RESEARCH ARTICLE

Climate vulnerability assessment of fish and invertebrates in the U.S. South Atlantic large marine ecosystem

J. Kevin Craig[1‡*], Brendan J. Runde[2‡], Nathan M. Bacheler[1‡], Michael L. Burton[1‡], Roldan C. Muñoz[1], John A. Quinlan[3], Mark W. Nelson[4], Samantha M. Binion-Rock[1], G. Todd Kellison[1], Joseph W. Smith[1], R. Wilson Laney[5], George R. Sedberry[6], James W. Morley[7], Stephen J. Poland[8], Russell Brodie[9], Lauren Gentry[10], Karla Gore[11], Jason E. Rock[8], Matthew W. Johnson[12], Jared Flowers[13], Chip Collier[14]

1 NOAA Southeast Fisheries Science Center, Beaufort Laboratory, Beaufort, North Carolina, United States of America, **2** The Nature Conservancy, Charlottesville, Virginia, United States of America, **3** NOAA Southeast Fisheries Science Center, Miami Laboratory, Miami, Florida, United States of America, **4** Electronic Consulting Services Federal, LLC, Fairfax, Virginia, United States of America; in support of NOAA Fisheries Office of Science and Technology, Silver Spring, Maryland, United States of America, **5** Department of Applied Ecology, North Carolina State University and United States Department of the Interior, Fish and Wildlife Service (retired), Raleigh, North Carolina, United States of America, **6** NOAA Office of National Marine Sanctuaries (retired), Savannah, Georgia, United States of America, **7** Department of Biology, Coastal Studies Institute, East Carolina University, Wanchese, North Carolina, United States of America, **8** North Carolina Division of Marine Fisheries, Morehead City, North Carolina, United States of America, **9** Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Jacksonville, Florida, United States of America, **10** Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg, Florida, United States of America, **11** NOAA Fisheries, Southeast Regional Office, St. Petersburg, Florida, United States of America, **12** NOAA Southeast Fisheries Science Center, Galveston Laboratory, Galveston, Texas, United States of America, **13** Coastal Resources Division, Georgia Department of Natural Resources, Brunswick, Georgia, United States of America, **14** South Atlantic Fishery Management Council, Charleston, South Carolina, United States of America

‡KC, BR, NB, and MB are Joint Senior Authors
* kevin.craig@noaa.gov

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Abstract

Trait-based climate vulnerability assessment (CVA) is a rapid and repeatable approach to simultaneously assess the vulnerability of a large number of species to projected regional changes in climate. We conducted the first CVA in the U.S. South Atlantic Large Marine Ecosystem for 71 ecologically, economically, and culturally important fish and invertebrate species. The CVA was conducted by a 16-member panel based on scoring 12 biological sensitivity attributes and seven climate exposure factors. About two-thirds of the species were considered highly vulnerability to future climate projected under the RCP 8.5 emissions scenario, with diadromous species, invertebrates, and deepwater reef fishes the most vulnerable functional groups. Ocean acidification, sea surface temperature, and salinity were the exposure factors with the greatest influence on climate vulnerability, while population growth rate, population status, and early life history traits were the most important biological sensitivity attributes. More than two-thirds of the species had high potential for

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shifts in geographic distribution, due mostly to the prevalence of broadcast spawning, extensive larval dispersal, and high adult mobility of many species, and the generalist habitat requirements of several estuary-dependent and hard-bottom reef species. Some shifts in distribution have already occurred though potential relationships to environmental conditions associated with climate are not well-understood. Uncertainty analyses confirmed the robustness of the climate vulnerability rankings, but comparison of alternative types of elicited informed judgement did not always agree, suggesting higher uncertainty in climate vulnerability for some species. In addition, several species may benefit under future climate conditions, and climate effects on some species considered to be highly vulnerable may be of relatively small magnitude. These results can be used to prioritize conservation, research, and management efforts, and identify key uncertainties related to the impacts of future climate on fishery resources in the U.S. South Atlantic region.

Introduction

Physical and biological changes in the world's oceans are altering the distribution, productivity, and abundance of marine species [1–4]. The potential acceleration and the associated uncertainty of changes in future climate are major challenges for natural resource managers and policymakers [5–8]. Risk-based assessments to identify and rank species, habitats, and ecosystems in terms of climate vulnerability have emerged as a pragmatic approach to help prioritize research and management efforts, enhance communication among stakeholders, and facilitate adaptation to future climate conditions [9–12].

Trait-based climate vulnerability assessment (CVA) is a formal approach that evaluates the ecological and demographic traits of species to assess their susceptibility to potential stressors associated with future climate conditions [13]. The approach typically uses a combination of existing data and expert judgment to score the biological traits that underlie a species' sensitivity, adaptive capacity, and potential exposure to key environmental factors projected to change with future climate [12]. Advantages of the approach include the ability to rapidly and concurrently assess the relative climate vulnerability of a large number of species using a consistent, transparent, and repeatable methodology. Information from CVAs is particularly useful for identifying and prioritizing vulnerable species, including data-poor species, as well as for developing research, management, and conservation priorities. CVAs can also help inform habitat vulnerability assessments [14], social vulnerability assessments [15,16], and broader risk assessments that consider environmental factors associated with future climate in combination with other risks, such as overfishing [17,18]. Trait-based CVAs have been conducted for several ecosystems worldwide [19–21] including several U.S. large marine ecosystems [22–25], as well as for particular species groups (marine mammals [26]; salmonids [27]) and for local regions [28].

The U.S. Southeast Atlantic Large Marine Ecosystem [29] (hereafter 'South Atlantic') encompasses nearly 20,000 km of shoreline habitat and >100,000 km^2

of adjacent oceanic waters extending from the Florida Keys through North Carolina (Fig 1). The Gulf Stream, a rapidly northward flowing, western-intensified offshore current, is the dominant oceanographic feature in the region [30,31]. Earth system models predict the Gulf Stream will slow under future increases in CO_2 emissions due to weakening of the Atlantic Meridional Overturning Circulation (AMOC; [32]). A slower flowing Gulf Stream has potential consequences for regional ocean temperature and salinity [33–34], evaporation and precipitation [35,36], sea level [37], storminess [38], currents and upwelling [39,40], and primary productivity [41]. The South Atlantic also harbors diverse nearshore habitats, including extensive shallow water coral reefs that support diverse fish communities (e.g., Florida Reef Tract; [42]), and extensive

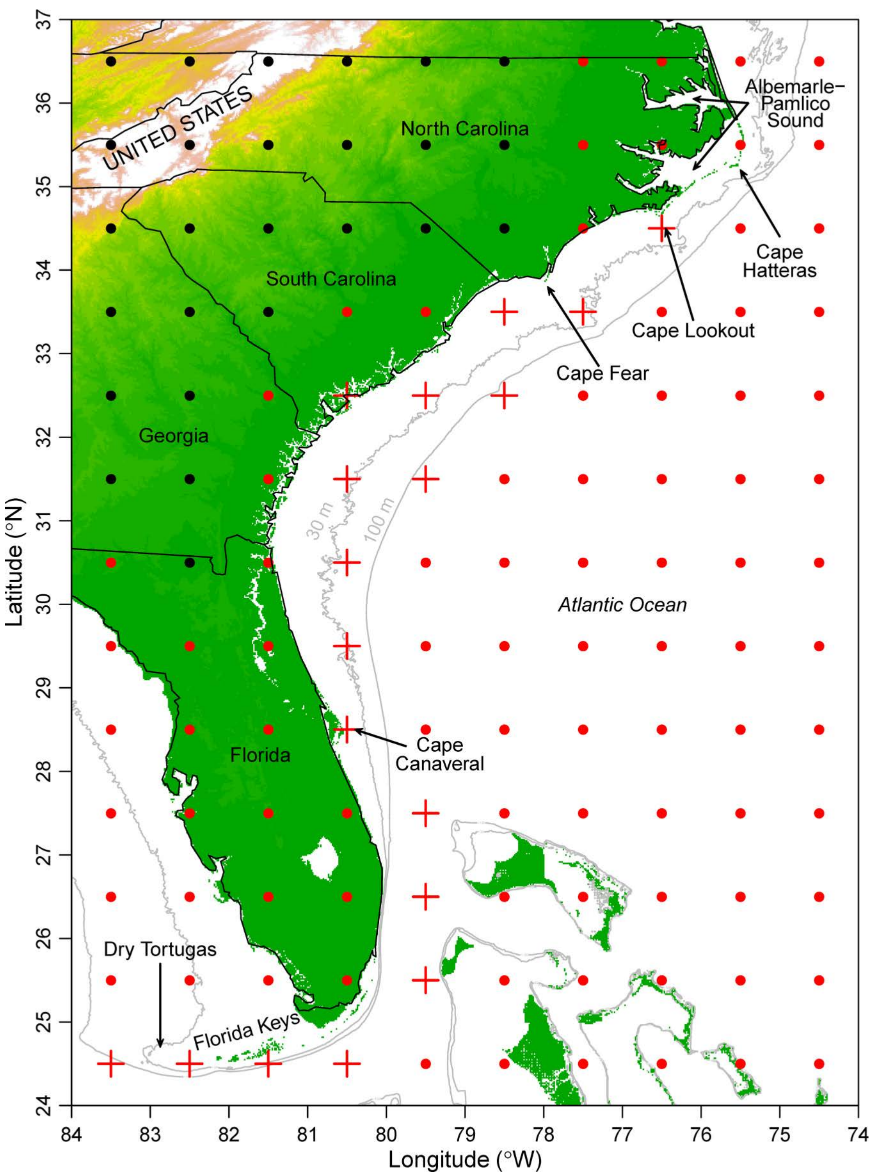

Fig 1. Study area for the South Atlantic CVA. Red symbols indicate all data nodes from the NOAA Earth Systems Research Laboratory (ESRL) Web Portal general climate model output. Red crosses indicate the particular nodes used to compute climate exposure for red snapper based on its distribution in the South Atlantic. Base maps are from the R package "maps" (https://cran.rproject.org/web/packages/maps/maps.pdf) which uses maps from naturalearthdata.com in the public domain.

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saltmarsh-dominated, lagoonal estuaries that serve as nursery grounds for many economically important species (e.g., Albemarle-Pamlico Estuarine System; [43]).

Over 100 fish and invertebrate species are managed in federal and state waters of the South Atlantic. Federal fisheries management in the region has focused on the snapper-grouper complex, which is composed of 55 species primarily associated with hard-bottom and rocky outcrops on the continental shelf and upper slope, and on several coastal migratory species [44]. The landings of most federally-managed species in the South Atlantic are increasingly dominated by the recreational fishing sector (>85%; [45]), a trend consistent with the rapid population growth along the coast and within coastal watersheds in the region [46].

While the South Atlantic is projected to warm at a slower rate compared to many north temperate marine ecosystems [33,47], multiple temperature indicators suggest the region has experienced recent oceanic warming, at least since the mid-2010s [46]. Other environmental factors associated with climate have also changed in recent years, including increasing ocean acidification (OA; [48]) and rising sea levels ([49]). Changing ocean conditions may be a contributing factor to recent declines in recruitment [50] and shifts in spatial distribution [51,52] documented for several species in the region.

Our objective was to assess the vulnerability of economically, ecologically, and culturally important marine fish and invertebrate species in the South Atlantic to projected oceanographic and environmental changes associated with future climate conditions in the region. We also evaluated the potential for each species to significantly alter its distribution based on intrinsic biological and life history characteristics. We used the NOAA Fisheries Climate Vulnerability Assessment Methodology, an established systematic approach based on available information and expert elicitation [53]. This CVA provides scientists and managers with information to better assess the potential effects of changing oceanographic conditions, environmental variability, and nonstationarity associated with future climate on the marine resources of the South Atlantic. Our results can help prioritize research and management as well as inform adaptive management plans to mitigate the negative effects, and maximize potential new opportunities, associated with changes in climate in the region.

Ethics statement

This study was subject to internal review through the NOAA Research Publication Tracking System (RPTS). This study was not reviewed by an Institutional Review Board because it was not based on Human Subject or Animal Research. This assessment was based on expert opinion and available literature, and the experts involved are authors on the paper. All individuals voluntarily participated via email or verbal response to an invitation from one of the senior authors (MLB).

Materials and methods

Overview

The geographic area of this CVA extends from Cape Hatteras, North Carolina through the Florida Keys, including the continental shelf and upper slope, as well as estuaries and their major riverine tributaries (Fig 1). A scientific panel was assembled to assess the climate vulnerability of 71 South Atlantic species by scoring biological sensitivity attributes and climate exposure factors. We followed the methodology described in Morrison et al. [53] that has been applied to several marine ecosystems [22–25,28]. This work builds on the results of Burton et al. [54] with substantial additional interpretation, new or revised visuals, and new or updated analyses. All analyses of the original data (S1 Data) were re-run and the most updated results are presented here.

Species selection

The primary criteria for selecting species were whether the species is: 1) managed under a fishery management plan (FMP); 2) important in recreational or commercial fishery landings; 3) considered ecologically important (e.g., forage species); or 4) of conservation concern (e.g., ESA-listed). Fishes and invertebrates that occur mostly in oceanic waters of the South Atlantic were the primary focus, though several diadromous and estuary-dependent species [43] as well species with extensive (e.g., circumpolar) migrations were also included. The 71 selected species were divided into nine functional groups based on life history characteristics and habitat preferences (Table 1): Coastal Fish (10 species; primarily occupy estuaries and the nearshore coastal ocean), Coastal Pelagic Fish (7 species; primarily occupy the upper water column of the continental shelf and seasonally migrate along the coast), Diadromous Fish (5 species; migrate between freshwater and oceanic habitats), Sharks (6 species), Invertebrates (9 species), Forage Fish (3 species; schooling species known to be important prey for piscivores), Pelagic Fish (3 species; occur in the South Atlantic but have circumpolar distributions), Reef Fish (23 species; primarily occupy hard bottom habitats on the continental shelf, 10–110 m depth), and Deepwater Reef Fish (5 species; primarily occupy waters >75 m on the continental shelf and upper slope). Of the 71 species, 80% are managed by the South Atlantic Fishery Management Council (SAFMC), mostly under the snapper-grouper FMP, 32% are managed via inter-state agreement by the Atlantic States Marine Fisheries Commission (ASMFC), and 54% have individual state-level FMPs (Table 1). Several species are also managed locally under U.S. National Park Service FMPs or as part of NOAA Highly Migratory Species FMPs. Two-thirds of the species considered here are subject to more than one management authority (Table 1).

Biological sensitivity attributes

Biological sensitivity attributes include intrinsic ecological and life history traits that affect a species' susceptibility, or capacity to respond, to environmental changes associated with climate, as well as extrinsic factors (e.g., fishing) that represent the effects of other external stressors [53,55]. We used the 12 biological sensitivity attributes described in the NOAA methodology [53] and used in CVAs for other regions [22–25]: Habitat Specificity, Prey Specificity, Sensitivity to Temperature, Sensitivity to OA, Adult Mobility, Dispersal of Early Life History Stages, Early Life History Survival and Settlement Requirements, Complexity in Reproductive Strategy, Spawning Cycle, Stock Size/Status, Population Growth Rate, and Other Stressors (e.g., disease, pollution, habitat loss) (S1 Text). For example, species that deposit and guard fertilized eggs on the bottom until hatching (e.g., many nest-building species) often have limited dispersal of early life history stages and potentially higher vulnerability to changes in local environmental conditions, while broadcast spawners with widely dispersed, pelagic larvae that can colonize new areas are potentially less vulnerable to changing oceanographic conditions associated with climate.

Climate exposure factors

Climate exposure is the magnitude of change an organism is expected to experience as a result of overlap or exposure to particular oceanographic or environmental variables under projected future climate conditions [20,53]. Seven climate exposure factors were chosen based on their importance to species' productivity, data availability, and use in CVAs for other regions (S1 Text): (1) Sea Surface Temperature (SST), (2) Sea Surface Salinity, (3) Air Temperature (i.e., a proxy for estuarine and freshwater temperature), (4) Precipitation (i.e., a proxy for river flow and freshwater input), (5) Sea Surface pH (i.e., an indicator of OA), (6) Sea Level Rise (SLR), and (7) Upwelling/Currents. Data for five of the exposure factors (1–5 above) were available from Global Climate Model (GCM) projections and were downloaded from the NOAA Earth Systems Research Laboratory (ESRL) Web Portal [56,57] (S2 Text). We used the average of an ensemble of models from the Fifth Coupled Model Intercomparison Project (CMIP5) based on the Representative Concentration Pathway (RCP) 8.5 scenario. RCP 8.5 represents a high emissions scenario that assumes little to no stabilization of greenhouse gas emissions by 2100. This scenario has been used in most prior CVAs in the U.S. [22–24,26–28] and elsewhere [21]. While alternative, more moderate emissions scenarios (e.g., RCP 4.5) may be more plausible [58], they do not diverge considerably from RCP 8.5 until after the time frame of our analysis (2006–2055). GCM outputs were available as 1° gridded arrays of mean field and standard deviations for the periods 1956–2005 (historical time frame) and 2006–2055 (future time frame). Standardized change between the future and historical time periods was computed as ($Mean_{2006–2055}$ – $Mean_{1956–2005}$)/

Table 1. Functional group, common and scientific names, and management authority for 71 South Atlantic species. "Mgmt" is the management authority where "S" = South Atlantic Fishery Management Council, "M" = Mid-Atlantic Fishery Management Council, "A" = Atlantic States Marine Fisheries Commission, "G" = Gulf of Mexico Fishery Management Council, "B" = Biscayne Bay National Park, "N" = NOAA National Marine Sanctuaries, "H" = NOAA Highly Migratory Species, and "St" = one or more state-specific management plans (Florida, Georgia, South Carolina, North Carolina). "Sens" indicates biological sensitivity attributes, "Exp" indicates climate exposure factors, "Vul" indicates overall climate vulnerability. M = Moderate climate vulnerability (Yellow), H = High climate vulnerability (Orange), VH = Very High climate vulnerability (Red). Numbers indicate the proportion of bootstrap replicates (5,000 for each species) in each climate vulnerability category. A change in color within a row (species) indicates the category with the highest proportion of bootstrap runs differed from the original scoring.

						Bootstrap Results				
Functional Group	Species	Scientific Name	Mgmt	Sens	Exp	Vul	L	M	H	VH
Coastal	Common snook	*Centropomus undecimalis*	St, B	M	VH	H	0	0.01	0.44	0.56
Coastal	Red drum	*Sciaenops ocellatus*	A, St, B	M	VH	H	0	0	0.74	0.26
Coastal	Weakfish	*Cynoscion regalis*	A, St	M	VH	H	0	0.01	0.98	0.01
Coastal	Sheepshead	*Archosargus probatocephalus*	St, B	M	VH	H	0	0.01	0.99	0
Coastal	Southern flounder	*Paralichthys lethostigma*	St, B	M	VH	H	0	0.01	0.99	0
Coastal	Black drum	*Pogonias cromis*	A, St, B	M	VH	H	0	0.3	0.7	0
Coastal	Spotted seatrout	*Cynoscion nebulosus*	A, St, B	M	VH	H	0	0.28	0.71	0
Coastal	Striped mullet	*Mugil cephalus*	St	L	VH	M	0	0.9	0.1	0
Coastal	Atlantic croaker	*Micropogonias undulatus*	A, St	L	VH	M	0	0.94	0.06	0
Coastal	Spot	*Leiostomus xanthurus*	A, St	L	VH	M	0	1	0	0
Coastal Pelagic	Cobia	*Rachycentron canadum*	A, St	M	VH	H	0	0.02	0.98	0
Coastal Pelagic	Almaco jack	*Seriola rivoliana*	S	M	VH	H	0	0.46	0.54	0
Coastal Pelagic	Bluefish	*Pomatomus saltatrix*	M, A, St	L	VH	M	0	0.86	0.15	0
Coastal Pelagic	Blue runner	*Caranx crysos*		L	VH	M	0	0.99	0.01	0
Coastal Pelagic	King mackerel	*Scomberomorus cavalla*	S, G, St	L	VH	M	0	0.99	0.01	0
Coastal Pelagic	Greater amberjack	*Seriola dumerili*	S, B	L	VH	M	0	1	0	0
Coastal Pelagic	Spanish mackerel	*Scomberomorus maculatus*	S, G, A, St	L	VH	M	0	1	0	0
Deepwater Reef	Snowy grouper	*Hyporthodus niveatus*	S	H	VH	VH	0	0	0	1
Deepwater Reef	Speckled hind	*Epinephelus drummondhayi*	S, St	H	VH	VH	0	0	0	1
Deepwater Reef	Warsaw grouper	*Hyporthodus nigritus*	S, St	H	VH	VH	0	0	0	1
Deepwater Reef	Blueline tilefish	*Caulolatilus microps*	S, M	H	VH	VH	0	0	0.43	0.57
Deepwater Reef	Golden tilefish	*Lopholatilus chamaeleonticeps*	S, M	H	VH	VH	0	0	0.57	0.43
Diadromous	Blueback Herring	*Alosa aestivalis*	A, St	H	VH	VH	0	0	0	1
Diadromous	American shad	*Alosa sapidissima*	A, St	H	VH	VH	0	0	0.04	0.96
Diadromous	Atlantic sturgeon	*Acipenser oxyrinchus*	A	VH	H	VH	0	0	0.1	0.9
Diadromous	Striped bass	*Morone saxatilis*	A, St	H	VH	VH	0	0	0.3	0.7
Diadromous	American eel	*Anguilla rostrata*	A, St	M	VH	H	0	0	0.36	0.64
Forage	Anchovies	*Engraulis* spp.		L	VH	M	0	1	0	0
Forage	Atlantic menhaden	*Brevoortia tyrannus*	A	L	VH	M	0	1	0	0
Forage	Pinfish	*Lagodon rhomboides*		L	VH	M	0	1	0	0
Invertebrate	Eastern oyster	*Crassostrea virginica*	St	H	VH	VH	0	0	0	1
Invertebrate	Atlantic horseshoe crab	*Limulus polyphemus*	A	H	VH	VH	0	0	0.01	0.99
Invertebrate	Pink shrimp	*Farfantepenaeus duorarum*	St, S	H	VH	VH	0	0	0.08	0.92
Invertebrate	White shrimp	*Litopenaeus setiferus*	St, S	H	VH	VH	0	0	0.08	0.92
Invertebrate	Brown shrimp	*Farfantepenaeus aztecus*	St, S	H	VH	VH	0	0	0.14	0.86
Invertebrate	Caribbean spiny lobster	*Panulirus argus*	S, St, B	H	VH	VH	0	0	0.15	0.85
Invertebrate	Golden crab	*Chaceon fenneri*	S	M	VH	H	0	0	0.96	0.04
Invertebrate	Blue crab	*Callinectes sapidus*	St, B	M	VH	H	0	0	0.99	0.01
Invertebrate	Brown rock shrimp	*Sicyonia brevirostris*	S	M	VH	H	0	0.02	0.98	0

(Continued)

Table 1. (Continued)

Functional Group	Species	Scientific Name	Mgmt	Sens	Exp	Bootstrap Results				
						Vul	L	M	H	VH
Pelagics	Dolphinfish	*Coryphaena hippurus*	S, St	L	VH	M	0	1	0	0
Pelagics	Little tunny	*Euthynnus alletteratus*	St	L	VH	M	0	1	0	0
Pelagics	Wahoo	*Acanthocybium solandri*	S	L	VH	M	0	1	0	0
Reef Fish	Atlantic goliath grouper	*Epinephelus itajara*	S, St	H	VH	VH	0	0	0	1
Reef Fish	Nassau grouper	*Epinephelus striatus*	S	H	VH	VH	0	0	0	1
Reef Fish	Red grouper	*Epinephelus morio*	S, B	H	VH	VH	0	0	0	1
Reef Fish	Gag	*Mycteroperca microlepis*	S	H	VH	VH	0	0	0.02	0.98
Reef Fish	Scamp	*Mycteroperca phenax*	S	H	VH	VH	0	0	0.08	0.92
Reef Fish	Hogfish	*Lachnolaimus maximus*	S, B	H	VH	VH	0	0	0.26	0.75
Reef Fish	Mutton snapper	*Lutjanus analis*	S, B	M	VH	H	0	0	0.93	0.07
Reef Fish	Red snapper	*Lutjanus campechanus*	S, St	M	VH	H	0	0.05	0.87	0.08
Reef Fish	Redband parrotfish	*Sparisoma aurofrenatum*	St	M	VH	H	0	0.01	0.97	0.02
Reef Fish	Gray snapper	*Lutjanus griseus*	S, St, B	M	VH	H	0	0	1	0
Reef Fish	Red porgy	*Pagrus pagrus*	S, St	M	VH	H	0	0.11	0.89	0
Reef Fish	Emerald parrotfish	*Nicholsina usta*	St	M	VH	H	0	0.23	0.77	0
Reef Fish	Yellowtail snapper	*Ocyurus chrysurus*	S, B	M	VH	H	0	0.31	0.69	0
Reef Fish	White grunt	*Haemulon plumierii*	S	L	VH	M	0	0.68	0.32	0
Reef Fish	Gray triggerfish	*Balistes capriscus*	S, B	L	VH	M	0	0.82	0.18	0
Reef Fish	Belted sandfish	*Serranus subligarius*		L	VH	M	0	0.92	0.08	0
Reef Fish	Cubbyu	*Pareques umbrosus*		L	VH	M	0	0.92	0.08	0
Reef Fish	Slippery dick	*Halichoeres bivittatus*		L	VH	M	0	0.93	0.07	0
Reef Fish	Black sea bass	*Centropristis striata*	S, M, A, St	L	VH	M	0	0.95	0.05	0
Reef Fish	Lane snapper	*Lutjanus synagris*	S, B	L	VH	M	0	1	0	0
Reef Fish	Lionfish	*Pterois* spp.	N	L	VH	M	0	1	0	0
Reef Fish	Tomtate	*Haemulon aurolineatum*	S, St	L	VH	M	0	1	0	0
Reef Fish	Vermilion snapper	*Rhomboplites aurorubens*	S	L	VH	M	0	1	0	0
Shark	Dusky shark	*Carcharhinus obscurus*	H, A	H	VH	VH	0	0	0.03	0.97
Shark	Sandbar shark	*Carcharhinus plumbeus*	H, A	M	VH	H	0	0.01	0.89	0.1
Shark	Bonnethead shark	*Sphyrna tiburo*	H, A St	M	VH	H	0	0	0.92	0.08
Shark	Sand tiger shark	*Carcharias taurus*	H, A	M	VH	H	0	0.04	0.86	0.1
Shark	Atlantic sharpnose shark	*Rhizoprionodon terraenovae*	H, A, St	M	VH	H	0	0.04	0.96	0
Shark	Spiny dogfish	*Squalus acanthias*	M, A	L	VH	M	0	0.97	0.03	0

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Standard Deviation$_{1956–2005}$. Model outputs were not available for Upwelling/Currents and SLR (6–7 above); therefore, narratives were developed from the literature to inform the scoring for these two exposure factors (S3 Text), similar to other CVAs [22,23,25].

Species profiles and geographic distributions

Species profiles summarizing relevant information about the biological sensitivity attributes were developed for each of the 71 species from the scientific literature, stock assessment reports, and other sources (S4 Text). The geographic distributions of the 62 finfish species were obtained from the IUCN Red List distribution maps [59], a reviewed source of consistent spatial information. Distribution maps for the nine invertebrate species were manually constructed based on the scientific literature, commercial landings, and the judgement of the scientific panel. Distribution maps were imported into

Matlab [60] and overlaid with the grid nodes of the GCM model outputs to determine which data nodes to include for each species and exposure factor (Fig 1).

Scientific panel

A 16-member scientific panel was assembled to score the biological sensitivity attributes and climate exposure factors for the 71 species. The panel included professionals from federal fisheries agencies, academia, each of the relevant state fisheries agencies (Florida, Georgia, South Carolina, North Carolina), the NOAA Southeast Regional Office, and the SAFMC. Most panelists had scientific expertise with multiple functional groups and several also had management experience (i.e., member of a committee or advisory panel for a federal or state management body). The panel had a median of 26 years (range: 5–54 years) of experience working on fish and fisheries in the South Atlantic region.

Scoring biological sensitivity attributes and exposure factors

Each panelist independently scored the biological sensitivity attributes and climate exposure factors for 18–24 species based on the available information and their own scientific judgement. Each panelist was assigned species based on their knowledge of one or more functional groups as well as a random selection of the remaining species. Each species was scored by five panelists. Each panelist accounted for uncertainty in their own scoring by distributing their scores using a five-tally system across the possible range of scores (i.e., Low, Moderate, High, Very High). For example, because eastern oysters are sessile as adults, there is little uncertainty regarding sensitivity to Adult Mobility, and a panelist could place all five tallies in the Very High category for this attribute. More commonly, panelists spread their five tallies across multiple categories based on their judgement of the magnitude of uncertainty. A three-day, in-person workshop was convened where the panel discussed tabulated scores and determined final scores for each species.

Assessment of overall climate vulnerability

Overall climate vulnerability was determined for each species as described in Morrison et al. [53]. First, each scoring category was assigned a numerical value: Low (L) = 1, Moderate (M) = 2, High (H) = 3, and Very High (VH) = 4. The weighted mean of the scorer tallies was computed for each of the 12 biological sensitivity attributes and seven climate exposure factors. A logic rule was used to convert the weighted mean component scores into an overall biological sensitivity score and an overall climate exposure score: Species with three or more mean scores ≥3.5 were assigned to the Very High category, two or more mean scores ≥3.0 were assigned to the High category, and two or more mean scores ≥2.5 were assigned to the Moderate category; all other species were assigned to the Low category. An overall climate vulnerability score was then computed as the product of the biological sensitivity score and the climate exposure score. Overall climate vulnerability scores were then grouped into four qualitative categories as: 1–3 = Low, 4–6 = Moderate, 8–9 = High, and 12–16 = Very High.

The panel also scored each species as to whether the overall directional effect of anticipated environmental changes under future climate was likely to be positive, negative, or neutral [23–25,53]. Five panelists scored each species by distributing four tallies across three bins (Positive = 1, Negative = -1, or Neutral = 0). The weighted mean was computed and an overall directional effect of anticipated change under future climate was assigned for each species as follows: mean score > 0.33 = positively affected; mean score < −0.33 = negatively affected; and −0.33 ≤ mean score ≤ 0.33 = neutrally affected.

Uncertainty and leave-one-out analysis

Uncertainty in climate vulnerability was assessed using a bootstrap analysis [53,61]. The scorer tallies were randomly resampled with replacement 5,000 times for each biological sensitivity attribute and climate exposure factor. Climate vulnerability was computed for each bootstrap replicate as described above, and the proportion of the 5,000 replicates in each vulnerability category was tabulated.

A leave-one-out analysis was conducted to determine which biological sensitivity attributes and exposure factors were most influential in determining a species' climate vulnerability. The overall climate vulnerability score and assigned vulnerability category (i.e., L, M, H, VH) were determined for each species after leaving out the scores one at a time for each of the 12 biological sensitivity attributes and seven exposure factors. The bootstrapping and leave-one-out analyses were conducted in R version 4.4.1 [62].

Potential for change in distribution

The potential for each species to shift its geographic distribution in response to regional changes in climate was assessed using a subset of the biological sensitivity attributes related to movement, dispersal, and habitat requirements. For example, species that are highly mobile as adults, have dispersive larval stages, low habitat specificity, and are sensitive to temperature are more likely to shift their distribution under changing environmental conditions associated with climate than are sessile or low-mobility species with specific habitat requirements, low sensitivity to temperature, and restricted dispersal of early life history stages [63]. The potential for distribution shifts was assessed by applying the same logic model described above to the scores for Sensitivity to Temperature and the inverse of the scores for Adult Mobility, Dispersal of Early Life Stages, and Habitat Specificity [53].

Results

Climate vulnerability analysis

The 71 species were about equally divided among three climate vulnerability categories (Table 1; Fig 2): Very High (31%, 22 species), High (34%, 24 species) and Moderate (35%, 25 species). This pattern was driven by the biological sensitivity attribute scores, which were about equally distributed among the Low (35%), Moderate (34%), and High (31%) categories, with only Atlantic sturgeon (*Acipenser oxyrinchus*) having Very High sensitivity (Fig 2). Climate exposure scores for nearly all species (70 out of 71) were Very High, except for Atlantic sturgeon, which had a High climate exposure score. The 22 species categorized as Very High climate vulnerability included 11 species of hermaphroditic groupers and tilefishes that occur in continental shelf and upper slope habitats, six species of invertebrates that use estuarine or nearshore reef habitats, four anadromous species that return from the ocean to freshwater habitats to spawn, and one coastal shark species currently listed as endangered on the IUCN Red list of threatened species (dusky shark, *Carcharhinus obscurus*). The High vulnerability category included a mix of demersal estuary-dependent species, hard-bottom or coral reef associated fishes, several coastal sharks, and two crab species. The Moderate vulnerability category was about equally divided between relatively small, shelf-associated, hard-bottom reef fishes and pelagic species, with the latter group including inshore estuarine species (e.g., bay anchovy, *Anchoa mitchilli*), nearshore coastal migratory species (e.g., Spanish mackerel, *Scomberomorus maculatus*), and highly migratory species with circumpolar distributions (e.g., dolphinfish, *Coryphaena hippurus*). No species was determined to have Low climate vulnerability.

Uncertainty in climate vulnerability

The bootstrap analysis indicated the climate vulnerability categories were highly robust for most species (Table 1). For example, assigned vulnerability categories were >90% certain for 70% of the species, between 66–90% certain for 23% of species, and <66% certain for only 7% of the species. Compared to the original vulnerability scores, the bootstrap results indicated higher vulnerability (i.e., VH instead of H) for common snook (*Centropomus undecimalis*) and American eel (*Anguilla rostrata*) and lower vulnerability (i.e., H instead of VH) for golden tilefish (*Lopholatilus chamaeleonticeps*). For the remaining 68 species, the most prevalent vulnerability category from the bootstrap analysis was the same as for the

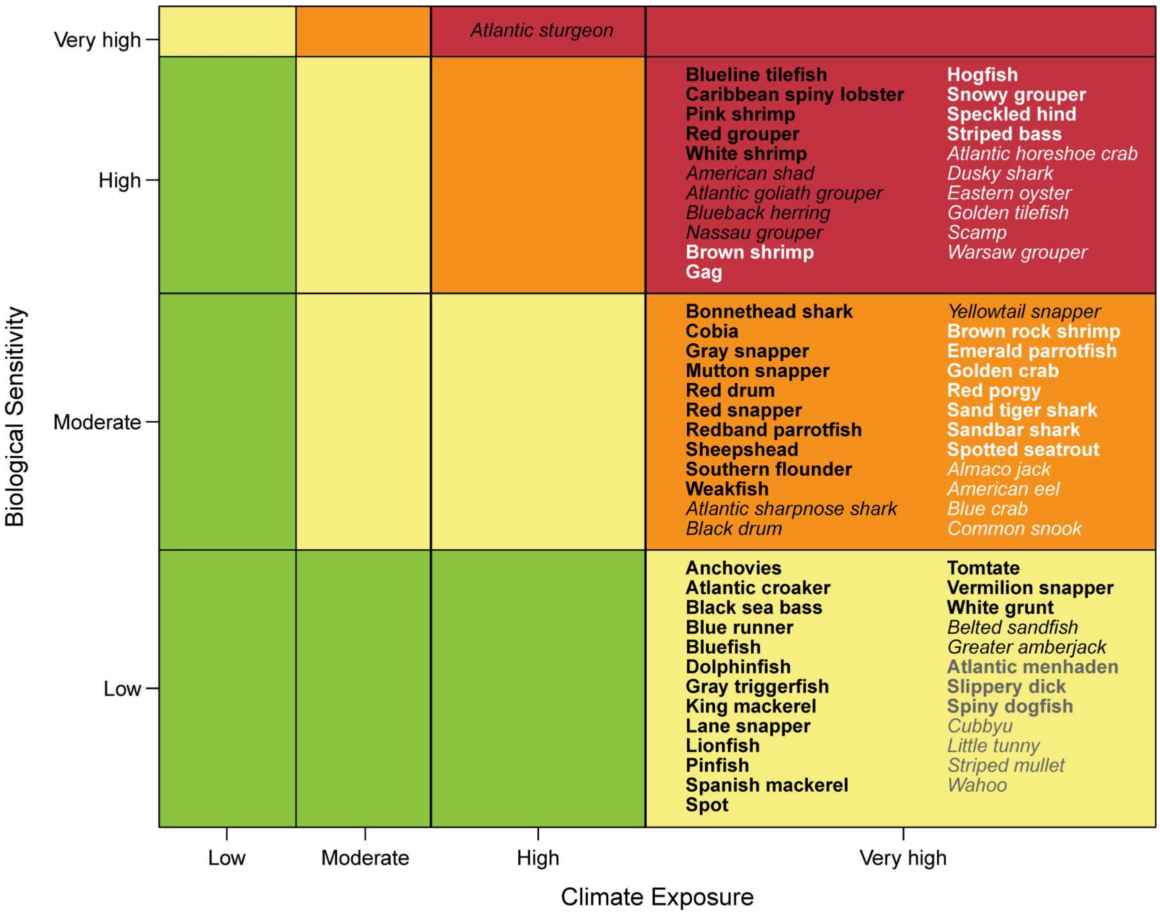

Fig 2. Overall climate vulnerability scores for 71 South Atlantic species. Colors represent Low (green), Moderate (yellow), High (orange), and Very High (red) climate vulnerability. Certainty in score is denoted by text font and text color: very high certainty (>95%, black, bold font), high certainty (90–95%, black, italic font), moderate certainty (66–90%, white or gray, bold font), low certainty (<66%, white or gray, italic font). See Table 1 for species scientific names, functional groups, management authorities, and full bootstrap results.

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original scoring. Across these 68 species, however, there was a > 25% probability of vulnerability being one category lower than assigned for seven species (black drum, *Pogonias cromis*; spotted seatrout, *Cynoscion nebulosus*; almaco jack, *Seriola rivoliana*; blueline tilefish, *Caulolatilus microps*; striped bass, *Morone saxatilis*; hogfish, *Lachnolaimus maximus*; yellowtail snapper, *Ocyurus chrysurus*), and a > 25% probability of vulnerability being one bin higher than assigned for one species (red drum, *Sciaenops ocellatus*) (Table 1).

Importance of biological sensitivity attributes and climate exposure factors

When averaged across the 71 species, the highest mean scores were for biological sensitivity attributes related to reproduction and early life history (e.g., Early Life History Survival and Settlement, Spawning Cycle, Complexity in Reproductive Strategy), while the lowest mean scores were for Prey Specificity, Sensitivity to Temperature, and Adult Mobility (Fig 3A). However, nine of the 12 attributes were scored as High or Very High for at least one species. Mean scores for Population Growth Rate and Stock Size/Status were intermediate but also showed the highest variability (i.e., largest interquartile range) across species.

There was considerable heterogeneity in mean scores both across the seven exposure factors, as well as across the 71 species in the degree of exposure to particular factors (Fig 3B). OA, Salinity, and SST had the highest mean exposure

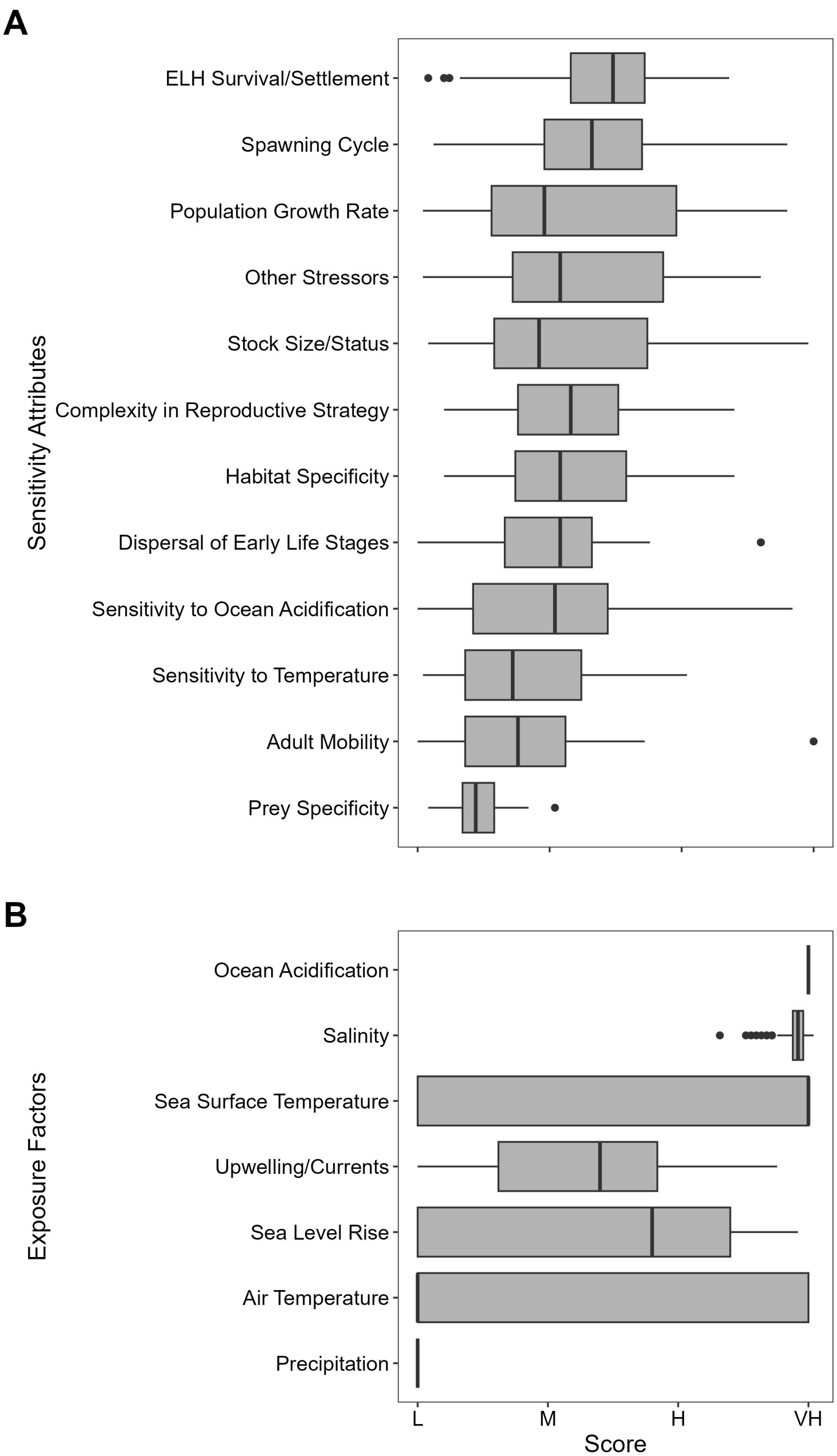

Fig 3. Distribution of (A) biological sensitivity attribute and (B) climate exposure factor scores across 71 South Atlantic species. Central bar indicates the median, shaded box indicates the 25th and 75th percentiles, whiskers indicate scores less than 1.5X the inter-quartile range, filled circles indicate outlying scores. Note the median score for SST and Air Temperature are very near the 75th and 25th quartiles, respectively. "ELH" = Early Life History.

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scores, with nearly all species considered to have high exposure to changes in OA. Mean exposure scores for Salinity and SST were also high but were more variable among species. Precipitation and Air Temperature had the lowest mean scores, with nearly all species having low exposure to changes in Precipitation. Mean scores for exposure to changes in Upwelling/Currents and SLR were intermediate, though at least some species scored Very High and some scored Low for these two exposure factors.

The leave-one-out analysis of the biological sensitivity attributes showed that Population Growth Rate was the most important attribute determining climate vulnerability, followed by Stock Size/Status, attributes related to early life history stages, and Habitat Specificity (Fig 4A). For example, removing Population Growth Rate resulted in a lower climate vulnerability ranking for 12 species (17%), mostly by one vulnerability category (e.g., H to M, or VH to H). These species included several sharks (e.g., sand tiger shark, *Carcharias taurus*; sandbar shark, *Carcharhinus plumbeus*), deepwater species (snowy grouper, *Hyporthodus niveatus*; blueline tilefish, *Caulolatilus microps*) and estuarine species (black drum; Atlantic horseshoe crab, *Limulus polyphemus*). Excluding any of the other biological sensitivity attributes altered the climate vulnerability category for <10% of the species. OA, Salinity, and SST were the primary exposure factors contributing to the climate vulnerability rankings (Fig 4B). The climate vulnerability category changed for 47 species (66%) when OA or Salinity were removed, 39 species (55%) when SST was removed, and eight species (11%) when Air Temperature was removed. No species was sensitive to Precipitation, SLR, or Upwelling/Currents.

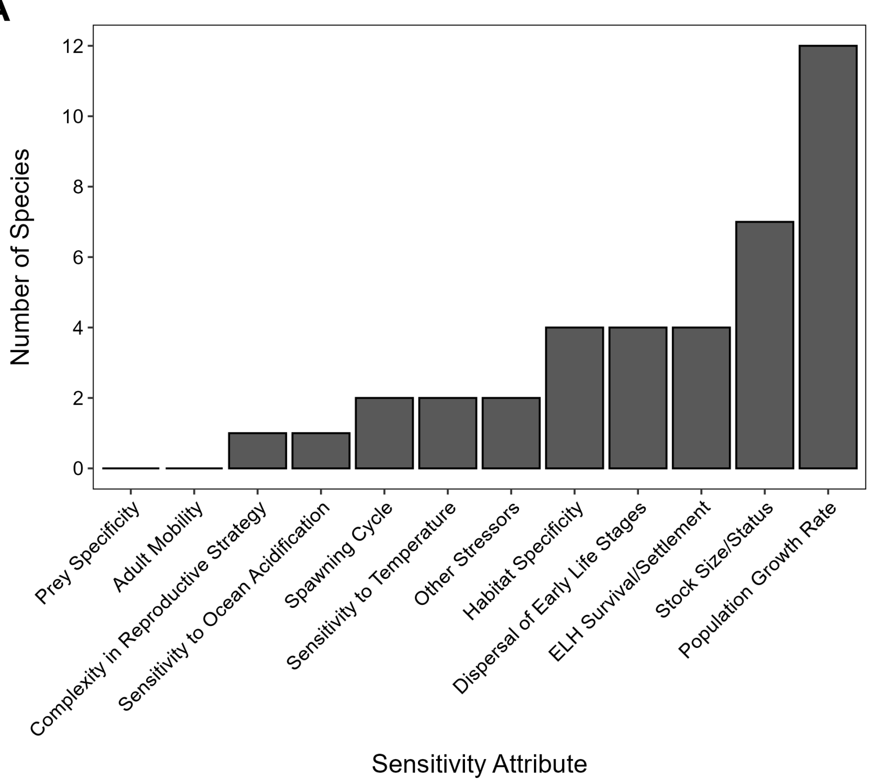
Potential for distribution shifts

The majority of species (69%, 49 species) had a Very High or High potential for shifts in distribution (Fig 5). The Very High category was composed of coastal sharks and species with ocean-basin (American eel), circumpolar (dolphinfish), or coastal (striped mullet, *Mugil cephalus*) migration patterns, while the High category included species with some combination of broadcast spawning and highly dispersed larvae (e.g., many snapper and groupers), extensive adult migrations (e.g., Spanish mackerel), or fairly generalist habitat requirements (e.g., many estuary-dependent species). Nineteen species (27%) had a Moderate potential and three species (4%) had a Low potential for shifts in distribution. Many of these species had either one or a combination of low mobility as adults (e.g., golden crab, *Chaceon fenneri*), fairly specific habitat requirements such as deepwater hard-bottom habitat (e.g., warsaw grouper, *Epinephelus nigritus*) or coral reef habitat (e.g., redband parrotfish, *Sparisoma aurofrenatum*), or specific estuarine or riverine spawning requirements (e.g., blueback herring, *Alosa aestivalis*). The bootstrap analysis indicated the potential for distribution shifts was > 90% certain for 59% of the species, between 66–90% certain for 20% of species, and <66% certain for only 21% of species (Fig 5).

Overall directional effects analysis

Based on the scoring for directional effects, over half of the species (51%, 36 species) were anticipated to be minimally impacted (i.e., Neutral) by environmental conditions associated with future climate, while negative effects were expected for 13 species and positive effects were expected for 22 species (Table 1, Fig 6). Species anticipated to be negatively affected included several diadromous species (e.g., American eel; American shad, *Alosa sapidissima*; blueback herring), benthic invertebrates with limited or low adult mobility (e.g., eastern oyster), species of conservation concern (e.g., Atlantic horseshoe crab; Atlantic sturgeon; Nassau grouper, *Epinephelus striatus*), and species where South Atlantic waters are near the southern limit (e.g., striped bass, *Morone saxatilis*; spiny dogfish, *Squalus acanthias*) or northern limit (e.g., Caribbean spiny lobster, *Panulirus argus;* Brown shrimp, *Farfantepenaeus aztecus*) of their geographic range. Species anticipated to be positively affected included several relatively small species that use estuaries (e.g., Atlantic croaker, *Micropogonias undulatus*; pinfish, *Lagodon rhomboides*; southern flounder, *Paralichthys lethostigma*) and continental shelf, hard-bottom habitats (e.g., tomtate, *Haemulon aurolineatum*; vermilion snapper, *Rhomboplites aurorubens*; gray snapper, *Lutjanus griseus*) as well as some highly migratory species (e.g., dolphinfish; wahoo, *Acanthocybium solandri*) and invasive species (i.e., lionfish, *Peterois volitans*). The bootstrap analysis indicated that none of the 71 species had

A



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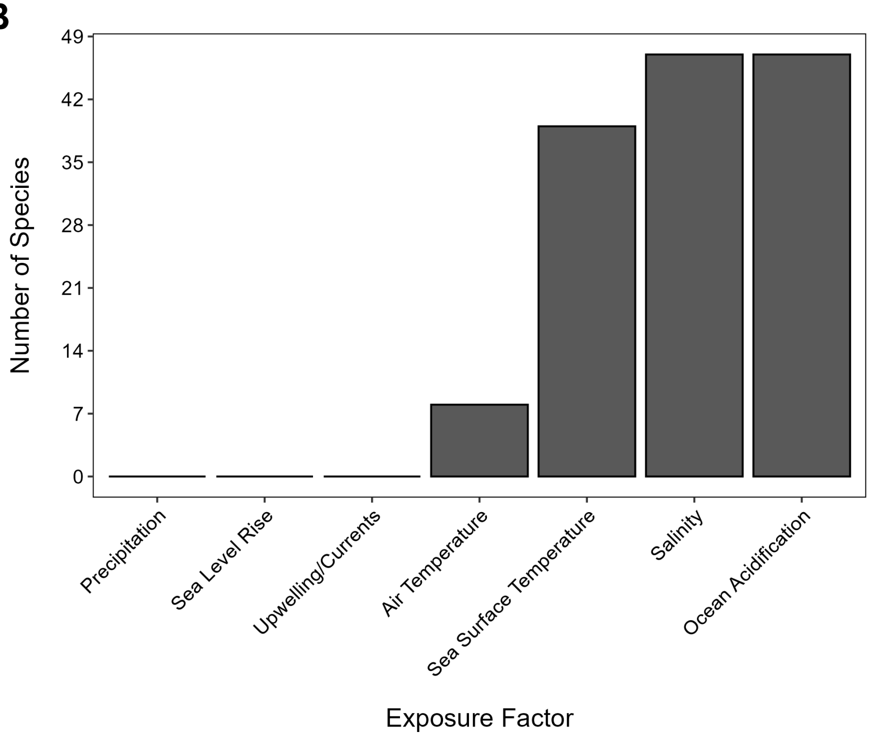

Fig 4. Leave-one-out sensitivity analysis of overall climate vulnerability to the effects of each (A) biological sensitivity attribute and (B) climate exposure factor. Y-axis indicates the number of species (out of 71) for which the climate vulnerability category changed when each factor was excluded. "ELH" = Early Life History.

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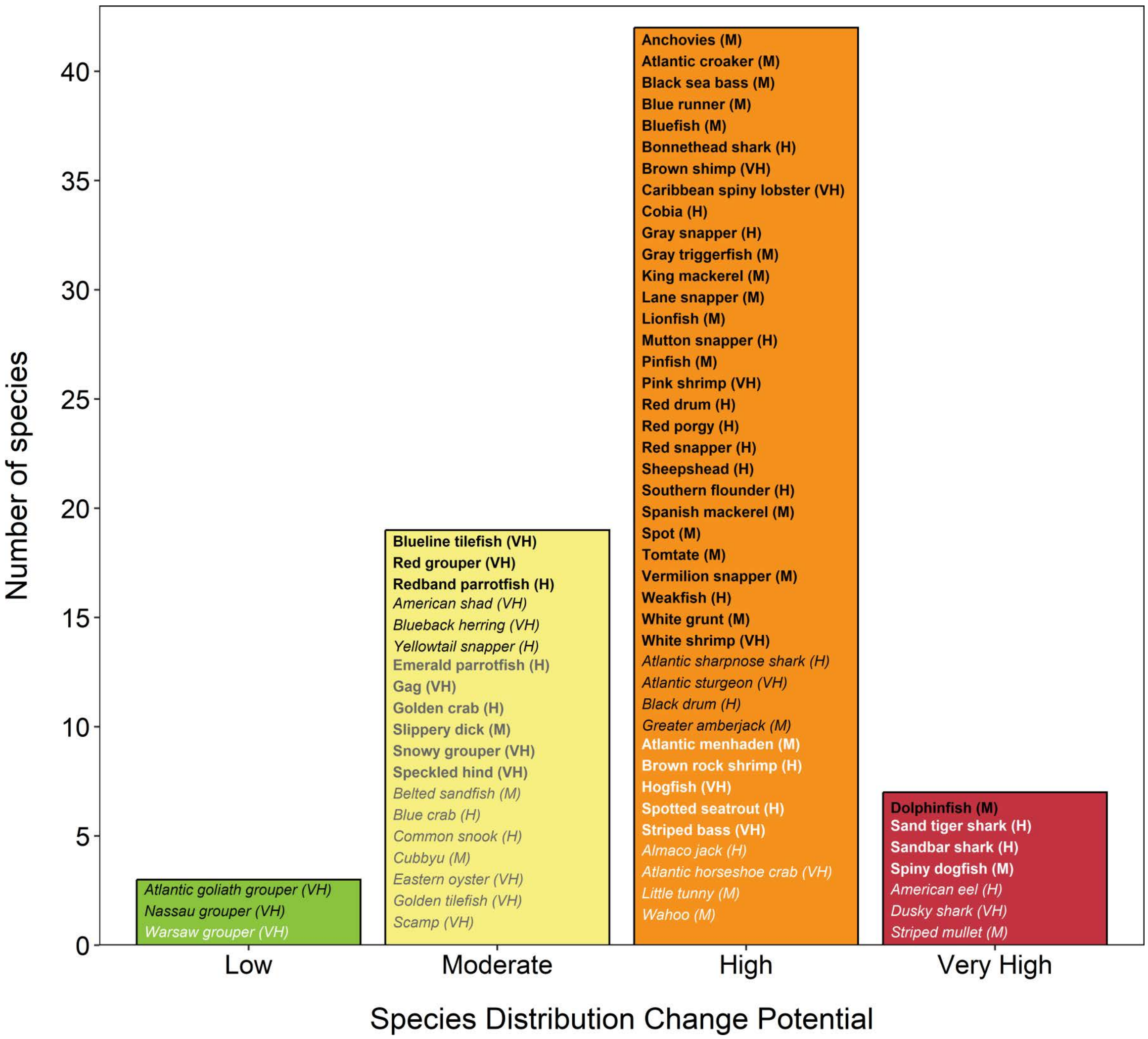

Fig 5. Potential for species distribution shifts based on a subset of biological sensitivity attributes. Colors represent Low (green), Moderate (yellow), High (orange), and Very High (red) potential for a shift in distribution. Certainty in score is denoted by text font and text color: very high certainty (>95%, black, bold font), high certainty (90–95%, black, italic font), moderate certainty (66–90%, white or gray, bold font), low certainty (<66%, white or gray, italic font). Abbreviations in () indicate the overall climate vulnerability category for each species: VH = Very High, M = Moderate, H = High, and VH = Very High.

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a higher probability of being assigned a directional effects category other than that from the original scoring (Table 2). Assignments to directional effects categories were >90% certain for 45% of the species, between 66–90% certain for 42% of species, and <66% certain for 13% of species.

Climate vulnerability of functional groups

Functional groups with High or Very High climate vulnerability were Diadromous Fish, Invertebrates, and Deepwater Reef Fish, while functional groups with mostly Moderate vulnerability were primarily pelagic and often highly migratory species (Fig 7, left column). Sharks as well as fish groups with an adult pelagic stage had High or Very High potential for distribution shifts, while Deepwater Reef Fish and Diadromous Fish had a Moderate to Low potential for distribution shifts (Fig 7, middle column). Overall, the functional groups expected to experience negative effects under future climate

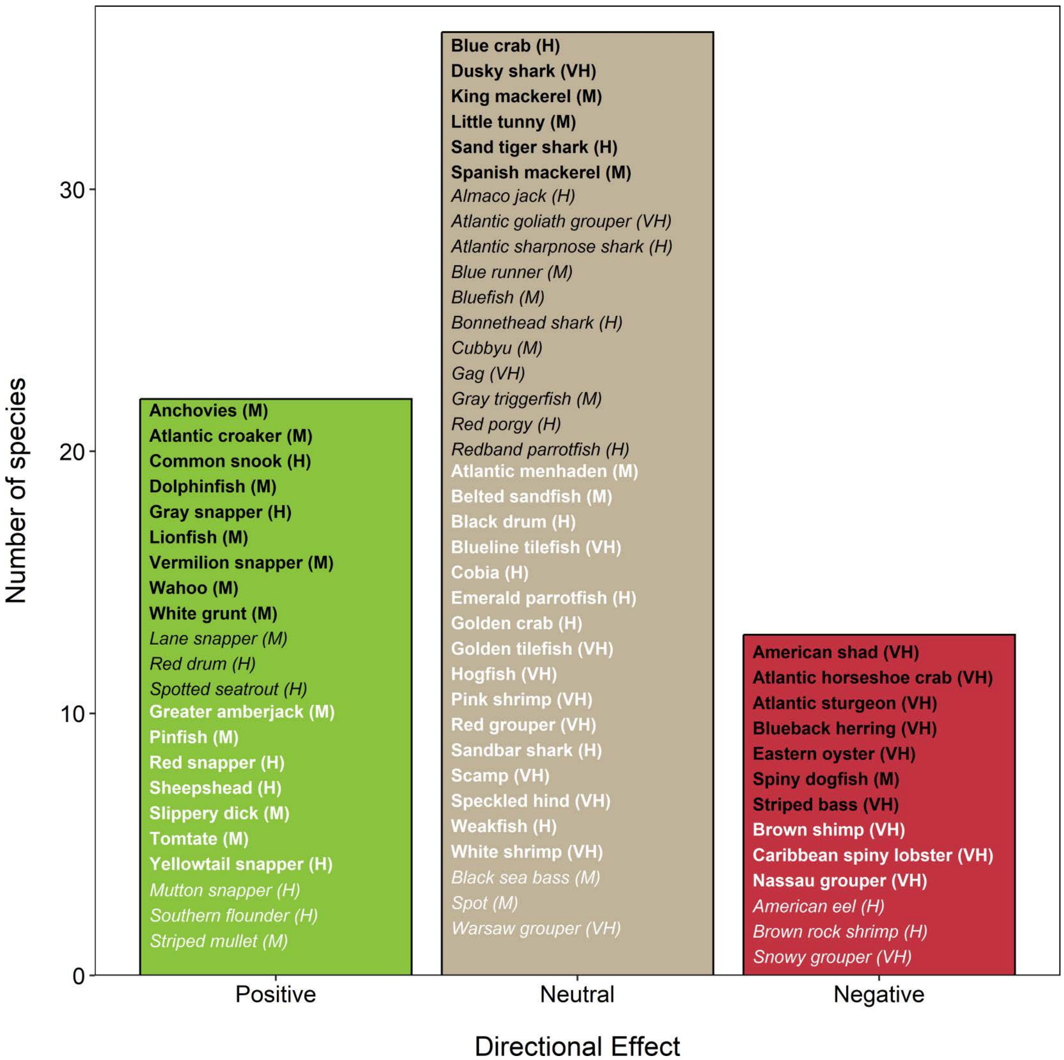

Fig 6. Directional effects of climate change for 71 South Atlantic species. Colors indicate species with anticipated neutral (tan), negative (red), and positive (green) effects of climate change. Certainty in score is denoted by text font and text color: very high certainty (>95%, black, bold font), high certainty (90–95%, black, italic font), moderate certainty (66–90%, white or gray, bold font), low certainty (<66%, white or gray, italic font). Abbreviations in () indicate the overall climate vulnerability category for each species (M = Moderate, H = High, and VH = Very High).

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were Diadromous Fish (100%) and Invertebrates (56%) while those expected to experience positive effects were Coastal Fish (70%), Pelagic Fish (67%), and Forage Fish (67%) (Fig 7, right column). Reef fish, the largest functional group (23 species), was also the most variable, and contained species in nearly all categories for climate vulnerability (Moderate to Very High), potential for distribution shifts (Low to High), and anticipated directional effects of future climate (negative to positive).

Discussion

This CVA indicates over forty species of finfish and invertebrate species (about two thirds of those considered) are highly or very highly vulnerable to projected changes associated with future climate conditions in the U.S. South Atlantic, meaning their abundance or productivity could be significantly impacted in the coming decades. The most vulnerable functional

Table 2. Anticipated directional effects of climate change for 71 South Atlantic species. Colors indicate species where the anticipated effects of climate change are negative (red), positive (green), or neutral (tan). Numbers indicate the proportion of bootstrap replicates (5,000 for each species) in each climate vulnerability category. See Table 1 for species scientific names.

		Bootstrap Results		
Species	**Original Scoring**	**Positive**	**Neutral**	**Negative**
Almaco jack	Neutral	0.08	0.92	0.00
American eel	Negative	0.00	0.43	0.57
American shad	Negative	0.00	0.00	1.00
Anchovies	Positive	1.00	0.00	0.00
Atlantic croaker	Positive	0.95	0.05	0.00
Atlantic goliath grouper	Neutral	0.02	0.92	0.06
Atlantic horseshoe crab	Negative	0.00	0.00	1.00
Atlantic menhaden	Neutral	0.00	0.69	0.31
Atlantic sharpnose shark	Neutral	0.07	0.90	0.03
Atlantic sturgeon	Negative	0.00	0.00	1.00
Belted sandfish	Neutral	0.11	0.89	0.00
Black drum	Neutral	0.32	0.68	0.00
Black sea bass	Neutral	0.00	0.58	0.42
Blue crab	Neutral	0.02	0.98	0.00
Blue runner	Neutral	0.07	0.92	0.01
Blueback herring	Negative	0.00	0.00	1.00
Bluefish	Neutral	0.03	0.94	0.03
Blueline tilefish	Neutral	0.00	0.78	0.22
Bonnethead shark	Neutral	0.00	0.92	0.08
Brown rock shrimp	Negative	0.00	0.44	0.56
Brown shrimp	Negative	0.00	0.17	0.83
Caribbean spiny lobster	Negative	0.00	0.22	0.78
Cobia	Neutral	0.32	0.68	0.00
Common snook	Positive	1.00	0.00	0.00
Cubbyu	Neutral	0.00	0.91	0.09
Dolphinfish	Positive	1.00	0.00	0.00
Dusky shark	Neutral	0.00	1.00	0.00
Eastern oyster	Negative	0.00	0.00	1.00
Emerald parrotfish	Neutral	0.15	0.85	0.00
Gag	Neutral	0.02	0.92	0.06
Golden crab	Neutral	0.12	0.88	0.00
Golden tilefish	Neutral	0.00	0.74	0.26
Gray snapper	Positive	0.99	0.01	0.00
Gray triggerfish	Neutral	0.08	0.92	0.00
Greater amberjack	Positive	0.70	0.30	0.00
Hogfish	Neutral	0.00	0.88	0.12
King mackerel	Neutral	0.05	0.95	0.00
Lane snapper	Positive	0.91	0.09	0.00
Lionfish	Positive	1.00	0.00	0.00
Little tunny	Neutral	0.00	1.00	0.00
Mutton snapper	Positive	0.57	0.43	0.00
Nassau grouper	Negative	0.00	0.31	0.69

(Continued)

Table 2. (Continued)

Species	Original Scoring	Bootstrap Results		
		Positive	Neutral	Negative
Pinfish	Positive	0.80	0.20	0.00
Pink shrimp	Neutral	0.00	0.87	0.13
Red drum	Positive	0.90	0.10	0.00
Red grouper	Neutral	0.10	0.89	0.00
Red porgy	Neutral	0.04	0.92	0.04
Red snapper	Positive	0.83	0.17	0.00
Redband parrotfish	Neutral	0.06	0.92	0.02
Sand tiger shark	Neutral	0.00	1.00	0.00
Sandbar shark	Neutral	0.00	0.79	0.21
Scamp	Neutral	0.00	0.83	0.17
Sheepshead	Positive	0.69	0.31	0.00
Slippery dick	Positive	0.80	0.20	0.00
Snowy grouper	Negative	0.00	0.42	0.58
Southern flounder	Positive	0.56	0.44	0.00
Spanish mackerel	Neutral	0.03	0.97	0.01
Speckled hind	Neutral	0.00	0.79	0.21
Spiny dogfish	Negative	0.00	0.00	1.00
Spot	Neutral	0.43	0.57	0.00
Spotted seatrout	Positive	0.90	0.10	0.00
Striped bass	Negative	0.00	0.00	1.00
Striped mullet	Positive	0.59	0.41	0.00
Tomtate	Positive	0.82	0.18	0.00
Vermilion snapper	Positive	0.98	0.02	0.00
Wahoo	Positive	1.00	0.00	0.00
Warsaw grouper	Neutral	0.00	0.61	0.39
Weakfish	Neutral	0.00	0.78	0.22
White grunt	Positive	0.98	0.02	0.00
White shrimp	Neutral	0.14	0.86	0.00
Yellowtail snapper	Positive	0.79	0.21	0.00

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groups were diadromous fishes, invertebrates, and deepwater reef fishes, but other functional groups also had species that were highly vulnerable (e.g., shelf reef fishes, sharks). Functional groups considered the least vulnerable and potentially positively affected under future climate included highly pelagic and migratory species, and nearshore and estuarine species with generalist habitat requirements and offshore broadcast spawning adults. One of the most prevalent responses of marine life to changing ocean conditions is to shift their geographic distribution [3], as has been documented or predicted for some South Atlantic species [51,52]. Indeed, we found 69% of the species considered here had a high potential for distribution shifts.

OA, SST, and salinity were the most influential exposure factors in determining climate vulnerability rankings. OA has been increasing in the South Atlantic due to a combination of increasing atmospheric CO_2, warming of continental shelf waters, and terrestrial nutrient inputs [48,64,65]. Increased acidification of marine waters negatively affects some species, for example, by impairing larval development and the calcification of hard structures (e.g., corals and shellfishes; [65–67]), but has also been shown to have little effect on other species [68]. SST is expected to continue increasing in the South

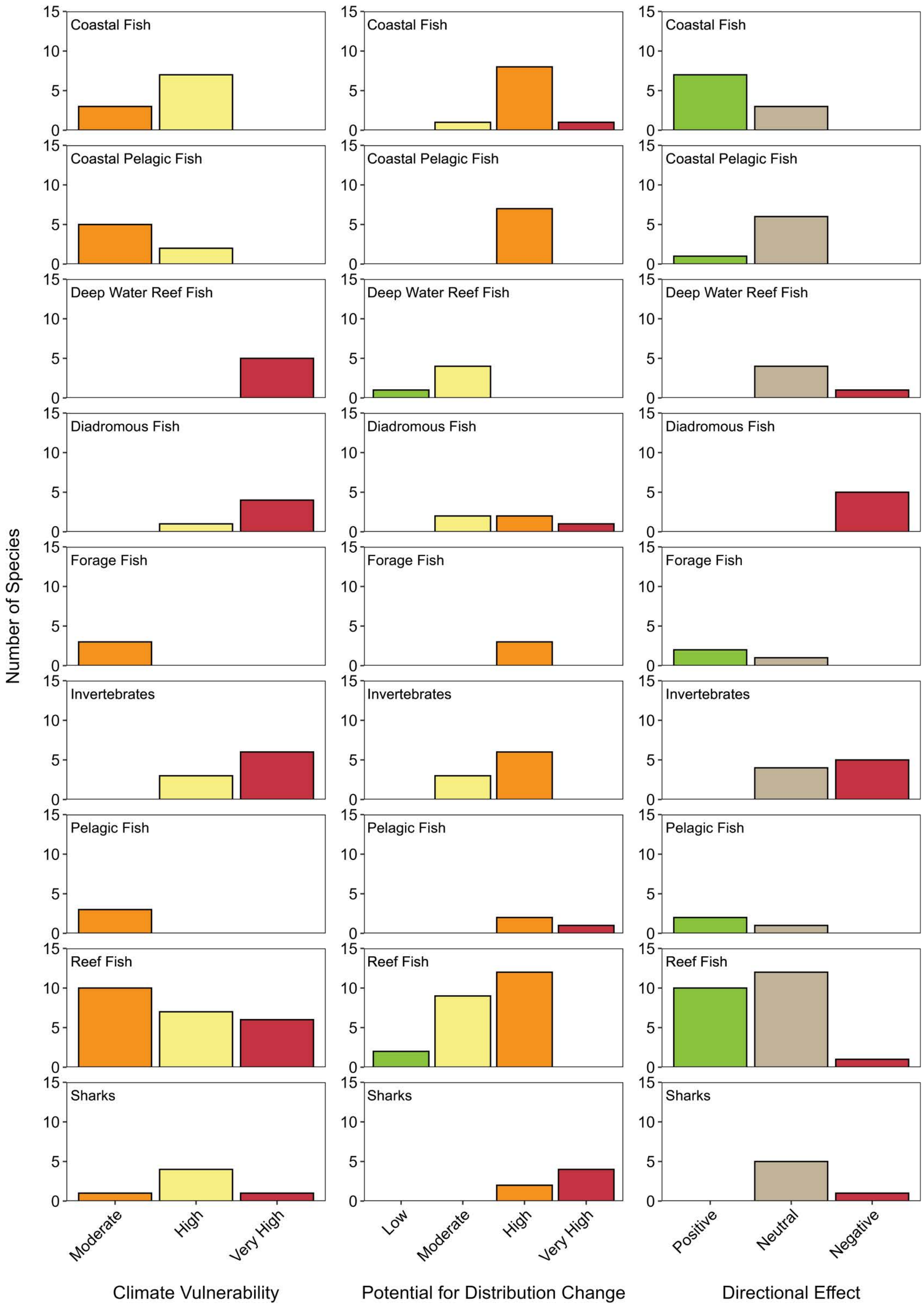

Fig 7. Functional group analysis of 71 South Atlantic species. (Left Column) overall climate vulnerability, (Middle Column) potential for distribution shifts, and (Right Column) directional effect of climate change. Y-axis is the number of species and colors correspond to x-axis categories.

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Atlantic [33,46], which can affect the physiology, oxygen demand, development, reproduction, and distribution of fishes in species-specific ways [67,69–73]. Salinity is also expected to increase in the subtropical Atlantic Ocean due to reduced precipitation and higher temperatures leading to increased evaporation [74,75]. Note that the exposure factors considered here may not only have direct effects on species, but may be indicators of other physical (e.g., stratification, nutrient upwelling) and biological (primary productivity, food availability) processes that are difficult to measure but are likely important for many species. It is also likely that interactions among the exposure factors and with other stressors influence fish and invertebrate species in the South Atlantic region.

Biological sensitivity attributes can be broadly categorized as either intrinsic (i.e., related to an organisms' life history characteristics) or extrinsic (e.g., related to attributes like stock size and population status). Biological characteristics such as intrinsic population growth rate and those related to early life history (e.g., reproduction, larval survival and settlement) had the most influence on climate vulnerability. The influence of extrinsic attributes mostly reflects the added vulnerability to climate-related environmental stressors anticipated for stocks that are also experiencing fisheries overexploitation. For example, Stock size/Population Status was particularly prominent in the vulnerability of anadromous species (e.g., Atlantic sturgeon) and several deepwater species (e.g., speckled hind, warsaw grouper) that are also considered overfished. Fishing is known to truncate population age and size structure, alter food web structure and biodiversity, and in some cases, degrade marine habitats, which can enhance sensitivity to other environmental stressors [2,69,76]. Some CVAs have excluded extrinsic attributes because of their ambiguous and indirect connection with climate [24], but certainly environmental changes associated with future climate may impede or enhance recovery from overexploitation even if these changes were not the proximate cause of population declines [77–79].

Species vulnerability based on the original scoring was altered for only a few species in the bootstrap analysis, suggesting the climate vulnerability rankings for the 71 species considered here are relatively robust. This conclusion is supported by the leave-one-out analysis, which indicated the vulnerability category changed for only 10–17% of species, and then by only one category (e.g., Very High to High), when individual sensitivity attributes or exposure factors were removed. The bootstrap analysis of directional effects (Positive, Neutral, Negative) gave similar results but generally indicated higher uncertainty in the likely response of some species to future climate conditions than the climate vulnerability analysis. For example, brown rock shrimp (*Sicyonia brevirostris*) showed nearly equal proportions of bootstrap runs in the Neutral (44%) and Negative (56%) categories, and red porgy (*Pagrus pagrus)* had bootstrap runs across all three categories. While these uncertainty analyses provide support for the climate vulnerability rankings, they pertain primarily to uncertainty associated with using thresholds and averages taken across multiple scorers, exposures factors, and sensitivity attributes to assess vulnerability [53].

Comparison of the directional effects analysis with the climate vulnerability analysis showed similarities but also important differences in how species will likely respond to future climate conditions. In general, the species expected to be positively or negatively affected under future climate agreed well with the climate vulnerability categories derived from scoring biological sensitivity attributes and climate exposure factors. For example, nearly all species for which negative directional effects under future climate were anticipated were also considered to have high climate vulnerability (spiny dogfish was the only exception). Further, no species anticipated to be positively affected under future climate was considered to have very high climate vulnerability (see Fig 6). Species anticipated to be positively affected were mostly small-bodied, rapidly growing species associated with shelf hard-bottom habitats (e.g., white grunt, *Haemulon plumierii*; tomtate), estuaries (e.g., pinfish, southern flounder), or species that are pelagic and highly migratory (e.g., wahoo, dolphinfish), while species anticipated to be negatively affected under future climate were mostly diadromous species (e.g., Atlantic sturgeon), invertebrates (e.g., eastern oyster), and reef fishes (e.g., snowy grouper).

Even so, about half of the species considered here were anticipated to be minimally affected (i.e., neutral) under future climate in the directional effects analysis, yet these same species were about equally distributed among the Moderate, High, and Very High categories in the climate vulnerability analysis. Further, more species were anticipated to experience positive effects (22 species) than negative effects (13 species) under future climate in the directional effects analysis, even though nearly two-thirds of species overall were categorized as highly vulnerable (H and VH) in the climate vulnerability analysis. Methodological differences used to characterize responses to future climate in the two analyses may be a contributing factor to these differences. The directional effects analysis is symmetrical with three categories (i.e., Positive, Negative, Neutral) and does not address the magnitude (only the direction) of species' likely responses under future climate. In contrast, the climate vulnerability analysis focuses on the magnitude of a potential negative response and the categories are progressive, with two "high vulnerability" categories (H, VH), one "moderate vulnerability" category (M), and one "low vulnerability" category (L). The intent of the additional "very high vulnerability" category (VH) is to insure species that are particularly susceptible to environmental changes associated with future climate are identified [53]. One consequence, however, could be an upward bias in the vulnerability scoring due to two "high" categories compared to one "low" category, compared to the directional effects analysis, which is symmetrical. Also, there is recent debate about the plausibility of various future CO_2 emissions scenarios [58] that could affect the climate exposure component of the climate vulnerability analysis. The RCP 8.5 scenario used here and in prior CVAs [21–24,26–28] is now considered less plausible than other more moderate emissions scenarios [80]. The use of GCM outputs from a single high-emissions scenario is another factor that may contribute to an upward bias in the climate vulnerability analysis. Alternatively, uncertainty in the directional effects analysis, which is based only on informed elicited judgement, was generally higher compared to the climate vulnerability analysis, which is based on scoring multiple factors using species-specific information (i.e., distribution maps, climate exposure factors, and biological sensitivity attributes). For example, there was $<66\%$ certainty in the directional effect of future climate for yellowtail snapper, mutton snapper, and southern flounder, which were considered to be positively affected yet also highly vulnerable under future climate conditions. Also, the high proportion of species anticipated to be minimally affected (51%) in the directional effects analysis suggests this analysis may not be particularly sensitive to how species will respond to future climate. The differences between the two analyses suggest additional uncertainty in climate vulnerability that is not captured in the bootstrap analyses. In particular, the vulnerability of the 12 species considered to be minimally affected by future climate yet categorized as highly vulnerable (Fig 6) should be considered with caution. Future work should consider additional methodological approaches, such as machine learning [81] and other data-driven approaches [82], as well as the use of GCM outputs from multiple CO_2 emissions scenarios to help reduce subjectivity and better characterize uncertainty in climate vulnerability.

Most of the assessed species were considered to have high (69%) potential for shifts in geographic distribution, while few species (4%) were considered to have low potential for distribution shifts. Most of the species considered here are broadcast spawners with relatively long (i.e., weeks) larval stage durations, which would presumably facilitate colonization of new habitats and shifts in distribution in response to changing oceanographic conditions [83]. Species without a highly dispersive egg and larval stage (e.g., diadromous fishes, some invertebrates) often had the highest climate vulnerability. Other species in the South Atlantic with limited dispersal of young, such as coastal sharks and anadromous species, are highly mobile and wide-ranging as adults, which may also facilitate shifts in distribution.

Few studies on shifting spatial distributions have been conducted for South Atlantic species. Some snapper and grouper species have shown indications of shifts in distribution to the north or south, as well as to deeper or shallower waters over the last two decades, though the role of oceanographic factors, spatial changes in productivity, or changing patterns in fishery harvest in driving these shifts is unknown [51]. For example, of the 17 species of snappers and groupers considered in both Cao et al. [51] and the current study, about half (9 species) showed evidence of distribution shifts within the South Atlantic (i.e., Cape Canaveral, Florida to Cape Hatteras, North Carolina). However, slightly more species showed shifts to the south than to the north and to shallower waters rather than to deeper waters, which is opposite to the general shift poleward and to deeper waters expected with increased warming [3,52,84]. Most notably, however, black sea bass (*Centropristis striata*), a species with high potential for distribution shifts in our analysis, showed the strongest evidence for shifts both northward and to deeper water among the species considered in Cao et al. [51]. The expansion of black sea bass populations in the U.S. Mid-Atlantic and Northeast shelf regions in association with warming temperatures has been well-documented, suggesting this species may be shifting or expanding its geographic range [14,85–87]. Other snapper and grouper species are strongly associated with structured bottom habitat, and whether suitable settlement habitat exists beyond these species' current geographic range [88], or whether they will respond to increasing temperatures [89], is largely unknown. Some estuary-dependent species that are common in northern areas (Atlantic croaker, [90]; summer flounder, *Paralichthys dentatus*, [91]) and southern areas (gray snapper, [92]) of the South Atlantic show evidence for range shifts. For example, a commercially viable fishery for white shrimp (*Litopenaeus setiferus*) has developed in Chesapeake Bay since the late 2010s [93] consistent with climate projections indicating penaeid shrimp thermal habitat will expand to the north [94]. Similar shifts in distribution across management jurisdictional boundaries may be expected for other species where the South Atlantic is at the northern limit (e.g., Caribbean spiny lobster) or southern limit (e.g., striped bass, spiny dogfish) of species' geographic ranges.

About half of the species considered here were also included in an analysis of projected shifts in thermal habitat for multiple North American large marine ecosystems over decadal times scales (i.e., to year 2100; [52]). In Morley et al. [52], projected shifts for South Atlantic species were much smaller than for more northern species, perhaps due to the anticipated slower rate of warming in more southern compared to more northern continental shelf ecosystems [33]. Nearly all of the 31 species in common between this CVA and Morley et al. [52] had a high potential for distribution shifts and were projected to shift northward in the coming decades, though the magnitude of the projected shifts are highly uncertain (see S1 appendix in [52]). Additional work is needed to reconcile potential shifts in distribution and the underlying mechanisms across different temporal and spatial scales in the South Atlantic and along the U.S. Atlantic seaboard.

Other CVAs using similar methods to the current study [21–25] showed both similarities and differences with the results reported here. Benthic invertebrates and diadromous species were among the most vulnerable functional groups for both the South Atlantic and the Northeast shelf, probably due to the low mobility and specific spawning habitat requirements of these two groups. Benthic invertebrates were also the most vulnerable functional group in a CVA for the northern Humboldt Current ecosystem [21] and in California state waters [28], while diadromous species were considered highly vulnerable for the California Current ecosystem [24]. OA and SST were important drivers of vulnerability for both the South Atlantic and Northeast shelf, and have been highly ranked among exposure factors in climate vulnerability assessments for other large marine ecosystems [21,24,25]. In contrast, salinity was an important exposure factor in the South Atlantic, but was only of moderate importance for the Northeast shelf and in other regions, perhaps reflecting the large number of species in the South Atlantic that use riverine, estuarine, and oceanic habitats at different life stages. Population Growth Rate was the most important biological sensitivity attribute contributing to the climate vulnerability of species in the South Atlantic, as has been found in some other CVAs [23–25], followed by aspects of the early life history (e.g., larval dispersal, survival of juveniles, settlement habitat requirements). This pattern reflects the importance of life history traits along the fast-slow continuum (*sensu* [95]) in mediating population responses to environmental change associated with climate [96–98].

There are several caveats to consider in the use of trait-based CVAs to assess vulnerability to future climate conditions. Use of informed elicited judgement has a long history in environmental science and can be an important source of information when data are limited [99–102]. However, results based on informed judgement can be affected by the particular panel selected [103], the method of elicitation [104], and the analytical approach used [105]. In addition, while considered the best available information at the time of this assessment, the data used here varied in terms of availability, quality, spatial scale, and the life stages for which they were collected [54]. Further, projections of future ocean conditions are highly uncertain, particularly at the scale of regional ocean features and coastal habitats important to many species [106–107]. As a result, the vulnerability rankings developed here may change as better information on future climate conditions and the responses of individual species to environmental drivers becomes available. Our results are best interpreted as a relative ranking of a set of chosen species' vulnerability to current projections of future climate conditions in the South Atlantic region.

This CVA can help inform how future climate in the South Atlantic will affect fisheries management, including recent initiatives to understand and mitigate cross-jurisdictional fisheries governance issues along the U.S. Atlantic seaboard [108]. Given the widespread potential for distribution shifts, we recommend the development and regular updating of species distribution models [51] for those species considered highly vulnerable to future climate conditions, and particularly those species that are of interjurisdictional management importance [109]. Environmental and oceanographic variables potentially affected by changes in climate have not been formally incorporated into the scientific advice informing the management of species in the South Atlantic. Results from this CVA can help prioritize species for the development and testing of management strategies that are robust to future changes in climate [110]. Finally, our results can be combined with other sources of risk (e.g., overfishing) in a formalized ecosystem-level risk assessment [17] or to inform other types of vulnerability assessments (habitat, [14]; social, [15]). Such efforts can help prioritize species and management issues in terms of the cumulative risk posed to meeting fisheries management objectives, hence, providing important strategic management advice [8]. Given that fishing-dependent communities are economically and socially vulnerability to changes in climate [15], effective and informed advice is a necessary prerequisite for building and maintaining resilient coastal communities.

Supporting information

S1 Data. Dataset. Climate vulnerability and directional effects scoring data.
(XLSX)

S1 Text. Supporting information. Description of climate exposure factors and biological sensitivity attributes.
(PDF)

S2 Text. Supporting information. General Climate Model (GCM) outputs for the five quantitative exposure factors.
(PDF)

S3 Text. Supporting information. Narratives for climate exposures factors: Sea Level Rise and Upwelling/Currents.
(PDF)

S4 Text. Supporting information. Species narratives.
(PDF)

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Author contributions

Conceptualization: J. Kevin Craig, Brendan J. Runde, Nathan M. Bacheler, Michael L. Burton.

Investigation: J. Kevin Craig, Brendan J. Runde, Nathan M. Bacheler, Michael L. Burton, Roldan C. Munoz, John A. Quinlan, Mark W. Nelson, Samantha M. Binion-Rock, G. Todd Kellison, Joseph W. Smith, R. Wilson Laney, George R. Sedberry, James W. Morley, Steve Poland, Russell Brodie, Lauren Gentry, Karla Gore, Jason E. Rock, Matthew Johnson, Jared Flowers, Chip Collier.

Methodology: Brendan J. Runde, Mark W. Nelson.

Project administration: J. Kevin Craig.

Writing – original draft: J. Kevin Craig, Brendan J. Runde, Nathan M. Bacheler, Michael L. Burton.

Writing – review & editing: J. Kevin Craig, Brendan J. Runde, Nathan M. Bacheler, Michael L. Burton, Roldan C. Munoz, John A. Quinlan, Mark W. Nelson, Samantha M. Binion-Rock, G. Todd Kellison, Joseph W. Smith, R. Wilson Laney, George R. Sedberry, James W. Morley, Steve Poland, Russell Brodie, Lauren Gentry, Karla Gore, Jason E. Rock, Matthew Johnson, Jared Flowers, Chip Collier.

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