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Contemporary and future distributions of cobia, *Rachycentron canadum*

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Abstract

Aim: Climate change has influenced the distribution and phenology of marine species, globally. However, knowledge of the impacts of climate change is lacking for many species that support valuable recreational fisheries. Cobia (*Rachycentron canadum*) are the target of an important recreational fishery along the U.S. east coast that is currently the subject of a management controversy regarding allocation and stock structure. Further, the current and probable future distributions of this migratory species are unclear, further complicating decision-making. The objectives of this study are to better define the contemporary distribution of cobia along the U.S. east coast and to project potential shifts in distribution and phenology under future climate change scenarios.

Location: Chesapeake Bay and the U.S. east coast.

Methods: We developed a depth-integrated habitat suitability model using archival tagging data from cobia that were caught and tagged in Chesapeake Bay during summer months and coupled those data with high-resolution ocean models to project the contemporary and future distributions of cobia along U.S. east coast.

Results: During the winter months, suitable cobia habitat currently occurs in offshore waters off North Carolina and further south, whereas during the summer months, suitable habitat occurs in waters from Florida to southern New England. In warmer years, the availability of suitable habitat increases in northern latitudes. Under continued climate change over the next 40–80 years, suitable habitat is projected to shift northward and decrease over the shelf.

Main conclusions: Habitat distributions suggest cobia overwinter offshore and could inhabit waters further north during warmer months, into state jurisdictions that do not have strict management regulations for cobia. When waters are warmer, distributions are projected to shift poleward and seasonal migrations may begin earlier. These results can inform resource allocation discussions between fishery managers and resource users.

KEYWORDS
archival tags, climate change, fisheries management, habitat suitability model, phenology, recreational fishery, temporal shifts

1 | INTRODUCTION

The distribution of many marine species has been changing worldwide as a result of climate change (Kleisner et al., 2016; Morley et al., 2018; Sunday, Bates, & Dulvy, 2012). Within the U.S. Northeast Continental Shelf, species along the southern Northeast Shelf have primarily shifted north-northeast, while species along the northern Northeast Shelf have shifted west-southwest (Kleisner et al., 2016). As climate change continues, species range distributions in this region are projected to shift on average between 100–600 km over the 21st century based on future greenhouse gas emission scenarios (Morley et al., 2018). Ocean warming in this region is projected to occur at a rate three times faster than the global average (Saba, Griffies, Anderson, Winton, Alexander, Delworth et al., 2016). A recent climate vulnerability assessment (Hare et al., 2016) suggested that of 82 species examined in the U.S. Northeast Shelf, over 50% are expected to experience changes in their distribution and that approximately half would be negatively impacted by climate change. Climate change is also impacting marine fish phenology, as migrations are often cued by changes in ocean temperature (Brown et al., 2016; Jansen & Gislason, 2011; Rose, 2005).

In recent years, various survey and oceanographic data combined with a suite of modelling techniques have been used to simulate the distribution of fishes historically (Hill, Tobin, Reside, Pepperell, & Bridge, 2016), in near real time (Hobday & Hartmann, 2006), seasonally (Hobday, Hartog, Spillman, Alves, & Hilborn, 2011) and into the future (Kleisner et al., 2017). Many studies use environmental data from the depth of data collection (e.g. bottom trawl survey), which would suffice for bottom-living species, but may not represent the full habitat description for species that use more of the water column. Further, there are many species that are not captured by fishery-independent or commercial fishery surveys. Data are particularly lacking for recreational fish species, which are, therefore, often overlooked when it comes to habitat modelling and projecting distributional shifts over any time period. Archival datasets generated from pop-off satellite archival tags (PSATs) or other data storage tags provide continuous records of temperature and depth of the animal, which allow habitats to be modelled in 3 dimensions (3D). Further, these types of tags can be fitted to species that may not be regularly caught in fishery dependent and independent surveys.

Cobia (*Rachycentron canadum*) is an important recreational fish species along the U.S. Gulf of Mexico and Atlantic coast from Florida to Virginia, as well as more northern states during the warmer months. The Atlantic cobia population is currently treated as a single stock and the boundary between it and the Gulf of Mexico stock is the border between Florida and Georgia (Perkinson et al., 2019). In the spring and early summer, Atlantic cobia migrate to inshore waters to spawn in bays and estuaries in North and South Carolina and within Chesapeake Bay (Shaffer & Nakamura, 1989). Over this time period (May-September), cobia are heavily targeted by recreational fishers, with the highest landings occurring in Virginia and North Carolina waters. Upwards of 225,000 trips targeting cobia are estimated to occur per year in Virginia alone and with anglers valuing cobia fishing between $488-$685 per trip; this recreational fishery is beneficial to coastal states (Scheld, Goldsmith, White, Small, & Musick, 2020). The Atlantic cobia total allowable catch limits were exceeded in recent years, and as a result of this high pressure, the National Marine Fisheries Service (NMFS) closed the fishery in federal waters (SAFMC, 2016; NCDENR, 2016; NOAA Fisheries, 2017). The states (except for South Carolina) did not undertake comparable measures to reduce fishing mortality in their state water (within 3 nautical miles of the coast). Overwintering habitat of cobia is not well known, primarily because cobia are not frequently targeted during the colder months, particularly north of Florida. Identifying the year-round distribution of Atlantic cobia will help managers determine the probability of occurrence of cobia in each state during each month and could drive more dynamic regulations that are informed by observed ocean conditions.

The migratory nature of cobia make them particularly sensitive to changing ocean conditions. If the distribution of cobia is shifting north, northern states that receive the resource later in the season will be more negatively impacted by early season closures. Anecdotal data suggest that over recent years, cobia are migrating into Chesapeake Bay earlier in the spring. Under climate change, if conditions become more favourable in Chesapeake Bay or further north, cobia phenology may shift, and fisheries managers will need to adjust for a cobia fishery that occurs earlier in Chesapeake Bay and more frequently in waters north of Virginia. The objectives of this study are to define the contemporary distribution of cobia along the U.S. east coast and project potential shifts in distribution and phenology of cobia under climate change. The findings can be generalized to approaches needed for a wide range of coastal migratory species.

2 | METHODS

2.1 | Tagging

During the summer months of 2016–2018, cobia were caught on rod and reel using typical recreational methods in Chesapeake Bay. Cobia were measured and a variety of tags were either externally or internally fit to them. Ten cobia were externally fit with PTT-100 PSATs (Microwave Telemetry), and 50 were surgically implanted with a G5 data storage tag (herein referred to as “Cefas tags”; Cefas Technology Limited) and acoustic transmitter (V16-4L/4H;

Vemco). To improve Cefas tag recovery, a conventional spaghetti tag (Hallprint) was attached to the Cefas tag and protruded from the incision so that fishermen were aware that the fish had an internal tag. Post-surgery and external dart tag attachment, fish were released. All fish capture, handling and surgical procedures were approved by the William & Mary Institutional Animal Care and Use Committee (protocol no. IACUC-2017–05–26–12133-kcweng).

2.2 | Habitat model

The habitat model implemented follows similar methods described in Eveson, Hobday, Hartog, Spillman, and Rough (2015). The model employs a ratio method which uses the ratio between habitat use and habitat availability to determine the habitat preference or suitability of the species, where a value above 1 represents habitat that is preferred or suitable (i.e. the conditions the fish occupied occurred in a greater proportion than they do in the available habitat data), below 1 represents non-preferred or unsuitable habitat, and equal to 1 represents no difference than random. A separate ratio was developed for each month of the year.

Habitat use data were generated from the PSATs and Cefas tags. Temperature and depth data were summarized by hour for each individual so that data from both tag types could be combined. A temperature histogram and associated densities with 0.5°C bins were created from 1.5–33.5°C for each individual for each month. The densities at each temperature were averaged for all individuals that were monitored during a given month of the year so that for each month there were mean densities over the entire temperature range. These densities represented habitat use for cobia each month of the year.

Habitat availability data consisted of extracted daily temperatures from Hybrid Coordinate Ocean Model (HYCOM) + Navy Coupled Ocean Data Assimilation (NCODA) Global 1/12° Reanalysis (GLBv0.08) over U.S. shelf waters from Maine to Florida over the time period cobia with tags were at-liberty (Ferris, 2019). All 40 layers from HYCOM were extracted each day and manipulated in R v.3.5.2 using the “ncdf4” (Pierce, 2019) and “abind” (Plate & Heiberger, 2016) packages. HYCOM layers are not equally spaced so we generated six depth bins over the depth range cobia used based on the archival tag data (0–250 m). The six depth bins were 0–20 m, 20–40 m, 40–60 m, 60–80 m, 80–100 m, 100–250 m. All temperatures for a given latitude and longitude from layers within a given depth bin were averaged over each day. Temperatures over all six depth bins for a given month of the year were combined, and a histogram and associated densities were generated from 1.5–33.5°C with 0.5°C bins. These densities represented habitat availability along the U.S. shelf each month of the year. A ratio was calculated at each temperature across the temperature range for each month by dividing the habitat use densities by the habitat availability densities.

To determine which areas were considered suitable cobia habitat over a specific time period (e.g. contemporary or future), 3D gridded temperature arrays (e.g. from HYCOM) were summarized into the six aforementioned depth bins by month so that for each month and every 1/12° of latitude and longitude there were six temperatures, one at each of the six depth bins. Ratios were then assigned to each grid cell at each depth bin based on the temperature in that grid cell and the specific month. To generate a single ratio value for a given latitude and longitude, a depth weighting factor was generated for each month. The depth weighting factor was calculated by taking the proportion of hourly depth observations from the combined PSAT and Cefas tags at each of the six depth bins each month. Based on the depth bin the ratio was in, the ratio was multiplied by the appropriate depth weighting factor. Once all ratios were weighted, the six weighted ratios at a given latitude and longitude for a specific month were summed over the water column to provide a single weighted ratio value at that latitude and longitude. Suitable habitat (herein referred to as “SH”) was considered to be any pixel along the U.S. shelf where the predicted ratio was greater than 1.

To validate the model predictions of suitable cobia habitat, acoustic telemetry data were used. A separate group of cobia only fitted with acoustic transmitters, but tagged over the same duration, were used for the validation procedure (i.e. acoustic detections from individuals that also received a Cefas tag were not included in the validation procedure). Acoustic detections from 31 cobia were used to validate the habitat model. Detections were downloaded from 175 receiver stations maintained by multiple agencies and organizations from New York to Florida. To determine SH for model validation, the habitat model was applied to daily HYCOM output summarized by month during the timeframe of acoustic detections (July 2017 – June 2019). The end result was monthly 2-dimensional (2D) raster surfaces with habitat suitability values in each grid cell. The validation approach was modified from Eveson et al. (2015); we initially calculated the proportion of detections (α) within SH for each month. However, this value may bias model validation if all receiver stations occur in SH. Therefore, we also calculated for each month and year the total number of receiver stations in SH (that received detections for that month) and divided it by the total number of receiver stations (that received detections for that year) to get a value (β). A score was generated by dividing α by β, where a score greater than 1 means the habitat model was better than random in predicting cobia habitat for that month and year (i.e. cobia were detected in a greater proportion in areas predicted to be SH than if they were randomly distributed among the receiver stations they were detected by that month).

2.3 | Contemporary projections

The habitat model was applied to the monthly climatologies as well as the coolest and warmest year along the U.S. shelf to determine contemporary cobia distribution. Monthly climatologies were based on daily HYCOM output from 1994–2015. The coolest year over that time period was 1996 (NOAA NCEI, 2019; NOAA Fisheries, 2019), whereas the warmest year was 2012 (Mills et al., 2013). Following the same methods from above, the final result for each monthly climatology was a 2D raster surface with habitat suitability values in each grid cell where values greater than 1 represented SH and values below 1 represented unsuitable habitat. The same steps were followed for each month for the coolest and warmest years. Rasters were created in R v.3.5.2 using the "raster" package (Hijman, 2019) and were displayed in ArcGIS 10.7.

2.4 | Climate change projections

Climate change projections of ocean temperature to the end of century were coupled to the cobia habitat model in order to project cobia distribution along the U.S. shelf. Expected monthly changes (i.e. deltas) in ocean temperature over an 80-year period were obtained from the NOAA Geophysical Fluid Dynamics Lab's (GFDL) CM2.6 high-resolution (1/10°) global climate model (McHenry, Welch, Lester, & Saba, 2019; Saba et al., 2016). NOAA GFDL's CM2.6 model resolves ocean circulation along the U.S. shelf (Kleisner et al., 2017; McHenry et al., 2019; Saba et al., 2016). The model simulations include a 1% increase in global atmospheric CO_2 per year, such that by year 70, CO_2 has doubled. The atmospheric doubling in CO_2 results in a 2°C increase in average global surface temperature, which is similar to the highest greenhouse gas emission scenario (RCP8.5) for the years 2060–2080 from the IPCC's 5th Assessment Report (IPCC, 2013). The 80 years of monthly ocean temperature deltas were regridded to match the HYCOM grid, summarized into the six depth bins and added to the monthly climatology layers generated from HYCOM. This produced an 80 year time series of ocean temperatures along the U.S. shelf for each month and depth bin. To evaluate average long term future trends, we aggregated the 80 year time series into four 20 year time periods (0–20, 20–40, 40–60 and 60–80). Similar to current projections, we followed the above methods, which resulted in 2D raster surfaces with habitat suitability values for each month for the four future time periods. We selected one future year that is predicted to be warmer than 2012 to assess how cobia distributions compared for an extreme future year. Mean temperatures at each depth bin over all months were summarized in Figure S1.

2.5 | Metrics

To quantify the amount of cobia SH over the year for the climatology, extreme contemporary years, four future time periods and future extreme year, we multiplied all habitat suitability values greater than one by the grid cell area. These values were summed over the entire U.S. shelf for each month to get a monthly total habitat suitability index value.

To evaluate habitat suitability from a management perspective, habitat suitability values were compared among U.S. east coast states within and among contemporary and future year projections. The habitat suitability values greater than one were multiplied by grid cell area and summed within each state's waters (within 3 nm of shore) for each month and then divided by that month's total habitat suitability index value (described above), so that for each state there was a proportional amount of SH present each month. The difference in proportional SH each month was calculated between the climatology and both extreme contemporary years. The same analysis was conducted in all shelf waters that were directly offshore of each state out to the shelf break. Some of the northeast states were combined if latitudinal estimates could not be calculated (e.g. Maine and New Hampshire were combined, as New Hampshire has a very small coastline).

TABLE 1 Tag information for cobia tagged with either a PTT-100 pop-off satellite archival tags (PSAT) or a Cefas G5 data storage tag (Cefas) in Chesapeake Bay, including total length when tagged, tagging date and days-at-liberty

Animal ID	Total length (cm)	Tag type	Date tagged	Days-at-liberty
C29796	116.8	PSAT	2016–08–14	178
C22787	129.5	PSAT	2016–08–17	182
C29795	96.5	PSAT	2016–08–20	182
C29793	124.5	PSAT	2016–08–30	84
A14128	78.7	Cefas	2017–07–08	301
C32022	121.9	PSAT	2017–08–25	84
C32024	127	PSAT	2017–09–04	180
A14158	139.7	Cefas	2018–06–01	366
A14135	100	Cefas	2018–06–28	406
A14144	120.1[a]	Cefas	2018–08–05	343
A14148	104.1	Cefas	2018–08–05	347
A14149	108	Cefas	2018–08–05	354
A14152	110	Cefas	2018–08–15	381
C32023	111.8	PSAT	2018–09–26	55
A14164	101.6	Cefas	2018–09–26	274

[a]Calculated from measured fork length using unpublished total length-fork length conversion equation.

3 | RESULTS

3.1 | Data retrieval

Data were available from 15 cobia (7 PSATs and 8 Cefas tags) ranging from 78.7 to 139.7 cm total length (mean ± *SD*: 112.2 ± 15.8 cm) (Table 1). Days-at-liberty ranged from 55 to 406 (248 ± 119 days) with PSATs remaining on cobia for an average of 135 ± 58 days. The days-at-liberty were substantially higher for cobia with internally implanted Cefas tags (347 ± 42 days) because such tags are not subject to early detachment from fish. Internally implanted tag data were only obtained when fishermen retained the fish and returned the tag (Table 1).

3.2 | Habitat model

Habitat suitability ratios were developed for each month (Figure 1). Colder months' ratios were higher because cobia selected (ratio > 1) temperatures that were less common (17–22.5°C). During warmer months, cobia selected more common temperatures (22.5–29.5°C) which resulted in lower ratios (Figure 1). Depth weighting factors were developed for each depth bin for each month. During colder winter months (December-March) and warmer summer months (June-September), cobia selected depths at 20–60 m and 0–20 m, respectively (Figure 2). During the fall and spring, cobia selected depths between 0–40 m. The validation of the habitat model showed scores >1 for every month when detections occurred (Table 2) indicating that the habitat model was successful at predicting cobia habitat.

3.3 | Contemporary distribution

3.3.1 | Climatology

The climatology of the monthly distributions of cobia SH within state waters (within 3 nm of shore) and all shelf waters differed substantially among states (Figures 3, 4, 5). For example, during winter months (December-February), the vast majority (>99%) of SH occurred beyond state waters off Florida-North Carolina, with the highest per cent SH occurring in shelf waters off South Carolina (30%–45%; Figures 3 & 5). During spring months, per cent SH began to increase in state waters (Figure 4, Table 3), particularly from Georgia-North Carolina, with the highest occurring in North Carolina (3%–6%; Figure 4). SH was still widely available in all shelf waters from Florida-North Carolina, with the highest percentage off South Carolina (37%–43%; Figure 5). In the summer, SH was present in states waters of North Carolina-Connecticut, with the highest percentage occurring in Virginia (4%–12%, Figure 4, Table 3). An extensive amount of SH still occurred in almost all shelf waters with the highest off Florida-Virginia (Figure 5). Further into fall months (October and November), SH began to shift away from state waters further north, but was still readily available in southern states' waters, particularly in North Carolina (15%; Figure 4, Table 3). SH in all shelf waters occurred from Florida-Virginia, especially off North and South Carolina (30%–50%; Figure 5).

3.3.2 | Extreme years

The distribution of cobia SH differed significantly in state and all shelf waters when comparing the climatologies to the extreme years except during the winter months (Figures 6 & 7). During spring, SH in state and shelf waters often occurred in states further north and in state waters earlier during the warmest year compared to the climatology. The opposite trends occurred during the coolest year. In the summer and into September during the warmest year, per cent SH increased in state and all shelf waters from Maryland-Massachusetts and decreased from Florida-North Carolina (Figures 6 & 7). For example, shelf waters off New Jersey in September increased from 8% to 27%, while North Carolina decreased from 22% to 11%, when comparing per cent SH for the climatology and warmest year. Opposite, yet less extreme differences occurred during the coolest year (Figure 7). During later fall months, there were no discernible patterns in SH.

3.4 | Future distribution

3.4.1 | Climatology

The distribution of future cobia SH in state and all shelf waters differed from contemporary distributions. During the winter, we

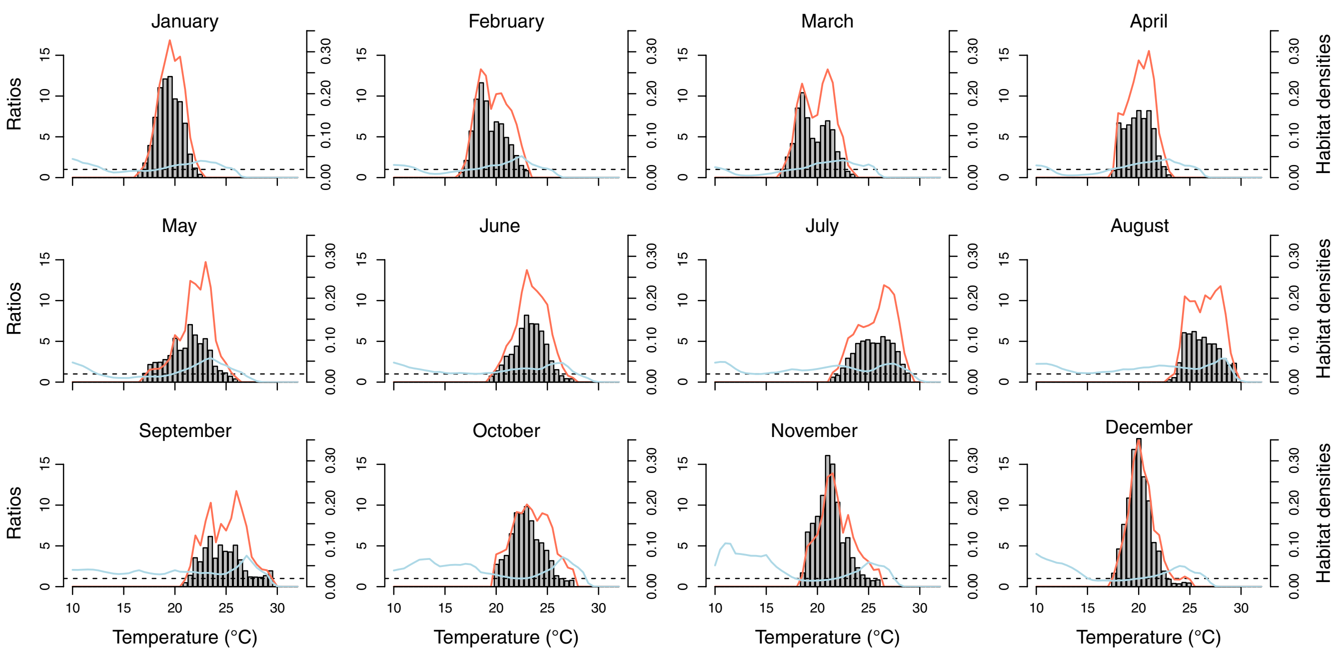


FIGURE 1 Habitat suitability ratios of cobia from 10–32°C (0.5°C bins) for each month (grey bars) for cobia. The ratios were generated from dividing the habitat use densities (red lines) and habitat availability densities (light blue lines) at each temperature

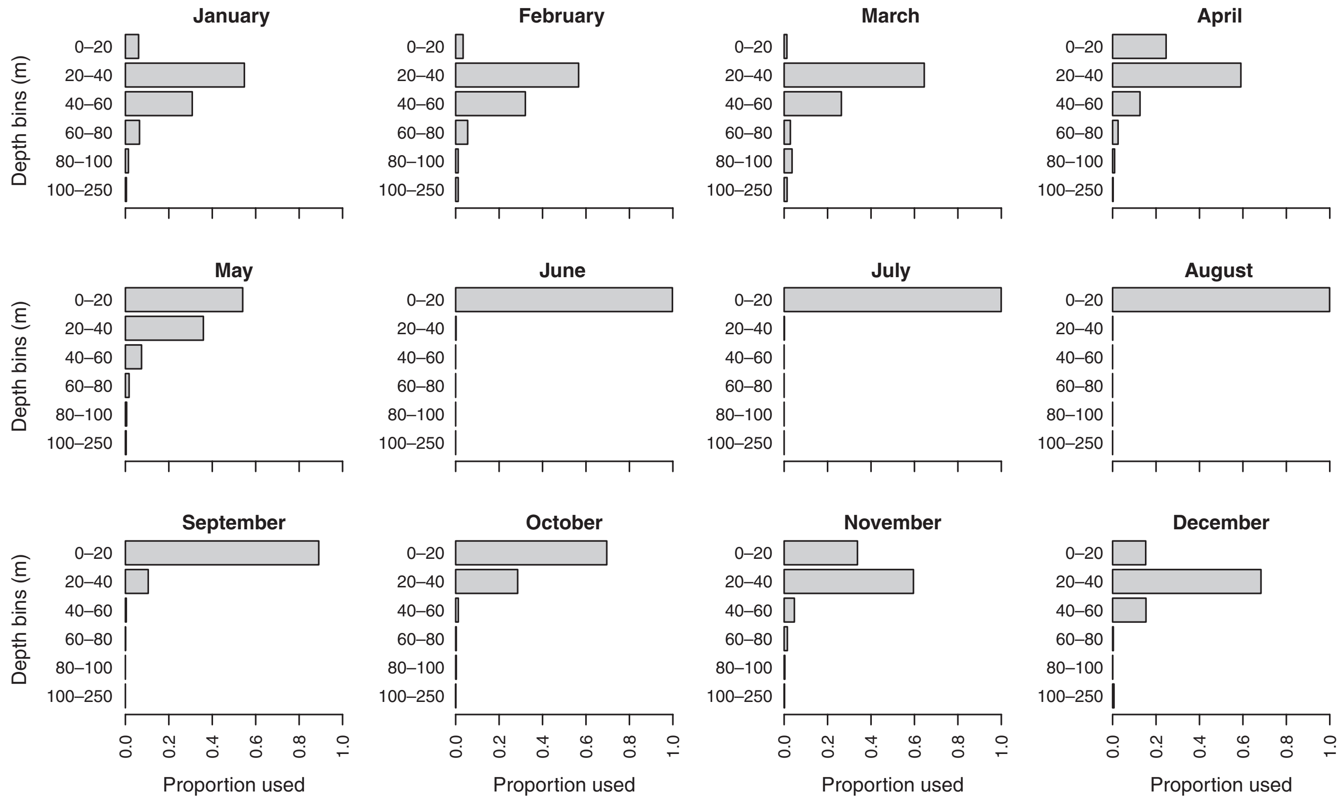


FIGURE 2 Depth weighting factors of cobia for each depth bin for each month

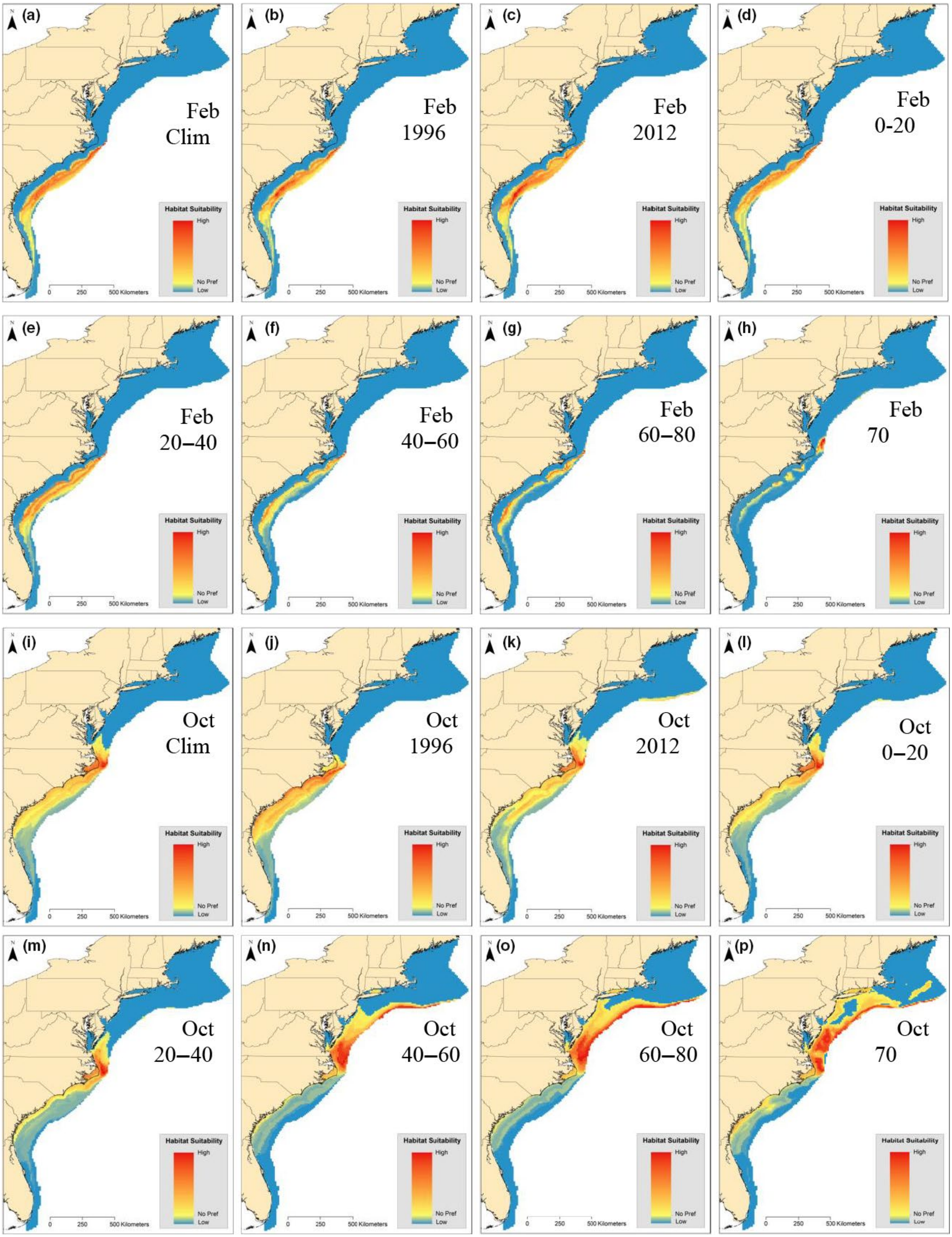
TABLE 2 Cobia habitat model validation table

Month	2017	2018	2019
January	–	–	NA
February	–	–	33.8
March	–	–	50.9
April	–	–	10.1
May	–	6.2	2
June	–	2.9	1.9
July	9.8	2.2	–
August	3.1	2.7	–
September	2.6	2.3	–
October	2.8	2.4	–
November	12.6	10.1	–
December	49.5	7.5	–

Note: A score greater than 1 indicates the habitat model was better than random at predicting cobia habitat for that month and year. A "–" indicates months where either there were no detections or there were no tagged fish in the water. NA represents when there was no acoustic receiver that received a detection in suitable habitat (SH) that month.

estimate SH distribution to remain relatively similar, except that the highest SH will occur off North Carolina instead of South Carolina (Figures 3 & 4). Per cent SH is projected to increase in state waters earlier and as far north as New Jersey in the spring the further into the future we go (Figure 4, Table 3). The highest per cent SH is projected in North Carolina and Virginia (up to 16%) state waters (Figure 4) and shelf waters (Figure 5). In the summer, we project the highest per cent SH to remain in Virginia state waters, although it is projected to decline in 60–80 years. Per cent SH is expected to increase gradually in state waters north of Virginia in the summer through September particularly in Maryland (~2% to ~ 5%), New Jersey (<1% to ~ 3%), and New York (1% to 2%) (Figure 4, Table 3). The percentage of SH in Virginia-Connecticut shelf waters is expected to gradually increase, while large decreases are expected off North Carolina-Florida overtime. In 40 years from now, we project New Jersey to have the most SH (>35%) of any state in the summer (Figure 5). We project SH to remain in state waters further into the fall as far north as Connecticut, but to remain the highest in North Carolina (Figures 3 & 4). SH is expected to occur in shelf waters from Florida-New Jersey, particularly off North Carolina, Virginia and New Jersey (Figure 5, Table 3).

FIGURE 3 Cobia suitable habitat projections along the U.S. east coast for each scenario (clim: climatology, 1996: coolest year, 2012: warmest year, 0–20, 20–40, 40–60, and 70: warm future year) for two months of the year; February and October. No pref on the legend represents a value of 1 meaning no difference than random. Above No pref represents habitat that is suitable whereas below indicates unsuitable habitat


(a)
Feb
Clim
(b)
Feb
1996
(c)
Feb
2012
(d)
Feb
0-20
(e)
Feb
20–40
(f)
Feb
40–60
(g)
Feb
60–80
(h)
Feb
70
(i)
Oct
Clim
(j)
Oct
1996
(k)
Oct
2012
(l)
Oct
0–20
(m)
Oct
20–40
(n)
Oct
40–60
(o)
Oct
60–80
(p)
Oct
70
Habitat Suitability
High
No Pref
Low
0 250 500 Kilometers
N

The general trend of the monthly total habitat suitability indices along the entire U.S. east coast shelf remained similar for each scenario, but the magnitude differed. The general trend showed that during the cooler months, total habitat suitability index was much lower compared to the warmer months. However, other than during the 0–20 and 20–40 year time periods, we project the future scenarios to have an overall decrease in total habitat suitability index for most months compared to contemporary scenarios (Figure 8). Total habitat suitability index for the warmest contemporary year was over 25% larger during the warmer months compared to all other scenarios.

4 | DISCUSSION

This is the first study to project cobia habitat distribution using a depth-integrated habitat model. We have developed an approach that can be applied to species that are ecologically and recreationally important like cobia that are not caught in large numbers in commercial fisheries or fishery-independent surveys and are underrepresented in species distribution modelling studies. McHenry et al. (2019) did create a habitat model for cobia caught in the NMFS fishery independent bottom trawl survey using surface and bottom conditions. However, they suggested a lack of SH north of North Carolina, which is not supported by recreational catch data in that region. A limitation of our approach is the use of only two variables in the model, temperature and depth. As tag technology advances, more variables could be incorporated into depth-integrated models. Despite this limitation, our depth-integrated habitat model captured temperature relationships throughout the entire water column. With the improvements in oceanographic model resolution, we have the capacity to generate depth-integrated climatologies of contemporary and future distributions. This approach could be particularly useful for species like cobia that use more of the water column, such as sharks, tunas and billfish species. With the increase in the number of species fitted with temperature and depth archival tags, we believe our approach could be valuable in describing the distribution of many species. Lastly, the majority of habitat modelling studies generate distributions at large scales. We have also demonstrated a method to determine a regional distribution (e.g. state level) where management and allocation is often discussed.

Although many other variables are known to influence species' distributions, temperature and depth appear to be major drivers for cobia. Cobia seem to migrate on temperature cues (Shaffer & Nakamura, 1989); therefore, it is likely that temperature throughout the water column has a strong influence on cobia distribution. Cobia are considered opportunistic feeders; therefore, if prey shift, cobia could simply change their prey option and may not need to shift. Cobia are known to associate with large animals like sharks and manta rays and congregate around hard structure; however, unfortunately these relationships are difficult to quantify and could not be incorporated into the model. It is currently unclear whether cobia would prefer these associations over using suitable temperatures or express these associations while in suitable temperature waters. It is important to note that the results from this study are based on data from cobia that spent their summer in Chesapeake Bay and caution is needed when extrapolating to cobia that summer in other states (e.g. South Carolina and Florida).

4.1 | Contemporary distribution

Contemporary distribution of suitable cobia habitat during the winter months suggests cobia prefer habitats offshore. Specifically, they prefer subsurface waters (20–60 m) offshore of North Carolina through Georgia beyond 3 nautical miles. These findings align with the lack of cobia catch in all states (inshore of 3 nautical miles) north of Florida during the winter months. This has been confirmed anecdotally from fishermen along the east coast and in NOAA's Marine Recreational Information Program (MRIP). These findings also agreed with a PSAT study that found all tags that reported after November 15 were located outside state waters (Jensen & Graves unpublished). It appears that during cooler months, cobia are selecting waters at the edge of the Gulf Stream and depths below the surface waters to access warmer water temperatures (~18–22°C). Although we believed limiting projections to U.S. shelf water was most appropriate for this species, it is likely that if projections extended further into the Gulf Stream, per cent SH would change offshore for each state. Cobia may have selected offshore waters instead of swimming over 1,000 km south into Florida as an energy saving strategy. Although there was some SH off Florida, the majority of SH occurring north of Florida supports the suggestion that Florida is a biogeographic boundary between the Atlantic and Gulf of Mexico stocks (Perkinson et al., 2019). Only one of 15 cobia were reported or detected in Florida respectively; therefore, water temperature characteristics observed off Florida during the winter months are less likely to occur in cobia records in this study. Preliminary data (Weng et al. unpublished) show that 19% (7 of 36 cobia) of acoustically tagged cobia in Chesapeake Bay were detected off Florida suggesting that for some fish, a long southern migration is preferred. It is currently unclear what may be driving these differences in overwintering locations. Differences in SH distribution between the climatology and the warmest and coolest years during winter months were minimal. These small differences may be due to slight shifts in the Gulf Stream that occur on a yearly basis.

Our data support the current notion that many cobia migrate inshore by mid-spring to late spring and early summer, which is thought to occur once temperatures approach 20°C (Lefebvre & Denson, 2012; Shaffer & Nakamura, 1989). Cobia begin spawning in April and May in South Carolina and North Carolina, respectively (Lefebvre & Denson, 2012; Perkinson et al., 2019), which corresponds to the occurrence of cobia SH in both states during those months. In addition, anecdotal evidence from fishermen and preliminary acoustic tracking data (Weng et al. unpublished) suggest that cobia begin migrating into Chesapeake Bay by May. This was also supported by the SH model. In May of the warmest year, an increase in per cent SH in states like Virginia and

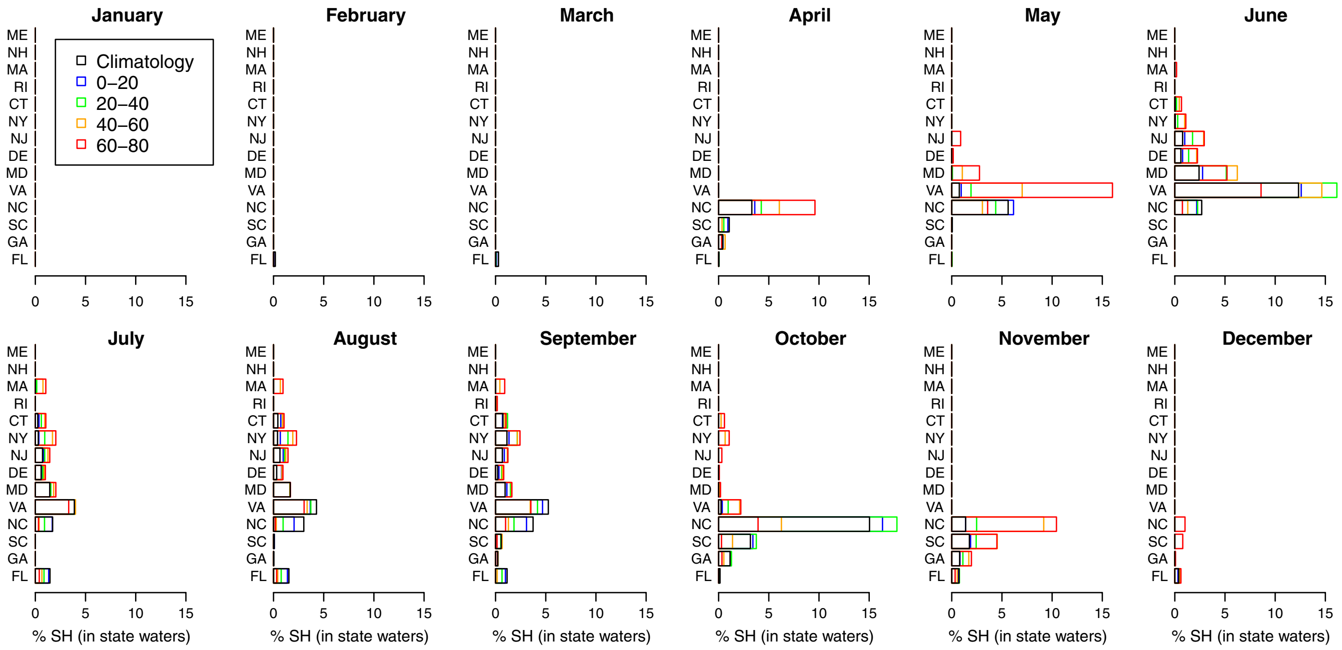


FIGURE 4 Per cent cobia suitable habitat (SH) available within the state waters (3 nm) of each state along the U.S. east coast for the climatology and four future time periods, 0–20, 20–40, 40–60, 60–80 years in the future. State acronyms: ME-Maine, NH-New Hampshire, MA-Massachusetts, RI-Rhode Island, CT-Connecticut, NY-New York, NJ-New Jersey, DE-Delaware, MD-Maryland, VA-Virginia, NC-North Carolina, SC-South Carolina, GA-Georgia, FL-Florida

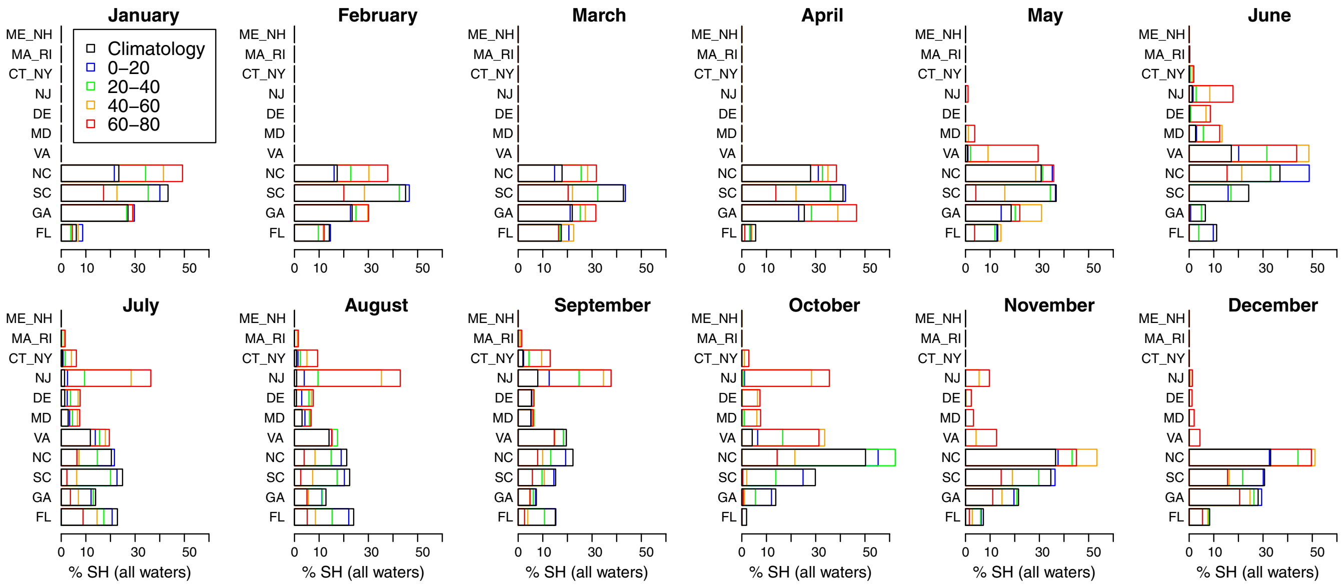


FIGURE 5 Per cent cobia suitable habitat (SH) available in shelf waters from the coast to the shelf off each state along the U.S. east coast for the climatology and four future time periods, 0–20, 20–40, 40–60, 60–80 years in the future. Some of the small states were combined. State acronyms: ME_NH-Maine/New Hampshire, MA_RI-Massachusetts/Rhode Island, CT_NY-Connecticut/New York, NJ-New Jersey, DE-Delaware, MD-Maryland, VA-Virginia, NC-North Carolina, SC-South Carolina, GA-Georgia, FL-Florida

Maryland suggests that during warmer years earlier migrations into Chesapeake Bay may occur. The opposite, yet smaller difference occurred during the coolest year indicating SH distribution along the U.S. east coast can easily shift from year to year. Despite the presence of SH in state waters, the majority of SH is beyond 3 nautical miles, suggesting that offshore areas still meet the thermal demands of cobia.

As expected, coastal habitats like Chesapeake Bay become most suitable for cobia during the summer months. From June-September, the most SH occurred in Virginia, the state with one of the most important spawning and feeding habitats for cobia along the U.S. east coast (Arendt, Olney, & Lucy, 2001; Perkinson et al., 2019). Interestingly, SH occurred in state waters from Maryland to Connecticut (i.e. Long Island Sound), suggesting cobia could inhabit these areas. The lack of SH in South Carolina and Georgia state waters indicate that cobia that summer in Chesapeake Bay prefer conditions in Chesapeake Bay and further north. This trend is consistent with genetics data and preliminary acoustic tagging data, which suggests there is sub-regional biological stock structure and that the cobia population inhabiting inshore South Carolina waters is genetically distinct from cobia in Virginia and North Carolina state waters (Perkinson et al., 2019). Suitable cobia habitat does exist beyond state waters as well, ranging throughout almost the entire east coast. A recent genetics study found separate genetic groups offshore of North and South Carolina (Perkinson et al., 2019) suggesting that it is not unlikely to find summer cobia habitat beyond state waters. This does assume that cobia that spawn inshore and offshore have the same thermal preference. A decrease in per cent SH in Virginia state waters during the warmest year suggests that during warm years, water temperatures of Chesapeake Bay may even exceed the thermal preference for cobia spawning. The large increase in per cent SH in waters off New Jersey in July-September aligns with recent anecdotal evidence of an increase in cobia catch in New Jersey. Increases in current spawning habitats (e.g. Chesapeake Bay) occurred during the coolest year.

TABLE 3 Major trends of cobia suitable habitat (SH) for each season (Winter: Dec.-Feb.; Spring: Mar.-May; Summer: Jun.-Aug.; Fall: Sept.-Nov.) for the contemporary period and 60–80 years into the future

Seasons	Contemporary	Future (60–80 years)
Winter	Offshore NC-FL; **SC**	Offshore NC-FL; **NC**
Spring	Offshore -> Inshore	Offshore -> Inshore; earlier
	State waters: GA-NC; **NC**	State waters: GA-NJ; **NC & VA**
	Shelf water: FL-NC; **SC**	Shelf water: FL-VA; **NC & VA**
Summer	State waters: NC-CT; **VA**	State waters: NC-MA; **NJ**
	Shelf waters: FL-CT; **FL-VA**	Shelf waters: FL-MA; **VA-CT**
Fall	Inshore -> Offshore	Inshore -> Offshore; later
	State waters: FL-VA; **NC**	State waters: FL-CT; **NC**
	Shelf waters: FL-VA; **NC & SC**	Shelf waters: FL-NJ; **NC, VA, NJ**

Note: This includes information about the projected per cent SH in state and all shelf waters, as well as the state or states where SH is estimated to be the highest (indicated in **bold**). State acronyms are as follows: FL-Florida, GA-Georgia, SC-South Carolina, NC-North Carolina, VA-Virginia, NJ-New Jersey, CT-Connecticut, MA-Massachusetts.

Contemporary SH for cobia suggests that they begin to make their offshore migration in the fall. Shifts in the percentage of SH in state waters north of North Carolina to shelf waters off North Carolina in October align with the notion that cobia leave coastal habitats in mid-September through mid-October and that the major fall fishery of cobia off North Carolina occurs during this time. Increases in the percentage of SH off New Jersey and Virginia during the warmest year during the fall may suggest that cobia stayed in Chesapeake Bay later and that the warm water offshore of New Jersey (inshore of the Gulf Stream) remained later into the fall than on average. This indicates how dynamic shifts in SH distribution can

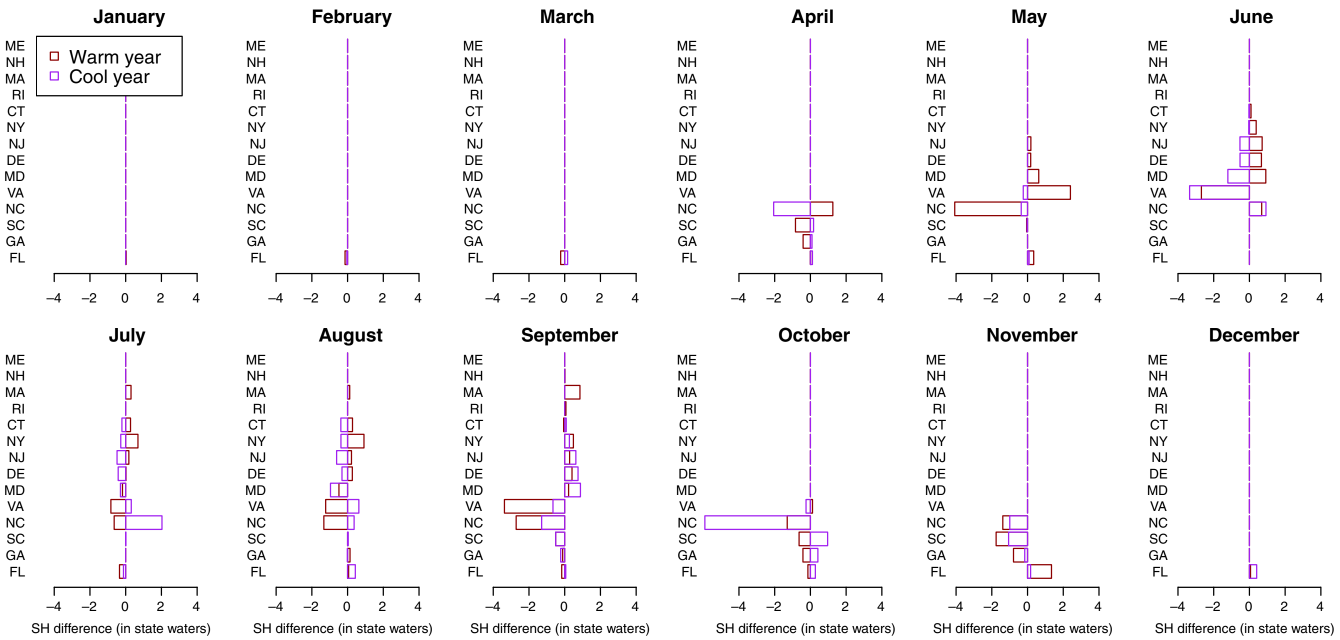


FIGURE 6 Difference in per cent cobia suitable habitat (SH) in state waters of each state along the U.S. east coast between the monthly climatologies and the warmest year (2012) and coolest year (1996). State acronyms: ME-Maine, NH-New Hampshire, MA-Massachusetts, RI-Rhode Island, CT-Connecticut, NY-New York, NJ-New Jersey, DE-Delaware, MD-Maryland, VA-Virginia, NC-North Carolina, SC-South Carolina, GA-Georgia, FL-Florida

occur through different states on a yearly basis, similar to during the spring months.

4.2 | Future distribution

The overall distribution of suitable cobia habitat is expected to shift northward (poleward) in the future, following the common trend of many other species that are either already or projected to experience poleward shifts (Kleisner et al., 2017; Morley et al., 2018; Sunday et al., 2015). Along the U.S. Northeast Shelf, highly mobile species, like pelagic fish and elasmobranchs, are projected to make the most extreme northward shifts due to their strong ties to seasonal oceanographic conditions to remain within their thermal preferences, to target environmental-influenced resources or to migrate at the right time for reproductive purposes (McHenry et al., 2019; Welch & McHenry, 2017). In the Northwest Atlantic, these shifts are expected to occur as a result of direct warming through climate change, a northward shift of the Gulf Stream, a retreat of the Labrador Current and an increase in more Atlantic temperate slope water entering the shelf (Saba et al., 2016). This warming may contribute to an increase in cobia fisheries in northern states' waters, like Maryland, Delaware, New Jersey and New York during the summer months. A corresponding reduction in the cobia fishery in states south of Virginia throughout parts of the year may occur. As expected, these trends become even stronger the further into the future we project because temperatures are warming at a faster rate further in the future. With these changes, cobia spawning in estuaries and bays further north such as Delaware Bay, New York/New Jersey Bight and Long Island Sound may occur. The potential for a cobia fishery to develop in waters beyond 3 nautical miles (e.g. New Jersey) will become more likely in the future as well, particularly in the spring–fall months, given the value that fishermen place on these fishing experiences.

We anticipate the timing of cobia migration to shift in the future. An increase in the percentage of SH in the next 40–80 years in Virginia in May, October and even November is projected and showcases the potential for cobia to arrive in Chesapeake Bay earlier and leave later. This expansion could lead to changes in the timing and duration of cobia spawning while inshore. Changes in the timing of spawning under climate change were projected in bluefin tuna (*Thunnus thynnus*), where spawning habitat was predicted to improve in early spring, but worsen in late spring within the Gulf of Mexico (Muhling, Lee, Lamkin, & Liu, 2011). These shifts in spawning could alter egg and larvae survival which depend on the precise timing of suitable water temperatures and favourable primary production conditions for their growth, feeding and survival (Durant, Hjermann, Ottersen, & Stenseth, 2007). The assumption behind these shifts is that cobia thermal preferences will not change. Species might behaviourally adapt to remain in preferred waters (e.g. cobia), but the capacity for rapid evolution is not well understood for most marine species (Hare et al., 2016).

Despite estimated shifts in the relative distribution of cobia SH throughout the U.S. east coast shelf, the overall habitat suitability is projected to decrease into the future, particularly beyond year 40. This is primarily driven by the thermal habitat exceeding the preferred temperatures over the majority of the year. Cobia appear to have a high thermal tolerance (32°C), but when stressed (e.g. exercised to exhaustion) at high temperatures mortality increases (Crear, Brill, Averilla, Meakem, & Weng, 2020); therefore, these temperatures are

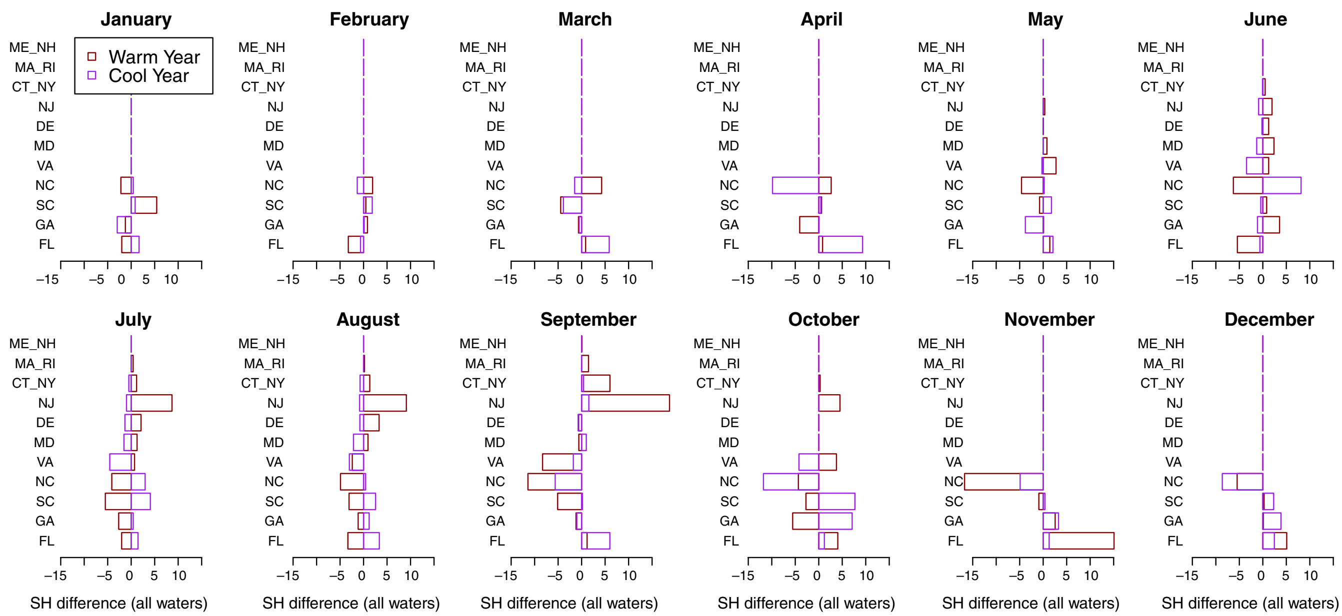


FIGURE 7 Difference in per cent cobia suitable habitat (SH) in shelf waters from the coast to the shelf off each state along the U.S. east coast between the monthly climatologies and the warmest year (2012) and coolest year (1996). State acronyms: ME-Maine, NH-New Hampshire, MA-Massachusetts, RI-Rhode Island, CT-Connecticut, NY-New York, NJ-New Jersey, DE-Delaware, MD-Maryland, VA-Virginia, NC-North Carolina, SC-South Carolina, GA-Georgia, FL-Florida

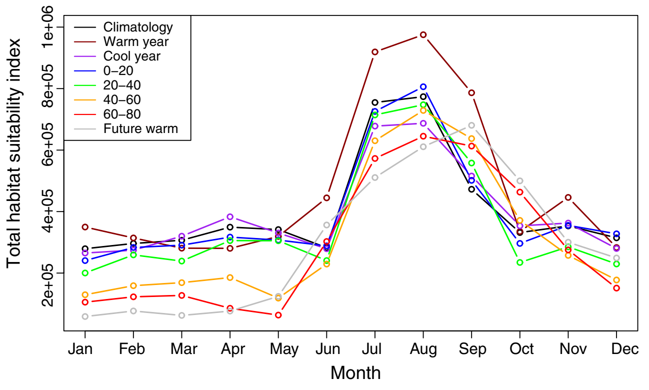


FIGURE 8 The total habitat suitability index for each month over the year for a given time period. The time periods include, the climatology, warmest contemporary year (2012), coolest contemporary year (1996), the future time periods including, 0–20, 20–40, 40–60 and 60–80 years in the future and a future warm year (year 70)

likely less preferred. SH reduction has been a common prediction in many climate change habitat distribution studies (Hare et al., 2016; Kleisner et al., 2017). For example, Kleisner et al. (2017) predict southern species like black sea bass (*Centropristis striata*) and butterfish (*Peprilus triacanthus*) and northern species like Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) will experience thermal habitat losses in the future. We do project increases in SH in September and October, which is likely driven by the warm temperature signature typical of summer extending into the fall months and thus creating more SH for cobia over the shelf.

4.3 | Management implications

A dynamic management strategy may be more suitable for a migratory species like cobia as opposed to the current static management approach. Dynamic management provides an opportunity to refine managed areas on a temporal and spatial scale and match the dynamic ocean (Dunn, Maxwell, Boustany, & Halpin, 2016; Maxwell et al., 2015; Welch et al., 2019). It is clear that cobia may shift their timing of migration and northern extent annually, especially in years with extreme temperatures, which will continue to occur in higher frequency. In addition, the need to have cobia fishing regulations in states north of Virginia may already be necessary based on the occurrence of SH off those states. Projecting cobia distribution prior to each year will help managers predict when this resource is expected to occur in each state. This strategy would help managers refine allocation assignments each year among states and be prepared for more extreme changes in the future (Lewison et al., 2015). As forecasting (3–9 month lead time) ocean models develop along the U.S. east coast, coupling them with our cobia habitat model can produce species' habitat distribution outputs on a time scale that would allow fisheries managers to act more tactical in real time.

The potential for cobia to expand their range northward under climate change is highly likely. We project the cobia fishery to increase or appear in states from Virginia to Connecticut. Currently, there are not strict management regulation for cobia in states north of Virginia that are comparable to those in southern states. As cobia continue to shift into new waters, the development of regulations in more northern states will become necessary to promote a sustainable cobia fishery. In addition, our SH projections suggest that cobia may spend more months in Chesapeake Bay (May-November), the location where the highest fishing pressure currently occurs. In the future, Virginia will have to decide whether seasonal adjustments in the cobia fishery are needed. As species shift their distributions as a result of climate change, it is imperative that we understand why and how these shifts are occurring so that both managers and fishers can ensure important resources continue to be fished sustainably.

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DATA AVAILABILITY STATEMENT

The data and the script supporting the results of this article are available in the Dryad repository (https://doi.org/10.5061/dryad.2fqz612kv).

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BIOSKETCH

The primary author's research focuses on the impacts of environmental change on marine species. Specifically, he is interested in quantifying shifts in species distributions, understanding animal movements and physiological responses relative to environmental change. His work assesses these shifts over seasonal, annual and multi-decadal time periods at a wide range of spatial scales.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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