responses may exist, because the timing and distribution of FSAs are discrete and well documented in some species (Erisman et al., 2017). Many large-bodied groupers form FSAs where individuals migrate long distances during specific times of the year to reproduce within large, temporary gatherings (Sadovy de Mitcheson & Colin, 2012). FSAs are critical life cycle events to species, often the only opportunities for fish to reproduce (Sadovy de Mitcheson & Erisman, 2012). Fishes that migrate to form FSAs may be particularly vulnerable to climate change, as migrants are adapted to adjust their behaviour with annual changes in weather, and warming may alter migration timing and arrival at spawning grounds (Sims et al., 2004). The decoupling of climatic variables between geographically separate breeding and nonbreeding grounds can result in mistimed migration and subsequent declines in reproductive success due to lowered food availability for offspring (Beaugrand, Brander, Lindley, Souissi, & Reid, 2003; Platt, Fuentes-Yaco, & Frank, 2003; Robinson et al., 2009). Also, warming is associated with reduced movement and activity in some aggregation spawners, which could decrease the frequency or extent of reproductive migrations in turn leading to declines in spawning intensity and reproductive output (Johansen, Messmer, Coker, Hoey, & Pratchett, 2014).

Nearly two-thirds of documented FSAs are degraded or have disappeared due to fishing (Russell et al., 2014), and climate-induced changes in the distribution and occurrence of FSAs could hold serious consequences for marine conservation. The high abundance of fish at FSAs during predictable periods and locations render FSAs vulnerable to fishing (Sadovy de Mitcheson & Erisman, 2012). Overfishing at FSAs reduces reproductive capacity by removing future egg production and interfering with mating (Erisman, Apel, MacCall, Román, & Fujita, 2014; Erisman et al., 2017; Rowe & Hutchings, 2003) and is associated with rapid declines in fish stocks, fishery collapses, extirpation of aggregations and even near extinction (Erisman, Allen, Pondella, Miller, & Murray, 2011; Sadovy de Mitcheson & Colin, 2012). Marked changes in phenology and distribution of spawning are likely to reduce the effectiveness of spatial and temporal regulations meant to protect FSAs from fishing (Lowerre-Barbieri et al., 2016). Negative impacts of overfishing and undermanagement on FSAs will likely be amplified by climate change, because fishing and changing environmental conditions can interact to create a double jeopardy situation that increases population size variability and heightens the probability of stock collapse (Anderson et al., 2008; Hsieh et al., 2006).

Changes in the dynamics of FSAs are likely to have serious impacts on species interactions, food webs and ecosystem structure (Erisman et al., 2017; Mourier et al., 2016). The ephemeral concentration of food resources at FSAs are associated with timed migrations by large migratory predators (e.g., sharks, tunas) that feed on aggregating fishes and mega-planktivores (e.g., whale sharks, manta rays) that feed on spawned eggs (Graham & Castellanos, 2012; Hartup, Marshall, Kottermair, & Carlson, 2013; Heyman, Graham, Kjerfve, & Johannes, 2001). Spillover of these rich resources can benefit adjacent areas (Cherubin, Nemeth, & Idrisi, 2011; Harrison et al., 2012). Likewise, the presence of predatory species that form FSAs (e.g., groupers) is important to the stability, structure and function of reef ecosystems (Boyd, Wanless, &

Camphuysen, 2006; Mourier et al., 2016; Sadovy de Mitcheson et al., 2012). Reduced abundance of groupers and other apex predators on reefs can alter community structure through changes in benthic dynamics, coral health, fish diversity, population demographics of lower trophic groups and resilience to climate change (Estes et al., 2011; Ruttenberg et al., 2011; Walsh, Hamilton, Ruttenberg, Donovan, & Sandin, 2012).

Here, we examine the potential impacts of climate change on the distribution and phenology of FSAs of Nassau Grouper (*Epinephelus striatus*, Bloch 1792), an iconic Caribbean species that migrates up to several hundred kilometres to spawn in aggregations of up to 100,000 individuals (NOAA, 2013). This species is endangered throughout its range due to overfishing of its FSAs (IUCN, 2017). We selected this species due to its importance for conservation and because the distribution of adult *E. striatus* and its FSAs are well documented (Kobara, Heyman, Pittman, & Nemeth, 2013; SCRFA, 2014). *E. striatus* conservation has predominantly focused on the designation of seasonal fishing closures and sales bans (NOAA, 2013). If climate change alters the distribution or phenology of spawning, the efficacy of these conservation measures could be compromised.

The objective of this study was to model projected 21st-century changes in the geographic distribution and phenology of *E. striatus* FSAs. We focused on answering three questions: (a) How may climate change affect the distribution, phenology and intensity of spawning in *E. striatus*? (b) What oceanic variables are responsible for the projected changes in the timing and distribution of FSAs? (c) Will changes in FSAs act as a "bottleneck" constraining overall shifts in species distribution? Our results will be used to assess the robustness of current-day conservation strategies for Nassau Grouper in the face of climate change.

2 | METHODS

To determine whether FSAs serve as a "bottleneck" constraining the adaptation of *E. striatus* to climate change, we compared changes in the distribution and phenology of spawning and nonspawning adult fishes, as well as modelled changes in grouper occurrence jointly across these two life history stages. Two biological datasets were used to develop separate species distribution models of spawning and nonspawning *E. striatus*: (a) the locations and months of *E. striatus* FSA formation were compiled from the scientific literature and an online database documenting FSA occurrence (SCRFA, 2014; http://www.scrfa.org; Supporting information Table S1 and Supporting information Appendix S1; $n = 283$); (b) point data on the monthly distribution of nonspawning adults were obtained from the Ocean Biogeographic Information System (OBIS; http://www.iobis.org; $n = 223$). The spatial and seasonal distributions of *E. striatus* observations are summarized in Figure 1. Nonspawning adults were observed year long, but the largest number of OBIS records were from March–September (blue bars in Figure 1b). In contrast, spawning occurs between December–April across most of this species' range, except in Bermuda where it occurs in June and July (orange points and bars in Figure 1). These observed months of peak spawner and nonspawner occurrence were used to constrain our focal season in some analyses.

Eight oceanographic variables were initially selected to examine how changing conditions may influence *E. striatus* distribution and phenology: (a) sea surface temperature (SST); (b) seasonal SST gradients (i.e., the difference in SST between month$_i$ and month$_{i-1}$); (c) surface chlorophyll (Chl) *a* concentration; (d) eddy kinetic energy (EKE); (e) geostrophic current velocity in the east/west (*u*) direction; (f) geostrophic velocity in the north/south (*v*) direction; (g) total speed of geostrophic currents; and

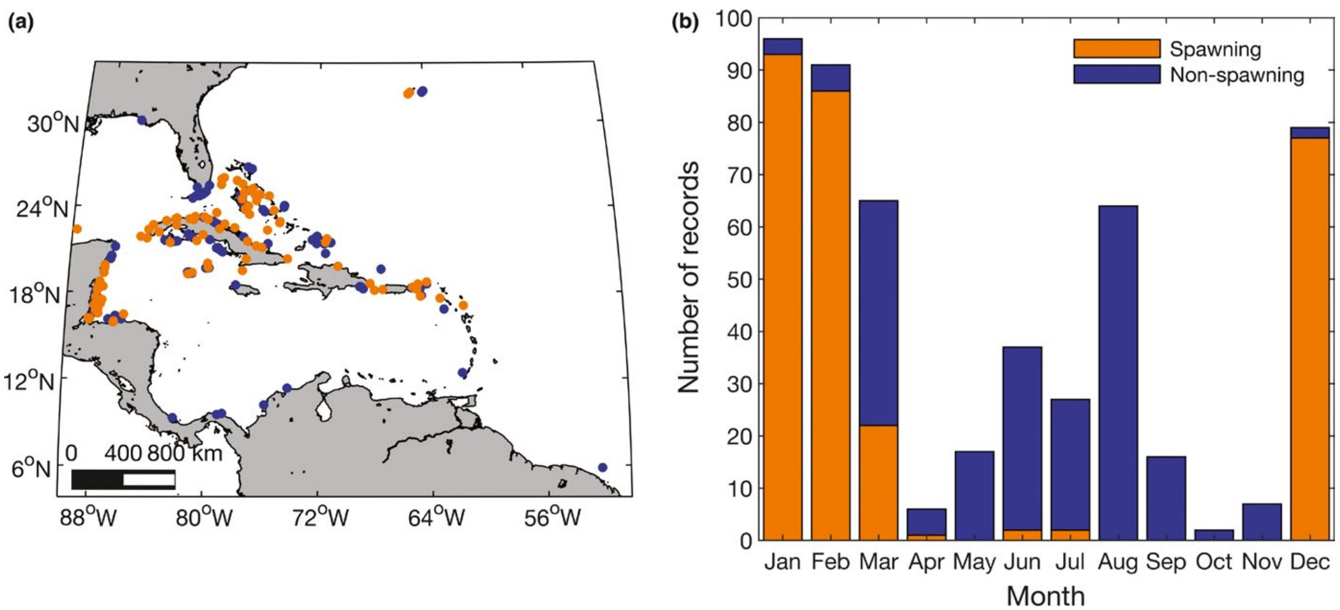


FIGURE 1 (a) Map of observed spawning aggregations of *Epinephelus striatus* from the Fish Spawning Aggregation (FSA) database in Supporting information Table S1 (orange circles) and nonspawning adult *E. striatus* observations from the Ocean Biogeographic Information System (OBIS) (blue circles). Map projection: Hammer-Aitoff. (b) Seasonal distribution of *E. striatus* observations from the FSA and OBIS databases

(h) vertical velocity (i.e., upwelling/downwelling). Details on the remote sensing data sources of these variables are provided in Supporting information Appendix S2. SST was selected as an independent variable to include in our analysis, because *E. striatus* can be induced to spawn in an aquaculture setting by manipulating temperature (Tucker, Woodward, & Sennett, 1996). Seasonal SST gradients were examined as an environmental covariate, because some reef fish species are known to spawn at thermal maxima, thermal minima, or during warming and cooling periods rather than at specific temperatures (Wooton & Smith, 2015). Lastly, many reef fishes have evolved to select spawning aggregation sites and times where currents favour retention of larvae close to shore and oceanographic conditions enhance primary and secondary production (Donahue, Karnauskas, Toews, & Paris, 2015; Karnauskas, Cherubin, & Paris, 2011). As a result, we considered Chl *a*, upwelling velocity, geostrophic currents and EKE as environmental covariates in our species distribution model, because they serve as proxies for conditions that can influence larval fish feeding and advection of fish eggs and larvae.

Data on all variables were extracted from 8–40°N and 60–93°W. We examined monthly climatologies of these variables, because FSAs recur at the same location each year, spawning migrations likely reflect learned behaviour that is repeated annually (NOAA, 2013), and the Greater Caribbean is a region characterized by reduced interannual climate variability (Deser et al., 2012). These characteristics coincide with the set of conditions where incorporating climatological data into species distribution models is often recommended (Mannocci et al., 2017). Furthermore, insufficient monitoring data are available at many *E. striatus* aggregation sites to assess how interannual climate variations may influence spawning. Observations of *E. striatus* FSAs and nonspawning adult occurrence were matched with data from each oceanographic dataset. If no data were available in the remote sensing grid cell of a fish observation, then data from surrounding grid cells were spatially averaged such that the spatial footprint for averaging was increased sequentially until each fish observation was associated with a complete set of environmental variables.

Projections of future oceanic conditions were made with one realization of the NOAA Geophysical Fluid Dynamics Laboratory Earth System Model (GFDL ESM2M; Dunne et al., 2012, 2013). At the global scale, this model has been shown to explain 99% of the spatial variability in SST (i.e., $r^2 = 0.99$), 96% of the variability in sea surface height, 80% of variability in sea surface salinity, 87% of variability in surface NO_3, 72% of variability in dissolved oxygen at 500 m and 54% of variability in chlorophyll concentration (Dunne et al., 2012, 2013). GFDL ESM2M has a resolution of 1° latitude/longitude in temperate-to-polar regions, but its resolution becomes finer in tropical regions decreasing to 0.33°. GFDL ESM2M was used to compare potential spawning habitat of *E. striatus* and nonspawning adult occurrence during baseline (1981–2000) and future (2081–2100) periods. Projections for the future period were based on Representative Concentration Pathways (RCPs) 2.6 and 8.5. RCP8.5 is a high end emissions scenario where anthropogenic influences on climate lead to an 8.5 W/m^2 change in radiative forcing by 2100, whereas RCP2.6 represents a scenario where substantial actions are taken to mitigate greenhouse gas and aerosol emissions (IPCC, 2013). Information on coral reef distribution from the Reefs at Risk database (Burke, Reytar, Spalding, & Perry, 2011) was projected onto the latitudinal/longitudinal grid used by ESM2M to constrain projections of fish occurrence to areas containing reefs. This was carried out because all records of *E. striatus* FSAs occur near coral reef promontories along the shelf edge (Sadovy de Mitcheson & Colin, 2012; NOAA, 2013; SCRFA, 2014; Supporting information Table S1 and associated references). To optimize comparability between observations and ESM2M, we undertook a model bias correction similar to those used in other studies of climate change impacts on tropical ocean ecosystems (Lehodey, Senina, Calmettes, Hampton, & Nicol, 2013; Logan, Dunne, Eakin, & Donner, 2014; Matear, Chamberlain, Sun, & Feng, 2015).

As locations of some FSAs remain undocumented, the FSA database in Supporting information Table S1 was considered to be in a presence-only format. We selected the Non-Parametric Probabilistic Ecological Niche (NPPEN) model to make projections of fish distribution, because NPPEN is capable of producing probabilistic maps of fish occurrence from presence-only data (Beaugrand, Lenoir, Ibañez, & Manté, 2011). For each life history stage of *E. striatus*, NPPEN was fit using all possible combinations of environmental variables (i.e., 127 possible models, excluding a null model) and the model that minimized the corrected Akaike information criterion (AIC_c; Hurvich & Tsai, 1989) was selected for use when making future projections. We assessed the relative importance of each environmental variable to *E. striatus* life history stages by calculating: (a) its summed Akaike weight across all possible models and (b) the difference between the AIC_c of the selected, multivariate model and each univariate model that incorporated an oceanic covariate (Burnham & Anderson, 2002). As different sets of variables were selected for each life history stage, we also ran simulations with a species distribution model that only used environmental covariates found to affect both FSAs and nonspawning adults. This was carried out to allow for more thorough comparisons of results across life stages. Using solely the variables affecting both life history stages, we also ran a simulation where we pooled data across life history stages to assess how this common form of model misspecification would impact results. Additional details about NPPEN and related analyses are described in Supporting information Appendix S2.

Monthly projections of fish distribution were made for the baseline and future periods using environmental variables from ESM2M. Changes in *E. striatus* spawning phenology between these periods were graphed and shifts in the weighted mean latitude of the probability of fish occurrence were calculated. We also computed the overall change in habitat suitability for *E. striatus* by integrating the probability of fish occurrence across all months and all locations with coral reefs and then comparing changes in this quantity between the baseline and future periods.

For RCP8.5, we determined what environmental variables were responsible for modelled changes in fish distribution and seasonality by assessing whether environmental conditions in a particular region or month fell outside the range of values associated with a probability of ≥0.35 fish occurrence according to NPPEN. The ≥0.35 threshold was selected, because it corresponded to the lowest 10th quantile of the probability of modelled fish occurrence in areas where fish were positively identified in the FSA and OBIS databases.

Lastly, we tested whether the ecological and thermal niche breadth of spawning and nonspawning *E. striatus* differed from each other, because a narrower niche breadth could be associated with a bottleneck in this species' response to climate change. Ecological niche breadth was measured following Smith (1982). Thermal niche breadth was calculated in the same way but only examined SST. Significant differences in the ecological and thermal niche breadth of spawners and nonspawners were assessed by comparing the 95% confidence intervals (CI) of these life stages (Supporting information Appendix S2).

3 | RESULTS

3.1 | Spawning aggregations

The location and timing of *E. striatus* spawning were best explained by SST, geostrophic currents in the *v* direction and seasonal SST gradients (Table 1). Akaike weights (w_i) shown in Table 1 indicated that there is a high level of confidence in this model compared to all other alternative models based on different combinations of environmental variables. The modelled probability of encountering FSAs was maximized at temperatures between 24–27.5°C, *v* of −5 to 6 cm/s and seasonal SST gradients of −1.8 to 0.8°C (Figure 2). The predominance of negative seasonal SST gradients in areas with a high probability of spawning is consistent with the fact that throughout most of its range this species spawns during winter months with cooling temperatures. The relative importance of each environmental variable based on summed Akaike weights indicated that SST, *v* and seasonal SST gradients all had similar effects on FSA distributions, whereas our second metric measuring the relative importance of oceanic

TABLE 1 Selection of environmental variables included in the Non-Parametric Probabilistic Ecological Niche (NPPEN) model based on minimization of the Akaike information criterion (AIC_c) and log likelihood

Model number	Log likelihood	AIC_c	ΔAIC_c	w_i	*k*	SST	SST gradients	Chl	*u*	*v*	EKE	Vertical velocity
Spawning aggregations												
1	2,016.3	4,038.5	0.0	0.9998	3	X	X			X		
2	2,022.5	4,053.1	14.6	0.0007	4	X	X			X	X	
3	2,024.7	4,053.5	15.0	0.0006	2	X				X		
4	2,031.9	4,067.8	29.3	4.42×10^{-7}	2	X		X				
5	2,031.1	4,068.3	29.8	3.39×10^{-7}	3	X	X	X				
6	2,029.5	4,069.0	30.5	2.37×10^{-7}	5	X	X	X		X	X	
7	2,033.0	4,071.9	33.4	5.51×10^{-8}	3	X	X				X	
8	2,034.5	4,072.9	34.4	3.38×10^{-8}	2	X			X			
9	2,033.5	4,073.1	34.6	3.08×10^{-8}	3	X	X		X			
10	2,036.4	4,076.9	38.4	4.67×10^{-9}	2	X	X					
Nonspawning adults												
1	1,691.2	3,390.5	0.0	0.9669	4	X	X		X			X
2	1,695.9	3,397.9	7.4	0.0234	3	X	X					X
3	1,697.5	3,401.0	10.6	0.0049	3		X		X			X
4	1,696.2	3,402.3	11.9	0.0025	5	X	X	X	X			X
5	1,699.3	3,402.7	12.2	0.0021	2		X		X			
6	1,702.8	3,409.7	19.2	0.0001	2		X					X
7	1,701.9	3,409.9	19.4	0.0001	3	X	X		X			
8	1,704.6	3,413.2	22.8	1.11×10^{-5}	2	X	X					
9	1,704.8	3,413.6	23.1	9.20×10^{-6}	2		X			X		
10	1,704.1	3,416.1	25.7	2.55×10^{-6}	4		X	X	X			X

Notes. Results are shown for both models fit using data on spawning aggregations and nonspawning adults. X indicates that an environmental variable was included in a given model. For brevity, only the ten models with the lowest AIC_c are listed. Abbreviated variable names and statistical parameters: w_i: Akaike weights; *k*: number of parameters in a model; SST: sea surface temperature; Chl: log-transformed chlorophyll concentration; *u*: geostrophic currents flowing in the east–west direction; *v*: geostrophic currents flowing in the north–south direction; EKE: log-transformed eddy kinetic energy. Final model selected for spawning aggregations: SST + *v* + seasonal SST gradient. Final model selected for nonspawning adults: seasonal SST gradient + *u* + vertical velocity + SST.

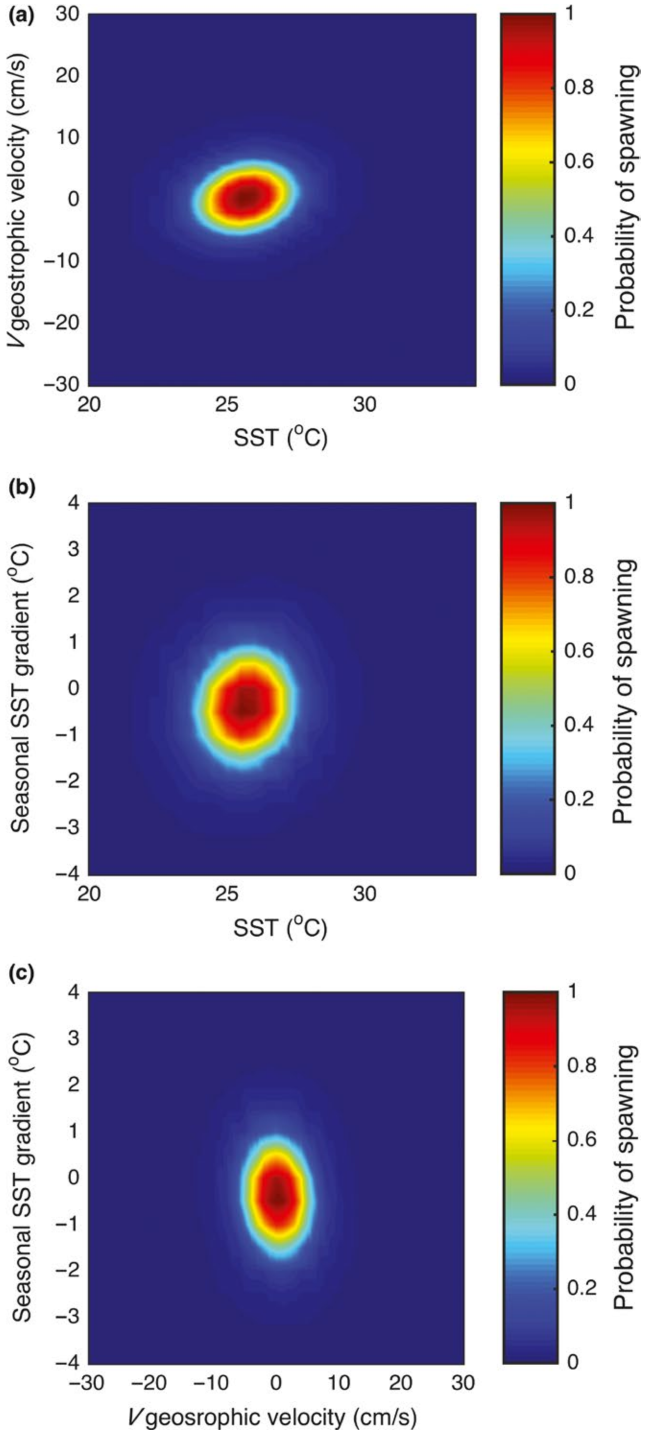


FIGURE 2 Modelled probability of *Epinephelus striatus* spawning as a function of sea surface temperature (SST), geostrophic currents in the north–south (*v*) direction and seasonal SST gradients. Positive geostrophic velocities indicate northward flow, whereas negative velocities are associated with southward currents. Positive (negative) values of seasonal SST gradients indicate that spawning occurs as temperatures warm (cool) seasonally. The optimal value (i.e., the value that maximized the probability of spawning) was used in the NPPEN model for the variable(s) not shown in a given bivariate plot

covariates (i.e., the univariate ΔAIC_c) suggested that SST exerted the strongest influence on FSA distribution (Table 2).

Historical projections of spawning activity indicated a high probability of spawning during winter around Cuba, the Mesoamerican barrier reef, the Bahamas and other areas of the Caribbean (Figure 3a). This coincided well with the observed distribution of *E. striatus* FSAs (Figure 1a; deviance explained (*D*) = 336.2, *df* = 280). Projections for 2081–2100 under RCP8.5 indicated a decline in the probability of spawning across the region (Figure 3e). This decline in spawning probability was consistent regardless of whether we focused on the historical spawning season (December–April) or integrated projections across the whole year to account for shifts in spawning phenology (Supporting information Figure S1). Suitable habitat for spawning was projected to decrease by 82% under RCP8.5 when data were integrated over the whole year. The largest declines in potential spawning habitat were observed around Cuba, Hispaniola, the Mesoamerican barrier reef, Puerto Rico and the Virgin Islands (Figure 3e). Under RCP2.6, climate change mitigation resulted in smaller declines in spawning habitat for *E. striatus*, with spatial patterns of projected spawning resembling those from the historical period (Figure 4c). Nevertheless, when integrated over the course of the year, there was still a 30% decrease in available spawning habitat under RCP2.6.

With unmitigated climate change, the areas with the highest probabilities of spawning were projected to shift northward. In 1981–2000, the maximum probability of spawning occurred at 14–26°N, whereas, in 2081–2100 under the RCP8.5 scenario, the maximum probability occurred at 26–30°N. An unexpected result was that, in 2081–2100 under RCP8.5, the probability of spawning remained relatively unchanged around Aruba, Curacao and Bonaire, suggesting these areas could serve as a climate refuge. When these changes were taken together, the mean latitude of spawning shifted northward by 329 km (2.96°) over the 21st century under RCP8.5. In contrast, only a 57-km (0.51°) northward shift in mean latitude was projected under RCP2.6.

We examined changes in environmental variables included in the NPPEN model of FSAs to identify the principal cause of declines in spawning habitat under RCP8.5. Winter temperatures were projected to rise by a mean of 2.6°C (*SD* = 0.2°C) across the Greater Caribbean by 2100, with winter SST across many areas exceeding 28°C (Figure 4a–b). Warming resulted in a contraction of habitats with suitable temperatures for *E. striatus* spawning. Currents in the *v* direction were projected to intensify, such that both southward and northward flowing currents became stronger (Figure 4c,d). However, current speed was not projected to increase to the point where it would restrict spawning habitat. Similarly, seasonal SST gradients during winter were not projected to undergo changes (mean change = −0.07°C ± 0.07°C *SD*) large enough to constrain the distribution of FSAs (Figure 4e–f).

We also investigated whether *E. striatus* spawning phenology is likely to shift under climate change. Under present-day

TABLE 2 Relative importance of environmental covariates affecting the distribution of *Epinephelus striatus* spawning aggregation sites and nonspawning adults

	Spawning aggregations		Nonspawning adults	
Environmental covariates	$\sum w_i$	Univariate ΔAIC_c	$\sum w_i$	Univariate ΔAIC_c
SST	1.0000	68.1	0.9928	99.0
SST gradients	0.9994	441.2	1.0000	29.5
Chl	<0.0001	332.7	0.0025	180.1
u	<0.0001	336.2	0.9766	84.6
v	1.0000	301.8	<0.0001	55.1
EKE	0.0007	466.4	<0.0001	127.9
Vertical velocity	<0.0001	381.9	0.9978	37.9

Notes. Variables exerting a greater influence on habitat suitability are characterizing by larger summed Akaike weights ($\sum w_i$) and a smaller univariate ΔAIC_c. Abbreviations for oceanic variables are the same as in Table 1.

climate, *E. striatus* spawns primarily between December–April, with peak spawning during December–February (Figure 1b). In Bermuda, spawning occurs in June and July. During the historical period, NPPEN correctly projected that peak spawning occurred in December–February, with high levels of spawning also projected in March (Figure 5a). Under RCP2.6., the probability of spawning remained high during January and February, but dropped below 0.5 in December and March, indicating a projected contraction of spawning season duration (Figure 5b). Under RCP8.5., almost all spawning occurred during January–March, with a curtailment of most December and April spawning (Figure 5c). This resulted in a slight delay in *E. striatus* phenology, as well as a contraction in spawning season length. Nonetheless, the most notable pattern in Figure 5c was the decline in spawning probability across all months under RCP8.5.

3.2 | Nonspawning adults

The most parsimonious model for nonspawning *E. striatus* included four variables: seasonal SST gradients, geostrophic velocity in the *u* direction, vertical velocity and SST (Table 1; $D = 48.1$, $df = 219$). Again, Akaike weights (w_i) were indicative of high confidence in selecting this model over other possible models based on different combinations of environmental variables. The ranges of environmental variables over which the probability of adult occurrence was maximal were −0.8 to 1.6°C for seasonal SST gradients, −6 to 6 cm/s for *u*, −0.003 to 0.002 cm/s for vertical velocity and 25–30.8°C for SST (Figure 6). Nonspawning adults occurred across a wider range of temperatures that were typically warmer than those utilized by FSAs. The preference for warmer temperatures among nonspawners was also evident when examining seasonal SST gradients, because this life history stage was principally found at higher gradients (an indicator of seasonal warming) than FSAs. It was not possible to directly compare preferences for current speed across life stages, because currents flowing in different directions were selected for inclusion in NPPEN. Nevertheless, Figures 2 and 6 suggest that both spawners and nonspawners were observed most frequently in areas with weak currents. Overall, summed Akaike weights indicated that nonspawning adult distribution was influenced to a nearly equal extent by all four environmental variables included in the selected model, whereas the univariate ΔAIC_c suggested that adult distribution was most strongly influenced by seasonal SST gradients and vertical velocity (Table 2).

When examining ecological niche breadth (Supporting information Appendix S2), no statistically significant differences were detected between spawning (mean: 0.06; 95% CI: 0–0.11) and nonspawning adults (mean: 0.06; 95% CI: 0–0.12). However, as hypothesized, the thermal niche breadth of spawners (mean: 0.71; 95% CI: 0.67–0.75) was significantly narrower than that of nonspawners (mean: 0.91; 95% CI: 0.89–0.94).

Based on the combined influence of the four variables that affected nonspawning *E. striatus* distribution, NPPEN projected a maximal probability of nonspawner occurrence across latitudes of 12–24°N during the baseline period (Figure 3b). This latitudinal range coincided well with the centre of the distribution of OBIS data on *E. striatus* occurrence for the historical period. Under RCP8.5, by 2100 the probability of nonspawner occurrence was reduced to ≤0.5 over nearly all of this species' historical range (Figure 3f). When integrated across time and space, there was a 45.9% decline in habitat suitable for nonspawning adults between 1981–2000 and 2081–2100 under RCP8.5. This change was accompanied by a slight northward shift of 78 km (0.70°) in mean latitude. Both the decrease in habitat suitability and the poleward shift in latitude were smaller among nonspawners than among FSAs under RCP8.5. In particular, the latitudinal shift among spawners occurred >4 times faster than among nonspawning adults.

To better understand the cause of these changes in suitable habitat under RCP8.5, we examined which environmental variables were likely to exceed the tolerance range of nonspawning adults. During the spring/summer months when nonspawning adults were most frequently observed, seasonal SST gradients and vertical velocity were not projected to change substantially under RCP8.5 (Figure 7). As was the case for *v*, currents in the *u* direction intensified under RCP8.5, with increases in eastward and westward velocities (Figure 7c,d). Nevertheless, changes in this variable did not constrain the future distribution of nonspawning adults. During

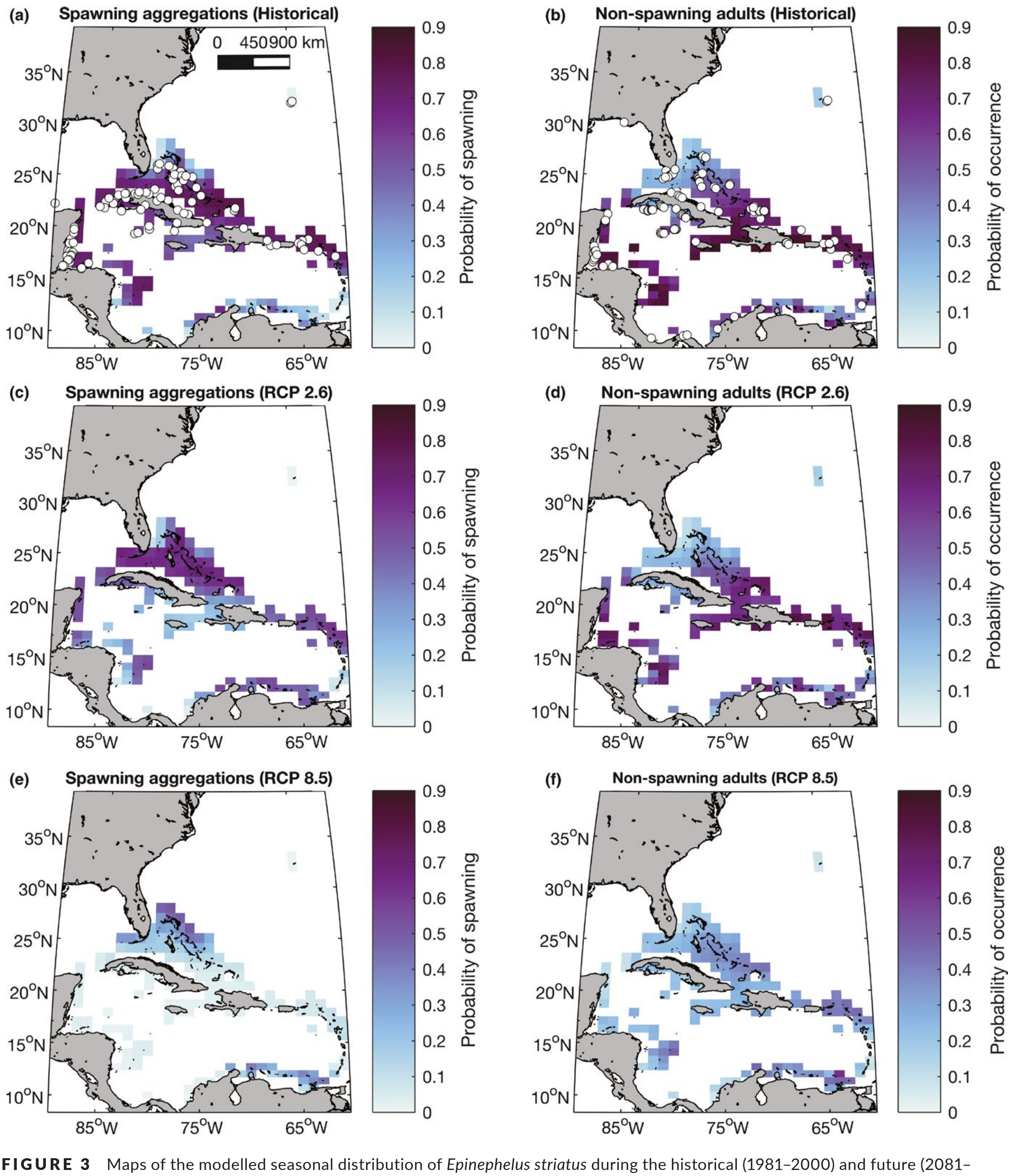


FIGURE 3 Maps of the modelled seasonal distribution of *Epinephelus striatus* during the historical (1981–2000) and future (2081–2100) periods. Left column: *E. striatus* spawning aggregations with data averaged over December–April at latitudes ≤30°N and over June–July at latitudes >30°N; right column: nonspawning adult *E. striatus* during March–September. These months were selected because they correspond to the historical peak in the seasonal occurrence of spawning aggregations and nonspawning adult *E. striatus* as displayed in Figure 1. Data for the future period are based on the RCP2.6 (c, d) and RCP8.5 (e, f) climate change scenarios. White circles indicate observations from the (a) Fish Spawning Aggregation database in Supporting information Table S1 and (b) Ocean Biogeographic Information System. Projection: Hammer-Aitoff

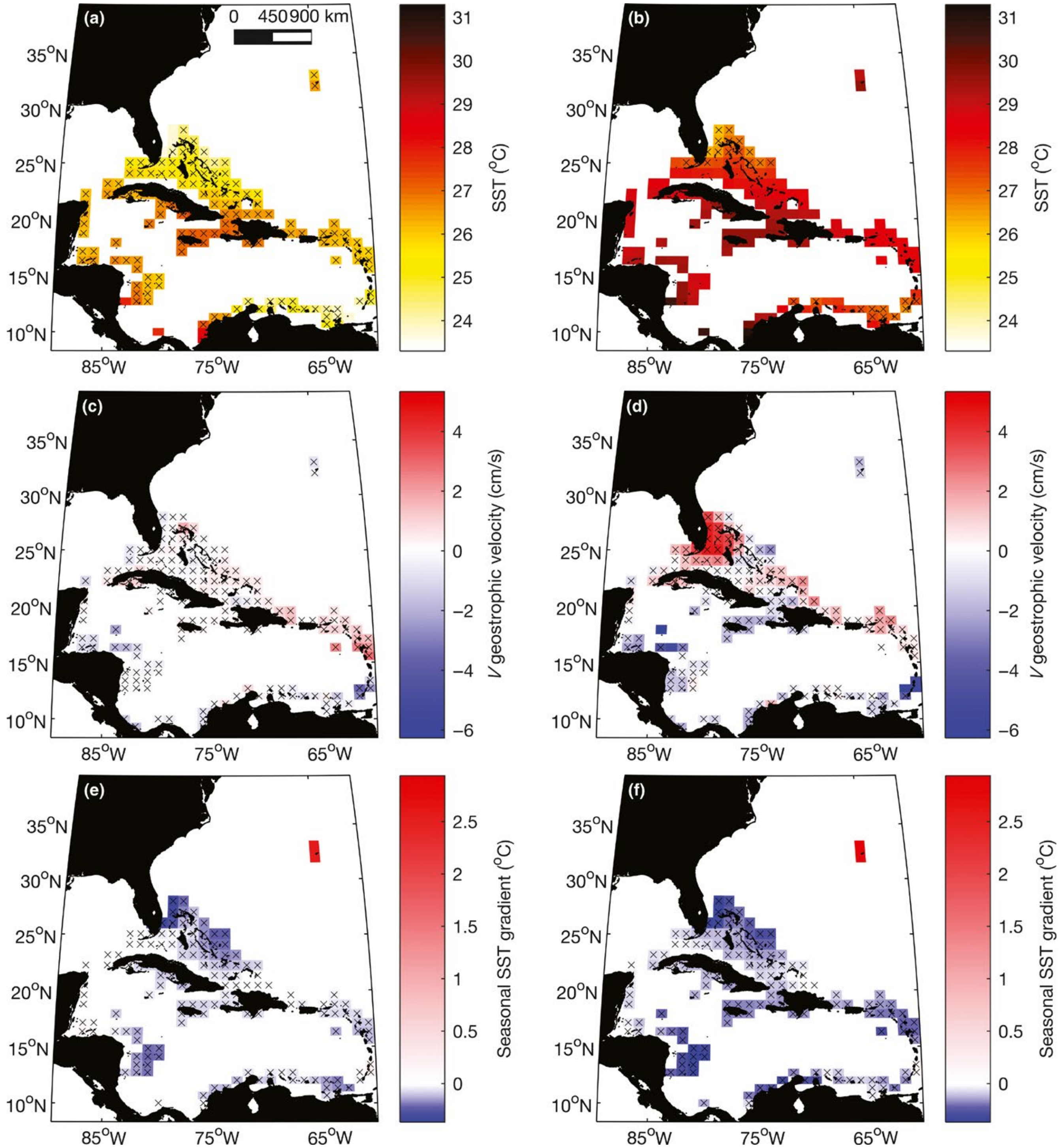


FIGURE 4 Changes in environmental conditions that affect the spawning habitat of *Epinephelus striatus*: (a, b) sea surface temperature (SST), (c, d) geostrophic currents in the north–south (*v*) direction and (e, f) seasonal SST gradients. The left-hand column shows climatological conditions during 1981–2000 based on historical simulations of the Geophysical Fluid Dynamics Laboratory Earth System Model (GFDL ESM2M), whereas the right-hand column shows conditions during 2081–2100 based on the RCP8.5 emissions scenario. Data are shown for December–April at latitudes ≤30°N and June–July at latitudes >30°N because these are principal months when spawning aggregations of *E. striatus* have been observed. The "×" symbol indicates conditions that are conducive to spawning based on the Non-Parametric Probabilistic Ecological Niche (NPPEN) model (i.e., SSTs of 23.9–27.4°C, *v* of −5 to 6 cm/s, seasonal SST gradients of −1.8 to 0.8°C). Map projection: Hammer-Aitoff

spring and summer months, SST was projected to rise by a mean of 2.8°C ± 0.2°C *SD*. This increase in SST restricted the projected distribution of nonspawners in the warmest areas of the Caribbean (e.g., Cuba, Jamaica, Haiti, Dominican Republic) but was not warm enough to compress the distribution of nonspawning adults in other regions (Figure 7h).

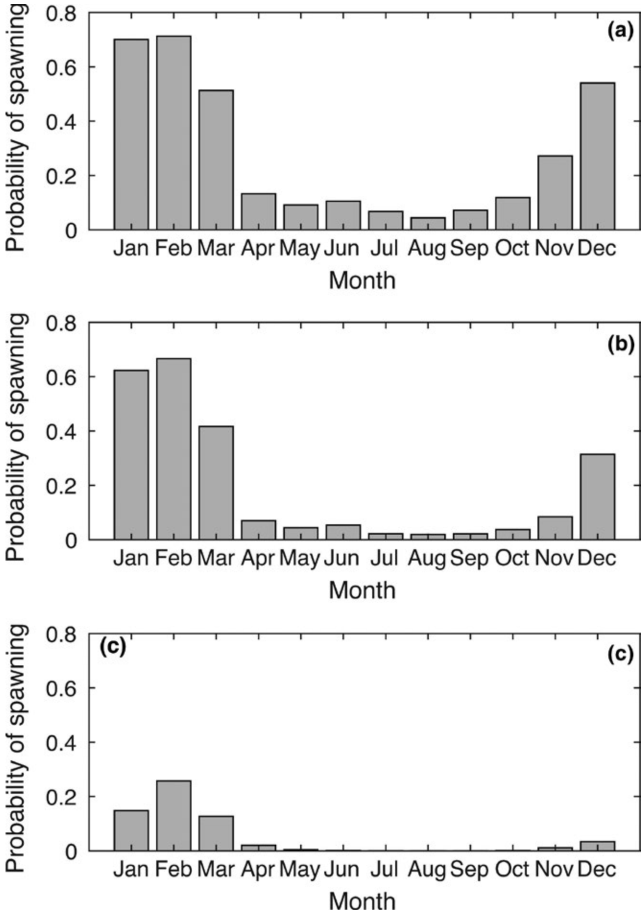


FIGURE 5 Modelled probability of spawning by *Epinephelus striatus* on a seasonal basis during the (a) baseline (1981–2000) and (b, c) future (2081–2100) periods. Results for the RCP2.6 climate change scenario are displayed in (b), whereas RCP8.5 is shown in (c)

As was the case with FSAs, nonspawning adults were projected to experience reduced changes in habitat suitability under RCP2.6 compared to RCP8.5. Spatial patterns associated with nonspawning adult probability of occurrence were generally similar under the historical baseline and RCP2.6 (Figure 3d), albeit with a slightly lower probability of occurrence in most areas of the Greater Caribbean under RCP2.6. The mean latitude of nonspawning adult occurrence shifted poleward by only 15 km (0.14°) under this climate change scenario. When results were integrated across all seasons, RCP2.6 was associated with an 11.0% reduction in suitable habitat for nonspawning adults by the end of the 21st century.

To assess whether inclusion of different environmental variables in the models of FSAs and nonspawning adults may have affected comparability across life history stages, we reran the NPPEN model using data on only changes in SST and seasonal SST gradients, because these were the two variables that exerted an influence on both *E. striatus* life history stages (Supporting information Figure S2). Results showed declines in habitat suitability and changes in latitudinal distribution that were extremely similar to those from the models selected based on minimization of the AIC_c. We also used this bivariate model to assess whether a species distribution model that pooled data across life history stages could accurately predict habitat suitability for *E. striatus*. For both FSAs and nonspawning adults, the pooled model overestimated habitat suitability when there was a low-to-intermediate probability of *E. striatus* occurrence, but underestimated habitat suitability at high probabilities of occurrence (Figure 8). This result implies that the pooled model was likely to underestimate changes in habitat suitability compared to models that explicitly included different life history stages. This pattern was more pronounced among FSAs than among nonspawning adults.

4 | DISCUSSION

Areas used by both spawning and nonspawning adult *E. striatus* could be identified based on spatial and temporal variations in temperature and hydrographic features. However, the specific conditions defining the habitat used by each life stage varied, with spawning fish using areas with colder temperatures, predominantly negative seasonal SST gradients and geostrophic currents flowing in a different direction than in areas predominantly used by nonspawning adults. Spawners appear to have a greater sensitivity to temperature than nonspawners as evidenced by their narrower thermal niche. When projecting how these stages respond to climate change, the integrated probability of occurrence decreased more among spawners than nonspawners under both climate change scenarios. Similarly, we detected a greater northward shift in distribution among spawners, as well as a slight delay and shortening of the spawning season. These changes in the probability of fish occurrence, geographic distribution and phenology were principally attributed to warming temperatures rather than changing hydrography. When taken together, these projections consistently indicate that *E. striatus* FSAs likely serve as a bottleneck constraining how this species responds to climate change.

Our results are consistent with previous research investigating the influence of temperature fluctuations on reef fishes in general and *E. striatus* in particular. In a study of 241 Indo-Pacific reef fish species, Mellin et al. (2016) found that seasonal deviations in monthly mean SST and human pressure (i.e., a multivariate index reflecting population density, fishing pressure, pollution and urban development) were the most important factors influencing the distribution of large-bodied fishes. Previous research rearing *E. striatus* in captivity demonstrated that temperatures of 24–27°C are most suitable for reproduction (Tucker et al., 1996), which matches our independent results from modelling the thermal preference of *E. striatus* FSAs (i.e., 24–27.5°C). Reflecting the sensitivity of the biogeographic distribution of reef fishes to changing temperatures, the range of several aggregating reef fishes has moved northward during recent decades in regions nearby our study area (Fodrie, Heck, Powers, Graham, & Robinson, 2009; Parker & Dixon, 1998). Under RCP8.5, the future range shifts and declines in the probability of occurrence projected here for *E. striatus* FSAs occurred at a faster rate than projected changes for other fish species in the Caribbean and Southeast United States. (Cheung et al., 2016; Hare, Wuenschel, & Kimball, 2012). However, precise comparisons with these studies are not possible due to differences in climate scenarios used and ecological modelling approaches.

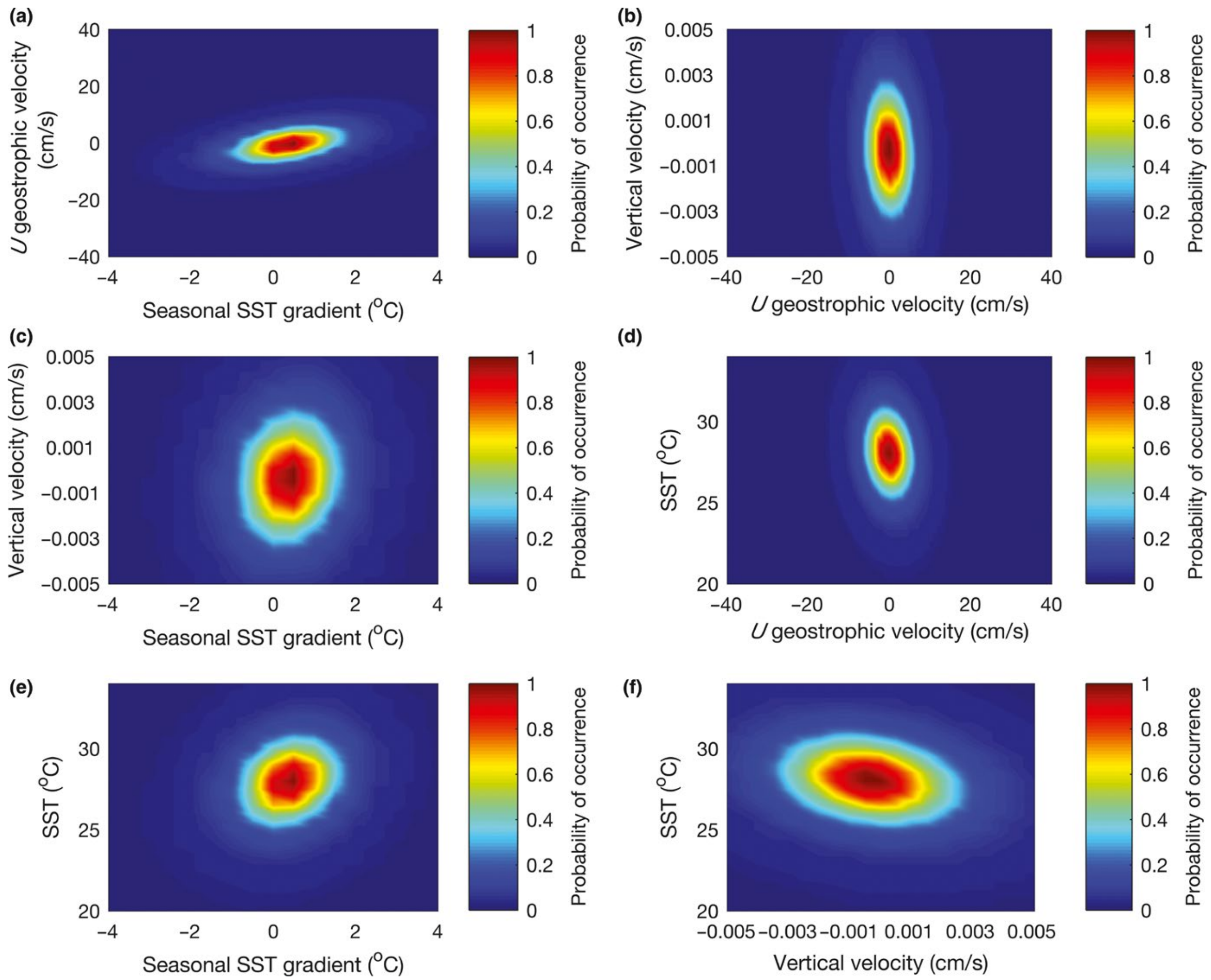
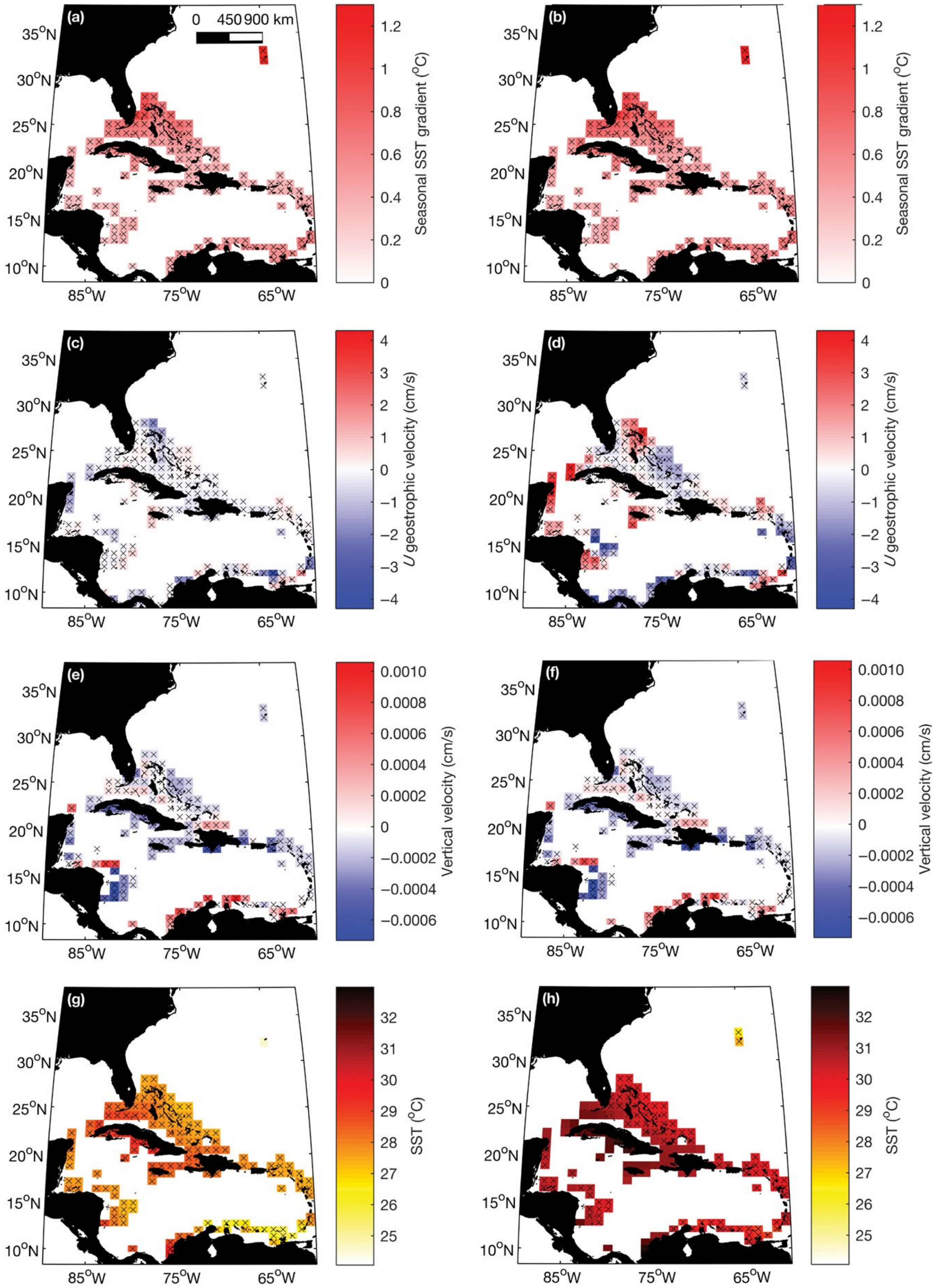


FIGURE 6 Modelled probability of the occurrence of *Epinephelus striatus* nonspawning adults as a function of seasonal sea surface temperature (SST) gradients, geostrophic currents in the east–west (*u*) direction, vertical velocity and SST. Positive (negative) values of seasonal SST gradients indicate that spawning occurs as temperatures warm (cool) seasonally. Positive (negative) geostrophic velocities indicate eastward (westward) flow. Upwelling (downwelling) is indicated by positive (negative) vertical velocity. The optimal value (i.e., the value that maximized the probability of fish occurrence) was used in the NPPEN model for the variable(s) not shown in a given bivariate plot

To the best of our knowledge, this represents the first study to model climate-related shifts in species distribution separately for spawning and nonspawning adults, highlighting this bottleneck effect. However, a few studies have observed differentiated responses to climate change and climate variability among separate fish life history stages. For example, mangrove jack (*Lutjanus argentimaculatus*), an Indo-Pacific reef fish, is sensitive to fluctuations in ocean heat content and sea surface salinity as an adult, but its growth rate is more responsive to precipitation as juveniles, reflecting an ontogenetic habitat shift where juveniles inhabit estuaries (Ong et al., 2015). Similarly, along the Northeast United States continental shelf, nearly half of the fish species exhibited out-of-sync shifts in their

FIGURE 7 Changes in environmental conditions that affect the habitat of nonspawning adult *Epinephelus striatus*: (a, b) seasonal sea surface temperature (SST) gradients, (c, d) geostrophic currents in the east–west (*u*) direction, (e, f) vertical velocity and (g, h) SST. The left-hand column shows climatological conditions during 1981–2000 based on historical simulations of the Geophysical Fluid Dynamics Laboratory Earth System Model (GFDL ESM2M), whereas the right-hand column shows conditions during 2081–2100 based on the RCP8.5 emissions scenario. Data are shown for March–September, which are the months when the greatest number of occurrences of nonspawning adult *E. striatus* has been observed. The “×” symbol indicates conditions that are conducive to these occurrences based on the Non-Parametric Probabilistic Ecological Niche (NPPEN) model (i.e., seasonal SST gradients of −0.8 to 1.6°C, *u* of −6 to 6 cm/s, vertical velocity of −0.003 to 0.002 cm/s, SST of 25.0–30.8°C). Map projection: Hammer-Aitoff


(a)
0 450 900 km
35°N
30°N
25°N
20°N
15°N
10°N
85°W
75°W
65°W
Seasonal SST gradient (°C)
1.2
1
0.8
0.6
0.4
0.2
0
(b)
(c)
(d)
U geostrophic velocity (cm/s)
4
3
2
1
0
−1
−2
−3
−4
(e)
(f)
Vertical velocity (cm/s)
0.0010
0.0008
0.0006
0.0004
0.0002
0
−0.0002
−0.0004
−0.0006
(g)
(h)
SST (°C)
32
31
30
29
28
27
26
25

distribution over a 31-year period when comparing larvae and adults, suggesting these life stages are responding differently to climatic variations (Walsh, Richardson, Marancik, & Hare, 2015). Among other marine organisms, a meta-analysis demonstrated that early life history stages of molluscs and corals have increased sensitivity to ocean acidification (Kroeker et al., 2013). Taken together these studies indicate that there is an imperative to consider interactions between each life history stage and climatic and biogeochemical variables when making projections of future changes in species distribution, abundance and phenology. This approach contrasts with most projections of marine organism responses to climate change made to date, which typically only consider the bioclimatic envelope of the adult life stage due to a lack of data on other life history stages (Ong et al., 2015). Consideration of the climatic niche of each life history stage will be especially important for migratory species that utilize different habitats throughout their life, because the rate of climatic changes can differ substantially between adjacent oceanic areas (Burrows et al., 2011).

A wide range of conservation measures focused on protecting *E. striatus* FSAs from overfishing have been implemented, including fishing moratoria, spawning season sales and fishing bans, establishment of marine protected areas, seasonal site closures, gear restrictions and other regulations restricting effort or catch (NOAA, 2013). Our results indicate that climate change also deserves consideration in local and regional conservation efforts for *E. striatus*. Even if current conservation measures are successful at protecting this species from overfishing and helping to restore FSAs, parts of the historical range of *E. striatus* may become inhospitable to spawning due to rising temperatures, potentially causing certain protected areas and fisheries management plans to fail at their stated goals. Other studies of climate change-induced shifts in species distribution, species richness and community composition have generated similar results regarding the future conservation value of terrestrial and marine protected areas (Albouy, Guilhaumon, Araújo Mouillot, & Leprieur, 2012; Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011). Conversely, areas where *E. striatus* spawning is projected to persist under climate change (albeit even at reduced levels) should be prioritized in conservation planning. Based on our model, such "thermal refuge" areas of spawning persistence under RCP8.5 could include the northern Bahamas and the Netherlands Antilles. Climate change mitigation will also aid *E. striatus* conservation, because 3.9 times more potential spawning habitat was projected to persist under RCP2.6 compared to RCP8.5

Our results do not suggest that there will be large shifts in *E. striatus* spawning phenology in most countries, so the effectiveness of existing temporal regulations (e.g., seasonal area closures and sales bans) will not be substantially affected. However, we detected a contraction in spawning season duration, with reduced spawning projected in December, March and April. Contracted spawning seasons are often associated with heightened recruitment variability (Mertz & Myers, 1994), which could jeopardize *E. striatus* reproductive success, impede population recovery in response to protection, and decrease resilience to fishing pressure.

To illustrate the conservation implications of this study, we describe two contrasting examples from the Bahamas and Belize. Both countries utilize seasonal fishing closures to protect *E. striatus* during its current-day spawning season (NOAA, 2013). Due to its location close to the northern edge of Nassau Grouper's distribution range, the Bahamas are projected to experience a modest 21% decline in the probability of spawning during the months of its seasonal fishing closure under RCP8.5. However, the months of peak spawning are projected to shift from December–February to January–March under this climate change scenario. As a result, this country may need to adjust the time period of its fishery closure for the closure to remain effective. In contrast, no change in spawning phenology was observed in Belize. However, a larger 95% decline in habitat suitable for spawning was projected under RCP8.5 across this country, suggesting that it will encounter serious challenges associated with conserving remaining populations of *E. striatus*.

Our projections of future *E. striatus* phenology and distribution correspond to changes in potential spawning habitat (i.e., the area where environmental conditions are suitable for spawning), whereas realized spawning habitat is dependent upon a number of factors not typically included in species distribution models, most importantly fish population size (Planque, Bellier, & Lazure, 2007). Due to historical overfishing, it is unlikely that today's population of *E. striatus* is able to occupy the full extent of its potential spawning habitat, so model projections should be interpreted as the maximal area where spawning could possibly occur. We also did not consider how species interactions between *E. striatus* and its prey, predators, competitors and recruitment dynamics could affect this species' range. This is a common drawback of species distribution models. The few species distribution models that explicitly incorporated interspecific interactions have obtained mixed results regarding their importance (Araújo & Luoto, 2007; Fernandes et al., 2013), indicating that this is an area that warrants additional research. Similarly, recent progress has been made using individual-based models to understand how climate change and climate variability can impact fish recruitment (Fiechter, Rose, Curchitser, & Hedstrom, 2015; Kristiansen, Drinkwater, Lough, & Sundby, 2011), thus representing another area where further research should be pursued.

Another concern specific to modelling FSAs is the time scale over which new FSA sites can become established in response to changing conditions. Spawning site fidelity is characteristic of *E. striatus* and there is some evidence that migration to spawning sites is a socially learned behaviour among this species and other fishes (Sadovy de Mitcheson & Colin, 2012; Starr, Sala, Ballesteros, & Zabala, 2007; Wooton & Smith, 2015). These behavioural characteristics may hinder or substantially delay the reconstitution of spawning sites that have been previously extirpated by overfishing. Similarly, such behaviour could circumvent the adoption of new spawning locations in response to climate change. However, *E. striatus* can be prompted to spawn in captivity by manipulation of temperature (Tucker et al., 1996), which demonstrates that its reproductive behaviour is directly responsive to environmental factors and implies that site fidelity may not undermine its capacity to adapt to climatic changes. Similarly, reports of novel or reconstituted spawning sites in Puerto Rico and the U.S. Virgin Islands (NOAA, 2013) provide additional evidence of the behavioural flexibility needed to colonize new FSA sites

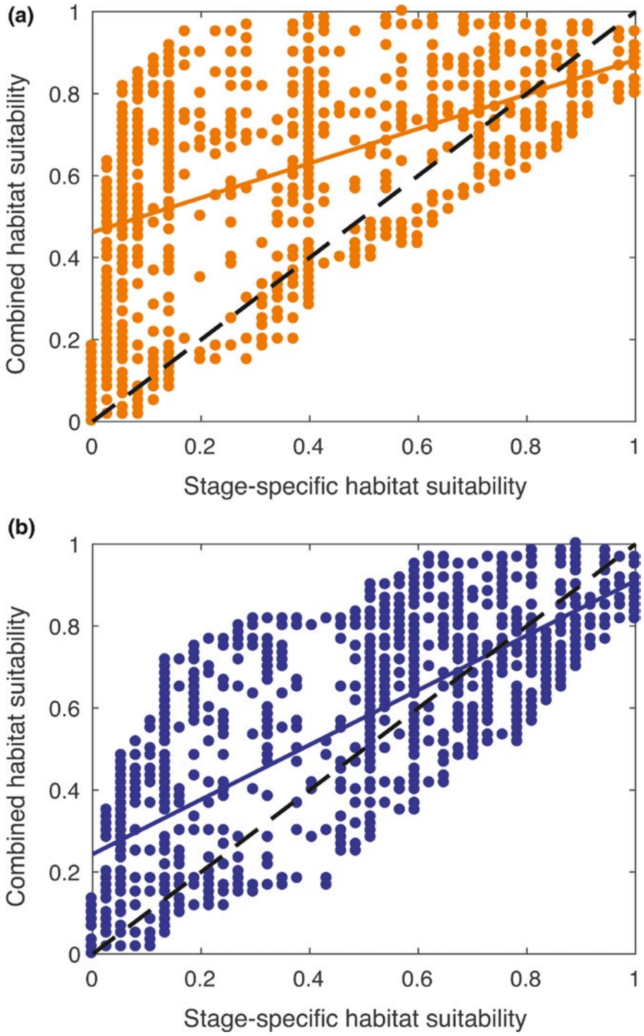


FIGURE 8 Comparisons between habitat suitability of *Epinephelus striatus* based on models that specify different life history stages and a model that pools data across all life stages. Stages-specific habitat suitability for fish spawning aggregations (FSAs) and nonspawning adults is shown in (a) and (b), respectively. Habitat suitability is modelled using monthly climatological data on sea surface temperature (SST) and seasonal SST gradients extracted from the GFDL ESM2M climate model for the years 1981–2000. The black, dashed line represents the one-to-one relationship between habitat suitability levels. The orange and blue lines in (a) and (b), respectively, are linear regressions between habitat suitability predicted with stage-specific models and the combined life history model. Regression formula for (a): $Y = 0.4618 + 0.4207X$, $r^2 = 0.24$, $p < 0.0001$, $n = 15{,}156$. Regression formula for (b): $Y = 0.2434 + 0.6672X$, $r^2 = 0.59$, $p < 0.0001$, $n = 15{,}156$

in response to climate change. Given this evidence, the centennial-scale changes projected here seem plausible.

Acclimation or adaptation to tolerate a broader range of temperatures could affect the accuracy of our projections. Experimental work has shown that transgenerational acclimation can compensate for changes in the aerobic scope of reef fishes across temperature changes of a similar magnitude to those projected for the late 21st century (Donelson, Munday, McCormick, & Pitcher, 2012). This would potentially preclude the need for fishes to migrate to new spawning grounds or shift their spawning phenology. However, other experiments have indicated that, given a choice, reef fishes are more likely to migrate to areas with preferred temperatures than remain in areas with suboptimal temperatures (Habary, Johansen, Nay, Steffensen, & Rummer, 2016), thus circumventing acclimation and indicating that range shifts are likely. The narrow and consistent set of temperatures associated with *E. striatus* spawning throughout its entire range suggest this species may have a limited adaptation capacity.

Due to our emphasis on climatological conditions, we may have underestimated the full range of conditions associated with spawning and adult fish occurrence, especially for oceanic variables that exhibit substantial interannual variability. Our results may also underestimate the extent of projected range shifts because we only made projections of *E. striatus* occurrence in areas coinciding with the present-day distribution of coral reefs. This may underestimate range shifts if this species begins to more heavily utilize habitats characterized by other hard substrates (e.g., oil rigs, artificial reefs) or if coral distribution shifts northward under climate change. However, the northward shift in reef distribution may be hindered by more severe impacts of ocean acidification on reefs at higher latitudes (Van Hooidonk, Maynard, Manzello, & Planes, 2014). Rather than shifting to higher latitudes, many fishes have coped with warming conditions by utilizing deeper depths (Perry, Low, Ellis, & Reynolds, 2005; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Walsh et al., 2015). Shifts in the depth distribution of *E. striatus* spawning are possible, because geomorphological features associated with spawning often extend to greater depths (Kobara et al., 2013; Starr et al., 2007).

In conclusion, by modelling two distinct life history stages we identified a more deleterious set of impacts of climate change on *E. striatus* than would be detected if solely the adult life stage were modelled. This result highlights the need for more studies to examine ontogenetic changes in a species' ecological niche throughout its full life cycle when making projections of climate change impacts. In the context of the greater Caribbean, many other species of groupers spawn in winter (Kobara et al., 2013; SCRFA, 2014) suggesting that these fishes may have similar thermal tolerances to *E. striatus* FSAs and may react similarly to climate change. In contrast, Caribbean snappers tend to spawn over much wider set of seasons (spring to fall) and thermal range (SCRFA, 2014) and, consequently, may be able to better cope with climate change. Collectively, these impacts could lead to alterations in the species composition of top predators on Caribbean reefs, a subject which should be further explored by expanding our modelling approach to additional species. Our research also highlights the need to conserve fish habitat in climate refuge where the effects of global warming on *E. striatus* and other protected species are projected to be less severe. Future work examining a greater diversity of climate models, ecological niche models and climate change scenarios may be useful to confirm the locations of such refugia because fine-scale spatial patterns can vary between models.

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DATA AVAILABILITY

Data on nonspawning fish distribution, environmental variables and the GFDL ESM2M model are all publicly available online at locations described in Supporting information Appendix S2. A summary of the FSA database is provided in Supporting information Table S1. Due to the endangered status of *E. striatus*, more detailed information on FSA location will only be made available for scientific purposes upon request to the authors.

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BIOSKETCHES

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SUPPORTING INFORMATION

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

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