

Range expansion of the invasive lionfish in the Northwest Atlantic with climate change

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ABSTRACT: Growing populations of invasive lionfishes *Pterois volitans* and *P. miles* have had detrimental impacts on native marine fish communities and transformed many of the reef ecosystems of the Northwest Atlantic Ocean. Over the last 3 decades, suitable environmental conditions and lack of natural biological controls have allowed lionfish populations to expand into areas ranging from the tropical waters of the Caribbean to the northern portions of the shelf break along the Southeast United States Continental Shelf (SEUSCS) during all months of the year. Under current climate conditions, continued expansion to waters further north or inshore from the shelf break is unlikely, given the physiological thermal tolerance of lionfish and the cooler temperatures of these waters. However, the geographic range of suitable environments may expand in the future with climate change. Here, we develop a conceptual model of the physical climate niche of lionfish and use projections of future ocean temperatures and salinities to explore potential lionfish habitat through the year 2100 under conditions of anthropogenic climate change. Without successful culling efforts or implementation of climate-change mitigation strategies, the spatial extent of suitable year-round lionfish habitat is expected to increase 45 % on the SEUSCS during the 21st century, covering 90 % of the region. Establishment of resident populations north of Cape Hatteras is unlikely. Nevertheless, in the coming decades, the potential impact of continued lionfish invasion on the valuable marine ecosystems of the SEUSCS is cause for concern.

KEY WORDS: Lionfish · Climate change · Biogeography · Invasive species · Southeast United States Continental Shelf · CMIP5

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INTRODUCTION

Climate change and variability have been associated with shifts in the geographic ranges of many species (Parmesan 2006, Thomas 2010), including marine fishes (Perry et al. 2005, Rose 2005, Nye et al. 2009, Pinsky et al. 2013). Continued warming is anticipated in the coming decades in response to anthropogenic emissions of greenhouse gases (IPCC 2013), and there is growing concern that future climate change will alter the distributions and productivity of fish species around the globe (Loukos et al. 2003, Cheung et al. 2009, 2010, Hare et al. 2012b).

In addition to these concerns, invasive species further threaten the health of marine ecosystems. Indo-Pacific red lionfish *Pterois volitans* and the morphologically similar devil firefish *P. miles* (hereafter collectively referred to as lionfish) were the first major marine fish invaders to become successfully established in the Northwest Atlantic Ocean (Whitfield et al. 2002). Lionfish were first spotted near Southeast Florida in the mid-1980s and have since spread throughout the continental shelves of the southeastern United States, Bermuda, The Bahamas, the Caribbean Sea, and the Gulf of Mexico (Schofield 2009, 2010, Morris & Akins 2009; for current sight-

ings see the online database Schofield et al. 2015b). The temperature and salinity tolerances of lionfish indicate that the species could survive as far south as Uruguay (Morris & Whitfield 2009), and recently one Caribbean-spawned adult lionfish was found off the coast of southern Brazil (Ferreira et al. 2015).

Ecologically, lionfish possess a unique appearance and hunting strategy (Morris et al. 2009, Albins & Lyons 2012), venomous spines that discourage predation by local predators (but see Maljković et al. 2008, Diller et al. 2014), high fecundity (Morris et al. 2009, 2011), and a wide range of habitat preferences (Fishelson 1975, Jud et al. 2011, Claydon et al. 2012). These traits, along with a generalist diet (Morris & Akins 2009, Muñoz et al. 2011), likely contribute to their invasion success and have resulted in the reduced abundance, recruitment, and diversity of native prey fishes (Albins & Hixon 2008, Green et al. 2012, Albins 2013). Lionfish may also affect the abun-

dance and behavior of commercially and ecologically important predators in the region, such as snapper and grouper, by competing with them for food and space (O'Farrell et al. 2014, Raymond et al. 2015).

In the Northwest Atlantic, lionfish are now well established on the continental shelf from South Florida to Cape Hatteras, North Carolina (Whitfield et al. 2007, 2014, Schofield 2009, 2010), a region known as the Southeast United States Continental Shelf (SEUSCS; 25 to 35.5° N). The SEUSCS exhibits a unique oceanographic climatology due to the influence of the warm Gulf Stream flowing northwards along the shelf break. During the winter months (December to March), an inshore–offshore temperature gradient develops between the cold, nearshore waters and the relatively warm waters of the Gulf Stream. These warm, offshore waters provide a refuge for lionfish while the well-mixed, shallow inshore waters are uninhabitable due to cold temper-

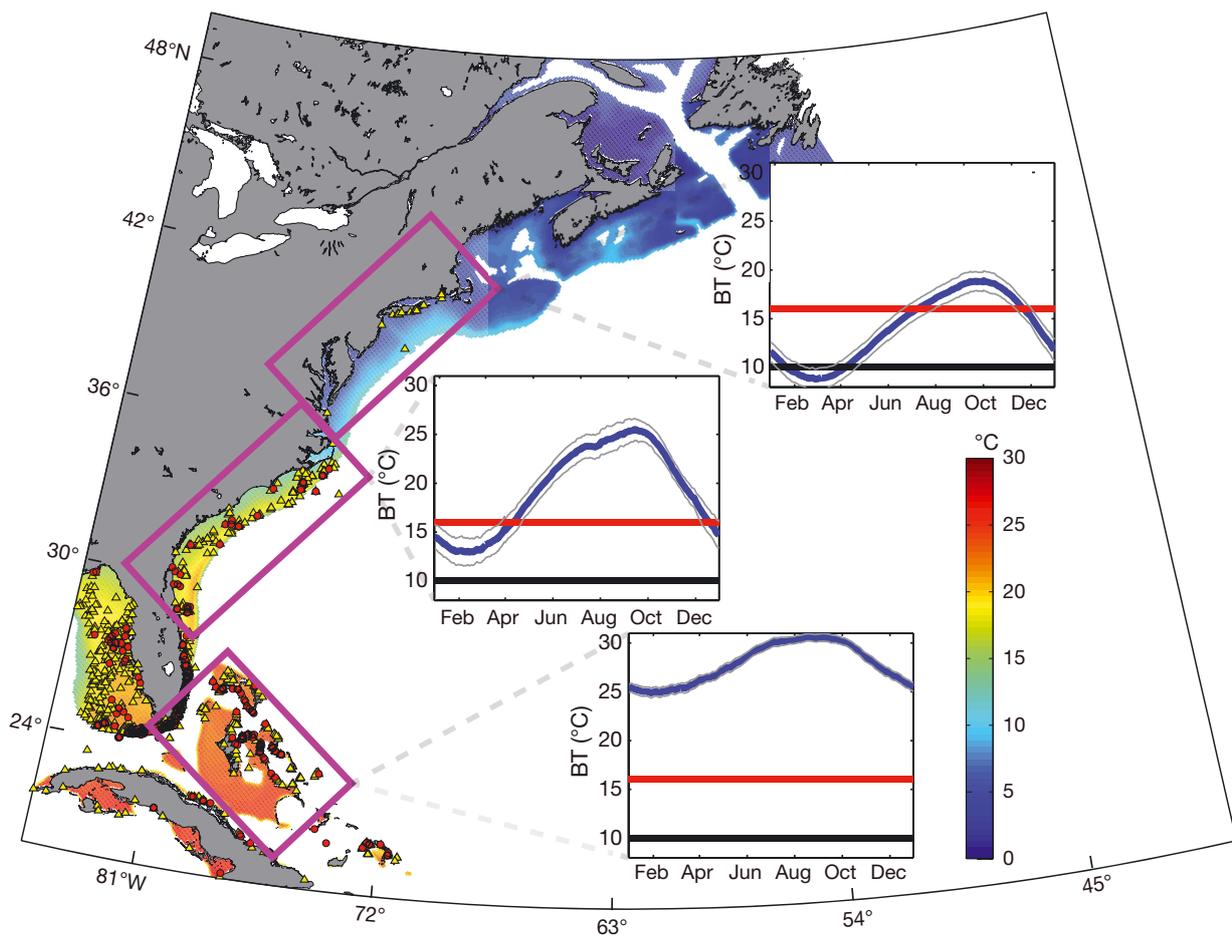


Fig. 1. Lionfish sightings and present-day mean winter (December to March 1987 to 2006) bottom water temperatures (BTs) on the Northwest Atlantic continental shelf (waters <200 m depth). Yellow triangles: summer lionfish observations; red circles: winter observations (Schofield et al. 2015b). The 3 time series illustrate daily averages of BTs on the continental shelf for example regions (boxed in pink) compared to critical physiological thermal limits for lionfish. Blue bold lines: BTs; thin gray lines: BTs \pm 1 SD; black horizontal lines: 10°C lethal minimum temperature for lionfish; red horizontal lines: 16°C lower feeding threshold (Kimball et al. 2004)

atures (Whitfield et al. 2002, 2014, Meister et al. 2005, Muñoz et al. 2011). This thermal gradient is reversed in the summer months (June to September), as the temperature of the shallow nearshore waters increase, allowing adult lionfish to move further inshore (Atkinson et al. 1983, Whitfield et al. 2007, Schofield 2009). Lionfish larvae are occasionally advected northward by the Gulf Stream and warm-core eddies (Hare et al. 2002), and young-of-the-year juveniles have been observed as far north as Long Island, New York during summer and fall months (Fig. 1, Whitfield et al. 2002). However, these individuals do not survive the harsh winters, and breeding populations have not been established north of Cape Hatteras (Kimball et al. 2004, Schofield 2009).

The waters of the Northwest Atlantic are expected to increase in temperature with future climate change (IPCC 2013), potentially permitting the species to invade new habitats in the coming decades. This range expansion, along with increased prey consumption by lionfish due to the increased metabolic rates associated with warmer water (Côté & Green 2012), could have severe negative consequences on the native ecosystems of the Northwest Atlantic.

Given the observed response of other fishes' distributions to climate change, it is expected that the range of invasive lionfish will shift as well. Specifically, we expect lionfish distributions to move further inshore and poleward as bottom temperatures warm in the future (Whitfield et al. 2014). Here, we seek to explore the sensitivity of the lionfishes' range to future changes in physical conditions along the continental shelf of the Eastern United States. We used an ensemble of 17 different climate models to investigate future bottom water temperatures (BTs) and salinities under different climate scenarios, and examined changes in the spatial and seasonal distribution of the fundamental niche of lionfish based on experimentally derived physiological tolerance limits. This approach is similar to a method previously used to estimate future distributions of the gray snapper *Lutjanus griseus* (Hare et al. 2012b).

MATERIALS AND METHODS

To explore the sensitivity of suitable lionfish habitat to future climate change, we required estimates of current BTs and salinities along the Northwest Atlantic continental shelf, projections of future changes in these properties in response to anthropogenic climate change, and a model describing the dependence of lionfish habitat on ocean conditions.

Projections of future changes in BTs and salinity

We obtained ocean temperature and salinity data from global coupled atmosphere–ocean general circulation models developed as part of the Climate Model Intercomparison Project phase 5 (Taylor et al. 2012) associated with the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2013). These data were provided by the Program for Climate Model Diagnosis and Intercomparison (PCMDI). For this analysis, we used climate models simulating historical (1987 to 2005) and future (2006 to 2100) time periods. The climate models for the future time period were forced with 2 Representative Concentration Pathways (RCPs): RCP 8.5 and RCP 4.5. RCPs represent the evolution of future changes in the amount of energy retained at the earth's surface based on temporal changes in a variety of factors such as greenhouse gas emissions, land use, and population growth (Moss et al. 2010, van Vuuren et al. 2011). RCP 8.5 represents a 'business-as-usual' scenario with no significant reductions in fossil fuel use, while RCP 4.5 represents an intermediately 'optimistic' scenario in which global greenhouse gas emissions reach a maximum during the 2040s and then decline during the second half of this century (Moss et al. 2010). Of the models that contributed to the PCMDI database, 17 had unique projections of hydrographic properties at monthly temporal resolution for both the historical and RCP 8.5 scenarios. Of these 17 models, 11 also had accompanying output for the RCP 4.5 scenario (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m546p225_supp.pdf).

The current generation of global general circulation models are relatively coarse in their spatial resolution (with horizontal grid spacing ranging from 0.5 to 1.4°; Table S1), and this resolution may inhibit proper representation of conditions along continental shelves. To improve representation of these habitats, coarse-resolution climate model simulations were statistically downscaled for the region of interest using a relatively high-resolution (ca. 7 × 7 km) Regional Ocean Modeling System (ROMS) simulation of the Northwest Atlantic hindcast over the 1958 to 2007 period (Kang & Curchitser 2013). Reanalysis data from the Simple Ocean Data Assimilation (version 2.1.6; Carton & Giese 2008) provided the initial and oceanic boundary conditions for this ROMS configuration. Air–sea fluxes were computed from the Coordinated Ocean-ice Reference Experiment (version 2; Large & Yeager 2009). The vertical dimension was represented with 40 terrain-following levels with

mixing determined by the K-profile parameterization (Large et al. 1994), and bathymetry derived from the 1' resolution Shuttle Radar Topography Mission (Farr et al. 2007).

Here, we used the last 20 full wintertime periods of the ROMS simulation (1987 to 2006) to create a high-resolution climatology (i.e. monthly mean and standard deviation, SD) of present-day conditions (BTs and salinity) for the Northwest Atlantic. We then used this high-resolution climatological information and applied the delta method (e.g. Hamlet et al. 2010, Hare et al. 2012a; Fig. S1 in the Supplement) to downscale the coarse-resolution data produced by the global climate models. In this approach, the present-day (1987 to 2006) conditions simulated by each climate model were subtracted from that model's simulation of conditions during the future period (2081 to 2100) to yield the projected change in conditions (i.e. the 'delta' BTs and salinity, referred to simply as the delta). The delta for each model was then re-gridded using nearest neighbor interpolation and added to the present-day climatology derived from the ROMS simulation, providing a high-resolution projection of the future evolution of BT and salinity in the Northwest Atlantic as represented by each global climate model. As our question of interest concerned long-term change associated with anthropogenic warming (and not changes related to interannual variability that may be associated with the North Atlantic Oscillation or meandering of the Gulf Stream), 20 yr averages were used to represent mean climate conditions. Additionally, we used multi-model averages of changes in conditions to explore variability in habitat area. This multi-model approach is often considered more accurate than approaches using single models (Randall et al. 2007, Reichler & Kim 2008), and the level of agreement among models can be used to provide an estimate of uncertainty in future habitat projections (e.g. Wethey et al. 2011).

The global climate models produce output at 4 or 6 h intervals, and these data were used to generate monthly averages that contributed to the PCMDI database. However, higher-frequency cold events (e.g. synoptic-scale events such as wintertime cold fronts) may be important when considering physiological stress on lionfish. Likewise, warm events that are short in duration may allow the activity of a torpid individual to increase to a level that permits sufficient feeding. In order to include consideration of events occurring at frequencies higher than those resolved by the monthly averages available from the PCMDI database, we calculated the SD of daily ROMS BT from the monthly mean at each modeled

location. This SD was later applied to consider the likelihood that high-frequency cold events (not represented by the monthly mean BT) would limit lionfish distribution in a region.

Lionfish distributions

Lionfish are habitat generalists that can survive under a variety of biological conditions. Here, we assume that the continental shelf habitats potentially susceptible to invasion contain suitable structural habitat, available prey, and no significant habitat limitation due to predation. Given the array of habitats in which lionfish thrive (Barbour et al. 2010, Jud et al. 2011, Claydon et al. 2012, Cure et al. 2014) and the variety of food items they consume (Morris & Akins 2009, Muñoz et al. 2011, Layman & Allgeier 2012), we believe these to be reasonable assumptions for exploration of potential habitat. Previous work on the species in its native range has noted a lack of correlation between presence of lionfish and rugosity, current speed, wave action, distance to freshwater sources, and proximity to other predators, including fellow lionfish (Cure et al. 2014). The same lack of correlation is true with structured habitat in the invaded range, with the exception of wave action (Anton et al. 2014). Prolonged exposure to low salinity (~10) does not alter lionfish behavior or physiology, but anything lower is considered fatal (Jud et al. 2015, Schofield et al. 2015a). Lastly, lionfish are a demersal species, so BT is believed to be more representative of their habitat than sea-surface temperature. Indeed, on the SEUSCS, surface temperatures appear to be poorly associated with lionfish presence in water deeper than 30 m (Kimball et al. 2004).

Based on this information, BT and present-day salinity are believed to be the primary factors influencing the fundamental niche of lionfish. Kimball et al. (2004) estimated that lionfish cease feeding under conditions colder than 16°C and die at ~10°C. The length of time at which lionfish can survive starvation (i.e. at temperatures colder than 16°C but warmer than 10°C) has not been determined, but Fishelson (1997) observed a group of adults that all survived 3 mo in experimental aquaria without feeding before cessation of the experiment. A study conducted in North Carolina waters tagged an established lionfish population over the course of a year and found lionfish overwintering for 3 mo in 14 to 16°C waters (Bacheler et al. 2015). The experiment also found high site fidelity for lionfish, as did Jud & Layman (2012). Therefore, periods of 3 mo during which tempera-

tures are between 10 and 16°C may be tolerable by adult lionfish.

A climate-niche model was created using salinity and BT thresholds supported by the observations described above. Areas (7 × 7 km) were considered potentially inhabitable by lionfish as long as the present-day salinity always exceeded 10 and the mean monthly BT – 1 SD (to account for daily variability in BT) never fell below the 10°C lethal minimum. If an area met these minimum criteria, we then calculated the number of months during which conditions were optimal for lionfish. We considered a period ‘optimal’ when the mean monthly BT + 1 SD was greater than 16°C. Optimal months per year were calculated using the ROMS simulation for present-day conditions (1987 to 2006) and for each downscaled climate projection in the 2041 to 2060 and 2081 to 2100 time periods. Because projected changes in salinity are small (~0.5 to 1.0 unit increase) throughout the region (IPCC 2013), this change was not believed to influence future lionfish distributions on the SEUSCS and was not considered further.

Modeled areas with potential lionfish habitat under present-day conditions were compared with lionfish sightings reported to the United States Geological Survey Nonindigenous Aquatic Species database (USGS-NAS; Schofield 2009, 2010, Fuller & Neilson 2015, Schofield et al. 2015b). Based on this comparison of the season of lionfish sightings and the duration of optimal months over the seasonal cycle (Fig. 2), we considered areas as habitable year-round if they experience 11 or 12 optimal months per year, seasonally habitable at 9 or 10 mo yr⁻¹, and potentially habitable at 8 mo yr⁻¹. Areas with fewer than 8 optimal months per year were not considered habitable. Results are presented using a single monthly BT derived from the average of all climate models in each time period, then repeated with individual climate models to display model agreement on a given range projection. In the latter scenario, total habitable area was calculated to include all areas where at least 50% of the models indicated habitable conditions.

Assessment of ROMS BT accuracy

Present-day BTs in the ROMS simulation were compared with NOAA winter, spring, and autumn bottom trawl survey data from 2003 to 2006. In these surveys, bottom trawls were conducted throughout the Northeast United States Continental Shelf in February, March, April, September, and October in

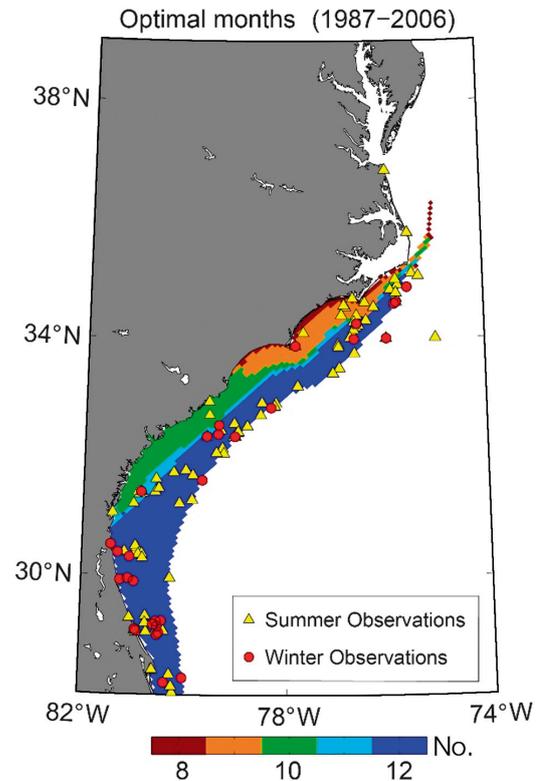


Fig. 2. Number of optimal months per year (i.e. when bottom water temperatures, BTs > 16°C) suitable for lionfish in the present-day (1987 to 2006) period. Summer (June to September) and winter (December to March) lionfish sightings are indicated with yellow triangles and red circles, respectively. An area with 11 or 12 optimal months per year is considered suitable habitat for lionfish year-round, 9 to 10 mo yr⁻¹ may be vulnerable to lionfish invasion seasonally, and 8 mo yr⁻¹ is considered the fewest months necessary for lionfish survival. Sightings of juvenile lionfish occur outside of these regions, but those individuals are not expected to survive winter periods

an unrelated effort to census fish abundance and diversity. Water temperature and depth were sampled during each trawl using a CTD (conductivity, temperature, and depth) instrument. These data were obtained from the resource survey reports of each expedition from the NOAA Northeast Fisheries Science Center website.

BTs sampled during the trawl surveys were matched to approximate locations in the ROMS simulation. For each point, the 4 yr (2003 to 2006) monthly average BTs from the ROMS simulation were recorded to develop observed and modeled climatological series that could be compared. If there were multiple temperature observations for each point across years, they were averaged. If the depth of the sample and the depth represented in the model grid were not within 50 m of one another, that sample was discarded; this occasionally occurred on the

shelf break where water depth changes rapidly with horizontal distance, and large discrepancies may exist between actual depth and depth represented by the model's 7×7 km grid spacing. The resulting datasets were all analyzed together, as well as stratified by month and depth in order to examine the sensitivity of model accuracy to these characteristics. Comparisons were analyzed using a non-parametric Wilcoxon signed ranks test for paired data ($\alpha = 0.05$), testing the null hypothesis that the model's monthly mean BT was not significantly different from the observed BT. Data did not meet normality assumptions required for parametric statistics.

RESULTS

Assessment of ROMS BT accuracy

Over the 2003 to 2006 period of NOAA trawl surveys examined here, there were 2395 samples suitable for comparison with the ROMS climatology developed for the same time period. Across all samples, the ROMS model averaged 0.06°C warmer than the observations, with some seasonal and bathymet-

ric variation. According to a Wilcoxon signed ranks test, the observed BTs were not significantly different than those in the model ($N = 2395$, $p = 0.42$), indicating that the ROMS simulation provides a suitable present-day representation of BTs on the continental shelf. Of the 5 months tested, only BT bias during February was greater than 0.1°C . Modeled BTs during February were 0.38°C warmer than the observations, and February was the only month for which modeled BTs were significantly different from observations ($N = 308$, $p < 0.01$). This bias is still rather small, as it is less than the average daily SD of 0.71 on the SEUSCS in February. The ROMS simulation was more accurate in shallow (10 to 50 m) waters than deeper (150 to 200 m) waters, regardless of the time of year.

Bottom water projections

Warming of bottom water during the 21st century is projected to be most substantial on the continental shelves (Fig. 3), with more extreme increases in BTs north of Cape Cod, Massachusetts. On the SEUSCS, the projected rate of BT warming is highest on the

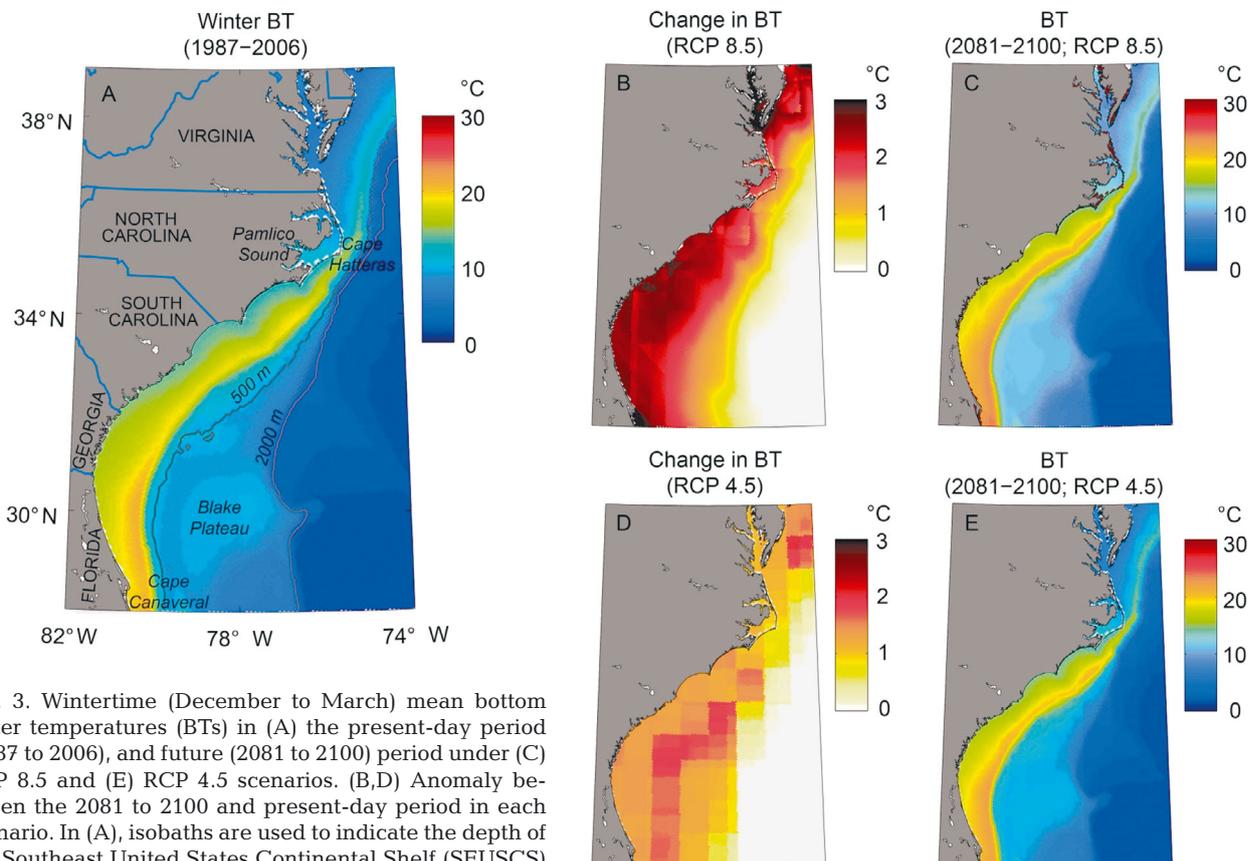


Fig. 3. Wintertime (December to March) mean bottom water temperatures (BTs) in (A) the present-day period (1987 to 2006), and future (2081 to 2100) period under (C) RCP 8.5 and (E) RCP 4.5 scenarios. (B,D) Anomaly between the 2081 to 2100 and present-day period in each scenario. In (A), isobaths are used to indicate the depth of the Southeast United States Continental Shelf (SEUSCS)

Table 1. Spatially averaged wintertime bottom water temperatures (BTs) and total lionfish habitat on the Southeast United States Continental Shelf (SEUSCS) for regions inhabitable year-round (habitable area), for 9 to 12 mo yr⁻¹ (seasonal area), and only if survival is possible near the extreme physiological temperature limit (with feeding possible for 8 to 12 mo yr⁻¹; extreme area). Percentages: change in habitat areas between the 2081 to 2100 and 1987 to 2006 periods

	SEUSCS temperature (°C)	Habitable area (km ²)	Seasonal area (km ²)	Extreme area (km ²)
RCP 8.5				
1987–2006	16.5	70315	99274	103733
2041–2060	17.6	85799	106624	108192
2081–2100	18.8	101773	111279	115150
100 yr change	2.3	31458 (+45%)	12005 (+12%)	11417 (+11%)
RCP 4.5				
1987–2006	16.5	70315	99274	103733
2041–2060	17.5	83251	104419	105595
2081–2100	17.8	89670	108143	109907
100 yr change	1.3	19355 (+28%)	8869 (+8.9%)	6174 (+6.0%)

shelves and decreases on the Blake Plateau. The magnitude of warming of bottom waters is rather limited (<0.2°C by the end of the century) beyond the Blake Escarpment into the deep ocean. Under the RCP 8.5 scenario, the average of the multiple climate models considered indicates that wintertime BTs on the SEUSCS are expected to rise 2.3°C above the 1987 to 2006 average to 18.8°C in the 2081 to 2100 period. In the same region, models simulate a 1.3°C increase by the 2081 to 2100 period under the RCP 4.5 scenario, leading to an average BT of 17.8°C (Table 1). In both scenarios, warming proceeds at a similar pace through the 2041 to 2060 time period, but then increases at a much faster rate in the second half of the 21st century under the RCP 8.5 scenario (Table 1).

Lionfish distributions

Most of the reported lionfish observations during the past 30 yr have occurred in areas that exhibit 11 or 12 optimal months (>16°C) per year (Fig. 2). This year-round habitat covers ~70 300 km² of the SEUSCS (Table 1). Under present-day conditions, lionfish have not been regularly documented in winter near inshore areas off the coast of Georgia and the Carolinas. However, lionfish have been found in these areas during summer months. These summertime (i.e. ‘seasonal’) habitats cover an additional ~29 000 km². Sightings at the extreme end of the lionfishes’ physiological cold tolerance (8 optimal mo yr⁻¹) are much rarer than sightings in areas with warmer winter temperatures (Fig. 2).

Under future scenarios of continued greenhouse-gas emissions, the number of months per year optimal for lionfish is expected to increase throughout the inner continental shelf of the SEUSCS. Under the RCP 8.5 scenario, optimal conditions are expected off Georgia and South Carolina year-round by the end of the 21st century, meaning that suitable habitat for lionfish will be present from the shelf break to the coast (Figs. 4 & 5). Suitable year-round habitat increases to 101 000 km² during this period—an increase of 45% over the presently suitable habitat range on the SEUSCS (Table 1). The increase in year-round habitat is similar under both RCP sce-

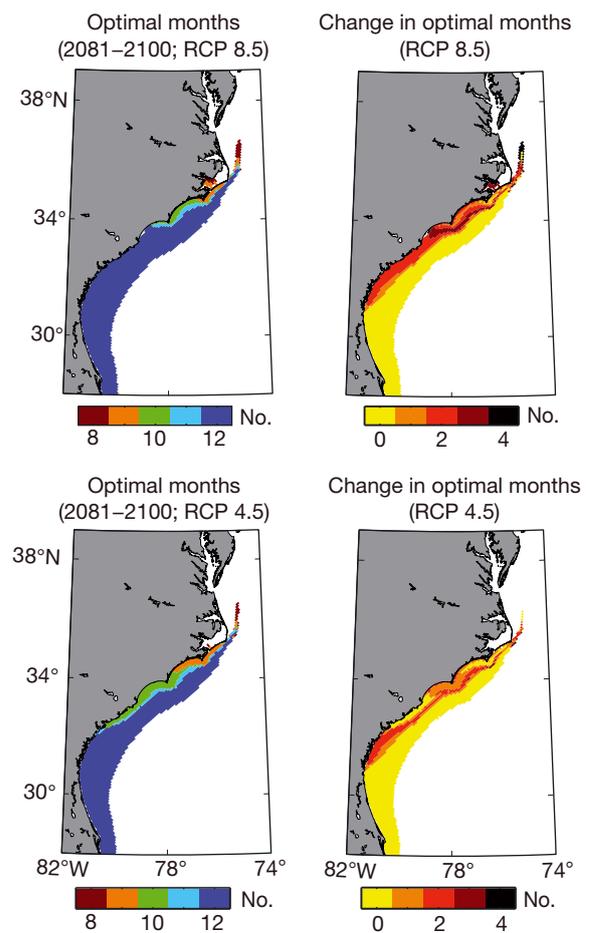


Fig. 4. Number of optimal months per year suitable for lionfish in the future (2081 to 2100) time period under (A) RCP 8.5 and (C) RCP 4.5 scenarios. (B,D) Shows the increase in number of optimal months between the present-day period (see Fig. 2) and the 2081 to 2100 period under each RCP scenario. White areas: uninhabitable in both time periods

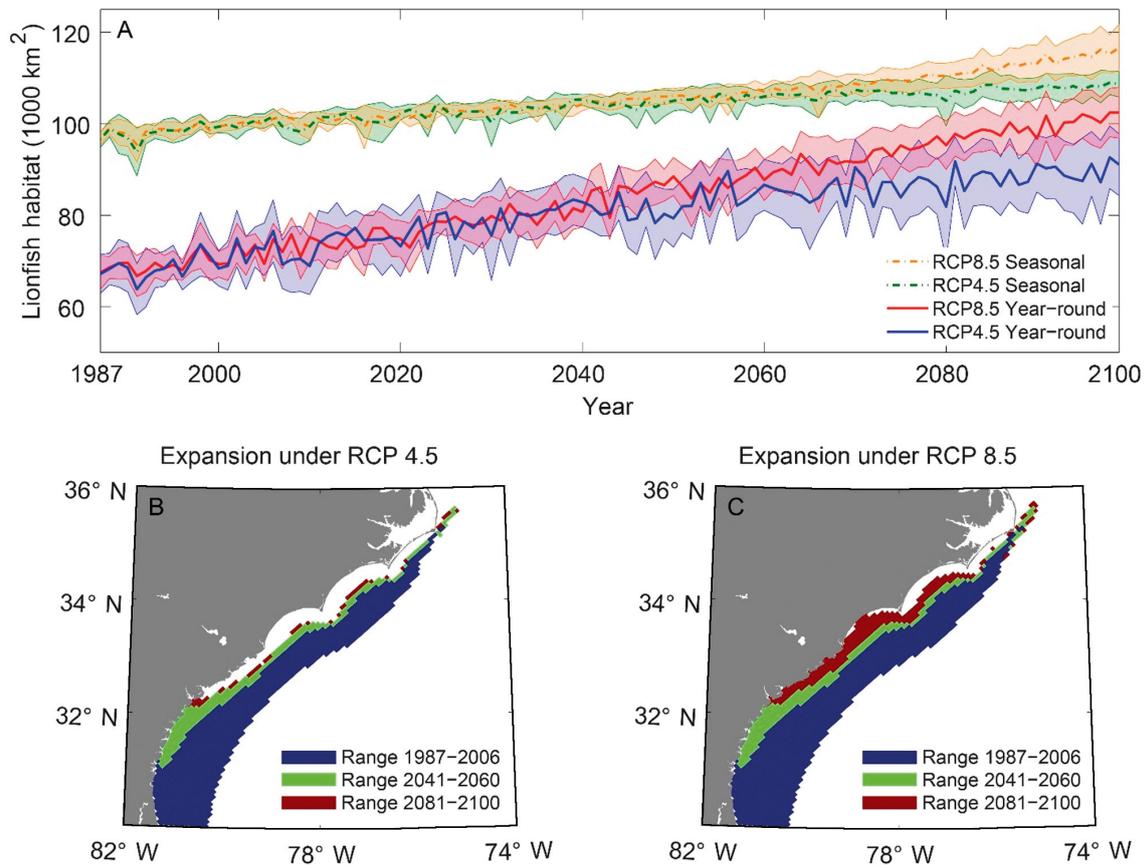


Fig. 5. (A) Average area of year-round (solid lines) and seasonal (dashed lines) habitat on the Southeast United States Continental Shelf (SEUSCS) under RCP 8.5 and RCP 4.5 scenarios. Shaded regions: 95% CI of habitat area projected by all models used in each situation. (B,C) Shows the present-day year-round range estimate (in blue) along with the areas of potential range expansion by mid-century (in green) and by the end of the century (in red)

narios until ~2050, when the 2 scenarios begin to diverge. Year-round habitat continues to increase under RCP 8.5, while habitat under RCP 4.5 exhibits limited increase in the second half of the century. Seasonal habitat (which includes year-round habitat) exhibits similar patterns, except that habitat areas under the 2 scenarios are roughly equivalent until the 2060s and then diverge during the last 3 decades of the century (Fig. 5). Given these results, new regions throughout the SEUSCS may face novel pressure of seasonal lionfish migration in the future under RCP 8.5, with seasonally suitable habitat expansion of up to 12%. These regions also face some of the sharpest increases in number of optimal months per year, with portions of the inshore SEUSCS gaining 3 mo of warm water suitable for lionfish (Fig. 4). This includes the southern region of the Pamlico Sound, North Carolina. Modeled habitat under RCP 4.5 shows similar results, although the Pamlico Sound remains uninhabitable through the end of the century (Fig. 4).

If lionfish are able to tolerate living at the extreme cold limits of their physiological tolerance, modeled habitat under RCP 8.5 conditions indicates that the northern region of Pamlico Sound will be threatened by seasonal lionfish invasion. Also, the locations of suitable year-round lionfish habitat could move ~100 km poleward within the Gulf Stream along the Outer Banks north of Cape Hatteras, reaching almost 37° N (Fig. 4). However, expansion into these extreme conditions is minimal under RCP 4.5, with only ~6000 km² of additional suitable habitat and little poleward expansion (Table 1).

The climate-niche analysis was repeated using each of the 17 individual climate models as replicates instead of the ensemble average. Using a threshold of 50% model agreement to define habitat area, we found that habitat expansion may be greater than that projected by the ensemble average BT; ~2000 km² of additional year-round habitat expansion is projected by using the 50% threshold in comparison to the ensemble average BT for RCP 8.5 conditions. A simi-

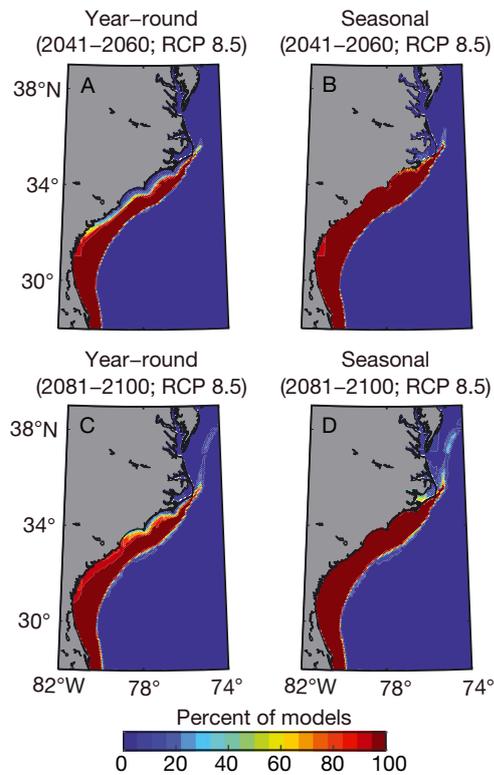


Fig. 6. Percentage of the 17 climate change models that project (A,C) year-round (11 or 12 optimal months per year) and (B,D) seasonal (9 or 10 optimal months per year) lionfish habitat for the (A,B) 2041 to 2060 and (C,D) 2081 to 2100 periods under RCP 8.5 conditions

lar increase in habitat area occurred when examining the seasonally threatened area. However, there were far less extreme habitats projected using this method, indicating that the projections of potential range under extreme conditions is sensitive to a few of the models included in the analysis of the ensemble average. Most of the climate models agree that the majority of the SEUSCS will be seasonally impacted by 2041 to 2060 (Fig. 6).

DISCUSSION

The aim of this investigation was to explore the potential for expansion of lionfish habitat associated with anthropogenic global warming. Based on future ocean temperatures projected by an ensemble of IPCC-style climate models, we anticipate a substantial increase in suitable lionfish habitat in the coming century. This increase in established (i.e. year-round) habitat is primarily due to an increase in BTs on the continental shelves of Georgia and the Carolinas, bringing temperatures in these regions to levels suit-

able for lionfish year-round. Under the RCP 8.5 scenario, the lionfishes' projected year-round range will expand to include almost the entire SEUSCS (~90%) by 2100, with the remaining area susceptible to seasonal invasion by the species.

Despite recent accelerated warming of BTs in the continental shelf north of Cape Hatteras (Forsyth et al. 2015), poleward expansion of lionfish habitat is limited. There is a distinct BT difference between the continental shelves north and south of Cape Hatteras due to the diversion of the Gulf Stream. Even with the 2 to 3°C increase projected under the RCP 8.5 scenario, wintertime BTs north of Cape Hatteras often fall below 10°C, and remain below 16°C long enough to prohibit lionfish survival during the winter (Fig. 3). As expected, the RCP 4.5 scenario leads to a smaller geographic expansion of BT niche for lionfish by the end of the 21st century, exhibiting about two-thirds of the increase in year-round habitat area compared to that simulated under the RCP 8.5 scenario. This is largely due to the decreased rate of expansion in the second half of the century associated with the RCP 4.5 conditions, reflecting the decreased greenhouse-gas emissions assumed under that scenario (Meinshausen et al. 2011, van Vuuren et al. 2011) and the associated decrease in the rate of ocean warming.

Most of the previous efforts to explore changes in fish distributions in response to future climate change have highlighted the potential for poleward expansion of habitats (Perry et al. 2005, Cheung et al. 2010, Hare et al. 2012b). The difference between those results and the inshore expansion we highlight here is largely a product of the regional scale of our analysis, the oceanographic characteristics specific to the SEUSCS, and the particular range of temperatures to which lionfish are sensitive. Our results emphasize the importance of implementing species distribution and climate models at regional scales, as the impacts of future climate change on a specific region or species of interest may differ substantially from the generalized trend emergent from global scale analyses. Many fish species will move poleward or deeper, but applying this simplified expectation while ignoring local oceanographic features may be inappropriate when considering changes at regional scales.

It is important to note the caveats of the techniques used here. Our projections of lionfish habitat are sensitive to assumptions regarding cumulative emissions of greenhouse gases in the coming decades. We explored the BT changes associated with 2 emissions scenarios—RCP 4.5 and RCP 8.5. The 'business as usual' RCP 8.5 scenario anticipates increasing rates

of emissions over time, whereas the RCP 4.5 scenario is more moderate and assumes that radiative forcing will stabilize by 2060. Of course, the exact evolution of future emissions is unknown. Note, however, that emissions during the last 5 yr have met or exceeded those expected under the RCP 8.5 scenario (Fuss et al. 2014), and continued 'business-as-usual' emissions seem increasingly likely. Additionally, our results indicate that expansion of established lionfish habitat will be fairly similar between these 2 scenarios through about the 2050s, after which the magnitude of invasion continues to increase in the more intense emissions scenario. Given these findings, our results describing invasion through the 2050s are insensitive to the particular emissions scenario that we follow.

Like most niche models, our model assumes that important physiological limits and behaviors of lionfish will not change in the future. We also assume that the current lack of biological control (i.e. limited predation by larger piscivorous fishes and sharks native to the region) will persist in the coming decades and will not limit lionfish habitat, even for individuals that may be weakened by sub-optimal physical conditions (but see Maljković et al. 2008, Diller et al. 2014). Furthermore, we focused on long-term changes associated with anthropogenic warming and intentionally utilized 20 yr averages of ocean conditions to limit variability in modeled temperatures that may be associated with natural modes of interannual variation. As such, this analysis projects where and when lionfish could be found, but not precisely where or when they will be found. Nor will seasonal populations of lionfish be present during all possible optimal months.

Finally, there are caveats associated with the USGS-NAS database that we used to indicate the general consistency between laboratory-derived thermal tolerances of lionfish and their observed distribution throughout the Northwest Atlantic. Most (but not all) of the observations are reported by civilians and are not the result of rigorous scientific surveys. These civilian reports occasionally lack details such as the method of observation, environmental conditions during observation, fish age, and fish size. Observations are likely biased due to the unevenly distributed observational effort (with more recreational dives during warm months than during winter) and lack of species' absence records. However, as our use of the data was to offer evidence that the observed distributions across the region are qualitatively similar to those derived from a simple climate-niche model incorporating physiological tolerances, we

found the USGS-NAS database particularly useful. If the impacts of lionfish on native fish and invertebrate populations are considered a significant management concern on the SEUSCS, then consistent scientific surveys to census the population are warranted along with continued efforts to examine the physical and ecological limitations on lionfish habitat. Such data, when coupled with observations and simulations of physical and biological conditions, would reduce the uncertainties associated with projections of future lionfish distributions.

Despite these caveats, we expect our results will be of value for fisheries managers and conservationists as they consider the likelihood of lionfish invasion in coming decades. Lionfish have already been found in coastal estuaries in South Florida and southern India (Jud et al. 2011, Prakash et al. 2012), and similar environments serve as required nursery grounds for commercially important fish species of the SEUSCS. This industry is valued at \$162 million (National Marine Fisheries Service 2014), and tourism and recreational fishing dependent on the health of the native fish communities also have a significant economic impact on the region. Georgia and the Carolinas are home to many ecologically and economically valuable estuaries and protected areas, and insight regarding the timing and likelihood of lionfish invasion is vital for effective control strategies and marine spatial planning.

Most niche-based species distribution models use the statistical relationships between the abiotic variables of a region and the presence or absence of a species in its observed range to project that species' habitat into new geographic areas. Using experimentally derived physiological limits to simulate future distributions—as we did here—is uncommon for fish species, but similar methodology has been applied across species in a variety of systems (Wetthey et al. 2011, Hare et al. 2012b, Overgaard et al. 2014, Glibert et al. 2014, Fly et al. 2015). Accounting for these physiological tolerances may improve model prediction for species in novel environments (Woodin et al. 2013) because interspecific interactions may be less relevant for invasive species (Peterson 2003). However, our model is still coarse in its representation of lionfish physiology and distribution, and improved understanding of the ability of lionfish to tolerate durations of sub-optimal conditions (i.e. cool periods when feeding is unlikely, but not fatal), reliable absence data on seasonal timescales, and a better geographic representation of benthic structure (Bernal et al. 2015) would help us narrow our estimates of habitat expansion.

In summary, the SEUSCS is expected to warm substantially over the coming decades, likely allowing lionfish to permanently invade structured benthic habitat on the continental shelf of Georgia and the Carolinas, but not the continental shelf of the Northeast United States. Habitat expansion by this invasive predator is likely to occur regardless of whether future emissions are more similar to the RCP 4.5 or 8.5 climate scenarios; however, the magnitude of continued invasion can be mitigated by large-scale decreases in greenhouse-gas emissions.

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