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Potential Range Expansion of the Invasive Lionfish in the Western Atlantic Ocean

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POTENTIAL RANGE EXPANSION OF THE INVASIVE LIONFISH IN THE WESTERN ATLANTIC OCEAN
IN RESPONSE TO FUTURE CLIMATE CHANGE

by

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DEDICATION

First and foremost, this thesis is dedicated to my parents, Peggy and Steven Grieve, to whom I am eternally grateful for everything they have done for me in my life. They have encouraged me to chase whatever paths appealed to me, provided structural, emotional, and financial support to allow me to pursue those paths, and bestowed their outstanding genetics – to which I am still attempting to utilize correctly. I would not have made it through without the respite of my friends who know who they are. Lastly, I owe everything to Ryan Rykaczewski for taking a chance on me and following through with remarkable and thoroughly undeserved patience.

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ABSTRACT

Lionfish (*Pterois volitans*) are an invasive, predatory fish native to the reefs of the Indo-Pacific. In the mid-1980s, lionfish were introduced off the coast of Miami, FL and have since transformed many of the reef ecosystems throughout the Western Atlantic Ocean. Although lionfish are found year-round as far north as Cape Hatteras, NC, they are confined to the warm Gulf Stream during winter months. Seasonal inshore expansion is possible in the summer, and further poleward expansion is limited by cold bottom-water temperatures in winter. Here, I use an ensemble of 17 different climate models to project lionfish habitat by the year 2100. Climate models were statistically downscaled using an existing Regional Ocean Modeling System, permitting a high-resolution (7-by-7 km) projection of bottom-water temperatures across the Western Atlantic Ocean. I compared these projections to the lower temperature thresholds of lionfish feeding and mortality, previously estimated to be 16°C and 10°C, respectively. Under the business-as-usual climate change scenario (RCP 8.5), lionfish habitat is likely to move inshore to the coastlines of the Carolinas, including the Pamlico Sound, NC. The spatial extent of suitable habitat in the South Atlantic Bight is expected to increase 35% by 2100, and seasonal range is expected to expand by 24%. These methods are broadly applicable to other niche models, especially for other hardy, generalist species sensitive to climate change. This work has applications for management and prevention of future lionfish invasions.

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LIST OF ABBREVIATIONS

| | |
|------------|---|
| BWT..... | bottom-water temperature |
| CMIP5..... | Climate Model Intercomparison Project phase 5 |
| ESGF..... | Earth System Grid Federation |
| IPCC..... | Intergovernmental Panel on Climate Change |
| MMT..... | mean monthly temperature |
| NOAA..... | National Oceanic and Atmospheric Administration |
| RCP..... | Representative Concentration Pathway |
| ROMS..... | Regional Ocean Modeling System |
| SAB..... | South Atlantic Bight |
| SD..... | daily standard deviation |
| SDM..... | species distribution model |

CHAPTER 1

INTRODUCTION

Invasive species are rampant in marine environments (Sorte *et al.*, 2010), yet few invasions by fish species have been documented (Baltz, 1991). Though uncommon, a few invasive fish species have been successful in disturbed marine areas such as the Mediterranean Sea (Golani *et al.*, 2002, 2007) and the Hawaiian Archipelago (Randall, 1987). Indo-Pacific red lionfish (*Pterois volitans*) and the morphologically-identical devil firefish (*Pterois miles*; hereafter collectively referred to as lionfish) are the first major fish invader into the Western Atlantic Ocean (Whitfield *et al.*, 2002). Lionfish were introduced near Miami, FL in the mid-1980s or 1990s, likely as the result of the aquarium trade (Hare & Whitfield, 2003; Semmens *et al.*, 2004) and have since spread throughout the continental shelves of the Southeastern United States, Bermuda, Caribbean Sea, and the Gulf of Mexico (Schofield, 2009, 2010). It is possible that lionfish could survive as far south as Uruguay (Morris & Whitfield, 2009), but are likely being deterred by the Amazon-Orinoco freshwater plume and the Southern Equatorial Current (Côté *et al.*, 2013). Native lionfish in the Indo-Pacific live almost exclusively on rocky and coral reefs (Fishelson, 1975; Schultz, 1986) but can be found not only in reefs (Whitfield *et al.*, 2007; Albins & Hixon, 2008; Green & Côté, 2009), but sea-grass beds (Meister *et al.*, 2005; Claydon *et al.*, 2012), mangroves (Barbour *et al.*, 2010), and estuaries (Jud *et al.*, 2011; Prakash *et al.*, 2012) in the invaded range.

Novelty confers certain advantages to lionfish, including a unique appearance and hunting strategy that may confuse potential prey, if prey recognize the lionfish as being a predator at all (Morris *et al.*, 2009; Albins & Lyons, 2012; Albins & Hixon, 2013). Lionfish possess venomous spines that discourage predation by local predators (but see Maljković *et al.*, 2008; Diller *et al.*, 2014), and their only predator in the native range, the bluespotted cornetfish *Fistularia commersonii*, is not present in the invaded range (Bernadsky & Goulet, 1991). Given these traits, along with a voracious, generalist appetite (Morris & Akins, 2009; Muñoz *et al.*, 2011), lionfish have been found to drastically lower abundance, recruitment, and diversity of prey fish in areas which they have invaded (Green *et al.*, 2012; Albins & Hixon, 2008; Albins, 2013). Benthic macroinvertebrates – the preferred prey of young and small lionfish – likely face similar consequences, but quantifying the impact of lionfish on this community requires further analysis (Muñoz *et al.*, 2011; Layman *et al.*, 2014). Lionfish may also affect abundance 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).

Lionfish are currently located throughout the outer shelf of the South Atlantic Bight (SAB) as far north as Cape Hatteras, NC (Schofield, 2009). Further northward expansion is presently limited by cold winter bottom-water temperatures in the Mid Atlantic Bight (Whitfield *et al.*, 2002, 2014; Kimball *et al.*, 2004). The SAB exhibits a unique oceanographic climatology due to the Gulf Stream transiting north through the continental shelf and redirecting towards Europe at Cape Hatteras. During the winter

months (December-March), a steep, inshore-offshore temperature gradient develops between the cold, nearshore waters and the relatively warm waters of the Gulf Stream. These warm waters provide a refuge for lionfish in the center of the SAB (Whitfield *et al.*, 2002, 2014; Meister *et al.*, 2005; Muñoz *et al.*, 2011), while the shallow inshore waters rapidly cool due to surface mixing (Atkinson *et al.*, 1983). This gradient is reversed in the summer months (June-August), allowing adult lionfish to move further inshore (Whitfield *et al.*, 2007; Schofield, 2009) as hot summer surface temperatures are mixed into the shallow inshore waters. Lionfish larvae are occasionally advected north by the Gulf Stream and warm-core eddies (Hare *et al.*, 2002), resulting in the presence of young-of-the-year juveniles as far north as the coast of Long Island, NY (Figure 1.1; Whitfield *et al.*, 2002). These individuals do not survive the harsh winters and have not established a breeding population (Kimball *et al.*, 2004).

Lionfish are unlikely to move further north under present conditions, as their current distribution is believed to be physiologically limited by cold tolerance (Kimball *et al.*, 2004). However, potential changes to their distributions in response to future climate change has not been investigated. Bottom-water temperatures at the northern edge of the lionfish's range have been increasing since regular observations were initiated in the 1970s, especially during winter months (Parker & Dixon, 1998). More warming is expected in the coming decades as a consequence of anthropogenic emissions of greenhouse gases (Stocker *et al.*, 2014). Additionally, the marine communities of the region are vulnerable to overfishing (Parker & Dixon, 1998; Lucey & Nye, 2010), with resultant declines in biomass and mean trophic level (Northeastern Fisheries Science Center, 2012). Such

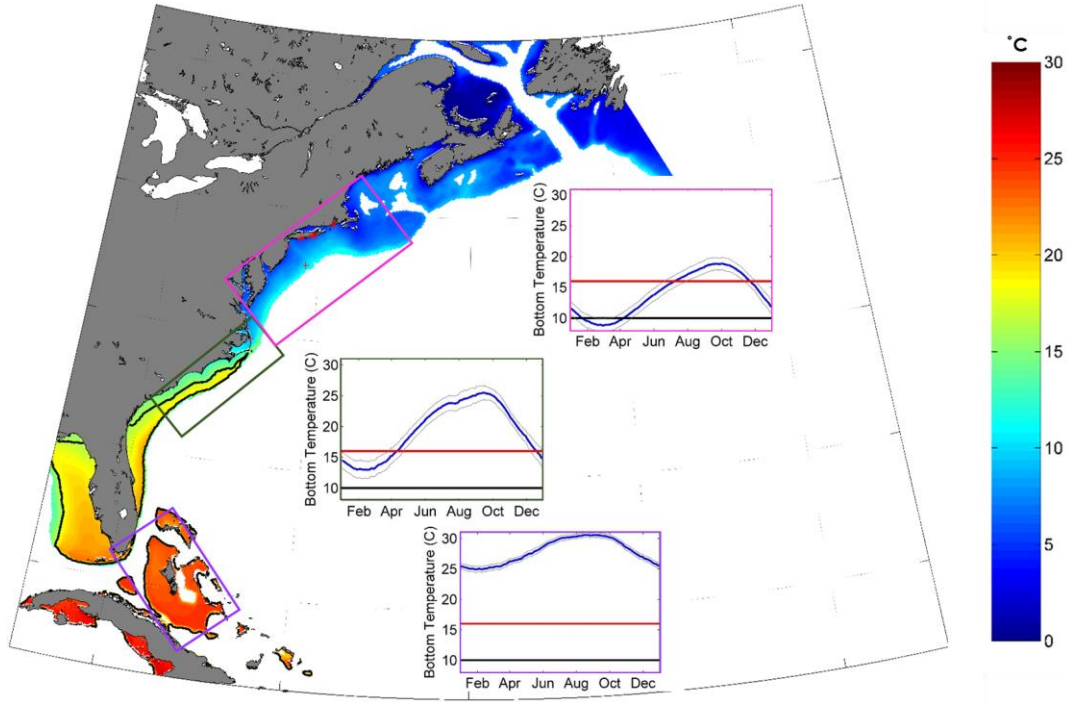


Figure 1.1: Comparison of potential lionfish habitats in the Western Atlantic Ocean over the present day (1987-2006) time period. Timeseries show the spatial average of annual bottom-water temperatures of the associated region throughout the year. Bottom-water temperatures are shown with blue lines ± 1 standard deviation (grey lines). Black horizontal lines indicate the 10°C lethal minimum temperatures for lionfish. Red lines indicate the lower feeding threshold for lionfish (Kimball *et al.*, 2004). The colorbar indicates winter (December-March) mean bottom-water temperatures. The black contour line shows suitable, year-round lionfish habitat, and juvenile outliers are indicated by red crosses (Schofield, 2009).

conditions are ripe for invasion, further increasing the opportunity for trophic cascades (Albins & Hixon, 2013) and regime shifts (Quero, 1998; Scheffer *et al.*, 2001; Daskalov *et al.*, 2007).

Many marine fishes have already shifted their range in response to climate change (Perry *et al.*, 2005; Rose, 2005; Parmesan, 2006; Nye *et al.*, 2009; Lucey & Nye, 2010), and many more are projected to in the future (Loukos *et al.*, 2003; Cheung *et al.*, 2009, 2010; Hare *et al.*, 2012). Many of these analyses utilize bioclimatic envelope models that project the fundamental niche – a combination of physical conditions tolerable to an organism – to estimate range instead of interspecific biological interactions (Hutchinson, 1957; Magnuson *et al.*, 1979). This is a popular way of conducting species distribution models, and they tend to be accurate despite their assumptions (Peterson, 2003; Jeschke & Strayer, 2008)

Given how other fishes have responded to climate change, it is expected that lionfish range will shift as well. Specifically, we expect lionfish to move further inshore (Whitfield *et al.*, 2014) and north within the northern branch of the Gulf Stream (Hare *et al.*, 2002). In this study, we use an ensemble of 17 different climate models to project future bottom-water temperatures under different climate scenarios and examine whether the fundamental niche of lionfish will move based on experimentally-derived physiological tolerance limits of lionfish. This approach has previously been used to estimate future distributions of the ecologically-similar gray snapper *Lutjanus griseus* (Hare *et al.*, 2012).

CHAPTER 2

METHODS

Bottom water projections

I obtained output from climate models used in the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC; Stocker *et al.*, 2014) from the Climate Model Intercomparison Project phase 5 (CMIP5; Taylor *et al.*, 2012) hosted on the servers of the Earth System Grid Federation (ESGF) . For this analysis, I used the historical model runs (1987-2005) to represent the present-day conditions and future model runs forced with continued greenhouse-gas emissions from 2006 to 2100 following Representation Concentration Pathway (RCP) 8.5 and RCP 4.5 (Moss *et al.*, 2010; van Vuuren *et al.*, 2011). These scenarios represent “business-as-usual” and an intermediately optimistic scenario where global greenhouse gas emissions level off by about 2050, among other factors (Meinshausen *et al.*, 2011). Seventeen of the CMIP5 models had unique, complete monthly projections of bottom-water temperatures (BWT) for both the historical and RCP 8.5 scenarios. Of these 17 models, 11 had accompanying RCP 4.5 models (Table 2.1).

All climate models used have relatively coarse spatial resolutions (Table 2.1), potentially obscuring important oceanographic factors along the eastern coast of the United States. To remedy this, all climate models were statistically downscaled with a high resolution (7-by-7 km) Regional Ocean Modeling System (ROMS) simulation of the

Table 2.1: Climate models used in this analysis

| Institution | Model | Experiment | Average Oceanic Horizontal Resolution |
|--|---------------------|--------------------|---------------------------------------|
| Beijing Climate Center | BCC-CSM1-1 | RCP 8.5 RCP 4.5 | 0.8° x 1.0° |
| Beijing Normal University GCESS | BNU-ESM | RCP 8.5 | 0.9° x 1.0° |
| Canadian Centre for Climate Modelling and Analysis | CanESM 2 | RCP 8.5 RCP 4.5 | 0.9° x 1.4° |
| Centro Euro-Mediterraneo per I Cambiamenti Climatici | CMCC_CESM | RCP 8.5 | 1.2° x 2.0° |
| | CMCC_CMS | RCP 8.5 RCP 4.5 | 1.2° x 2.0° |
| Centre National de Recherches Meteorologiques | CNRM-CM5 | RCP 8.5 RCP 4.5 | 0.6° x 1.0° |
| Institute for Numerical Mathematics | INM_inmcm4 | RCP 8.5 RCP 4.5 | 0.5° x 1.0° |
| Institut Pierre Simon Laplace | IPSL-CM5A-MR | RCP 8.5 RCP 4.5 | 1.2° x 2.0° |
| | IPSL-CM5B-LR | RCP 8.5 RCP 4.5 | 1.2° x 2.0° |
| Institute of Atmospheric Physics | LASG-CESS_FGOALS-g2 | RCP 8.5 RCP 4.5 | 0.9° x 1.0° |
| Japan Agency for Marine-Earth Science and Technology | MIROC5 | RCP 8.5 | 0.8° x 1.0° |
| | MIROC5-ESM | RCP 8.5 | 0.9° x 1.4° |
| | MIROC5-ESM-CHEM | RCP 8.5 | 0.9° x 1.4° |
| Max Planck Institute | MPI-ESM-LR | RCP 8.5 RCP 4.5 | 0.8° x 1.4° |
| NOAA Geophysical Fluid Dynamics Laboratory | GFDL-CM3 | RCP 8.5 RCP 4.5 | 0.9° x 1.0° |
| | GFDL-ESM2G | RCP 8.5 RCP 4.5 | 0.9° x 1.0° |
| | GFDL-ESM2M | RCP 8.5 RCP 4.5 | 0.9° x 1.0° |

Western Atlantic Ocean (Kang & Curchitser, 2013). Using an approach called the delta method (Figure 2.1; e.g., Hamlet *et al.*, 2010; Ramirez-Villegas & Jarvis, 2010), the BWT for each climate model in the present period (1987-2006, coincident with last 20 full years of Run 03 of the ROMS simulation) was subtracted from the BWT in the future period (2081-2100), giving the change projected for each model (the “delta” BWT, referred to simply as the delta). The delta was regridded using nearest neighbor interpolation and added to the present day BWT simulated by the ROMS model, providing a high-resolution representation of the Western Atlantic BWT in the future. Twenty-year averages were used for each time period in order to ameliorate noise related to inter-annual variability (e.g., phases of the North Atlantic Oscillation, meandering of the Gulf Stream) of the ROMS model. The delta method also reduces the chance that biases resulting from different initial conditions of each climate model are represented in the 2100 projections.

The climate models are run using 4 or 6 hour temporal resolutions, but are packaged as monthly averages from the ESGF. In order to consider physiological stresses on lionfish that may occur due to cold temperatures occurring at frequencies higher than monthly, for each area I calculated the average standard deviation, $SD_{M,a}$, of daily ROMS BWT away from the monthly means of each year using

$$SD_{M,a} = \frac{\sum_{y=1}^N \sqrt{\frac{\sum_{D=1}^n (T_{D,y} - \bar{T}_{M,y})^2}{n}}}{N}$$

where T refers to the bottom-water temperature of the specific day, D , in each month, M , of year, y . N and n refer to the number of years SD was calculated from and the

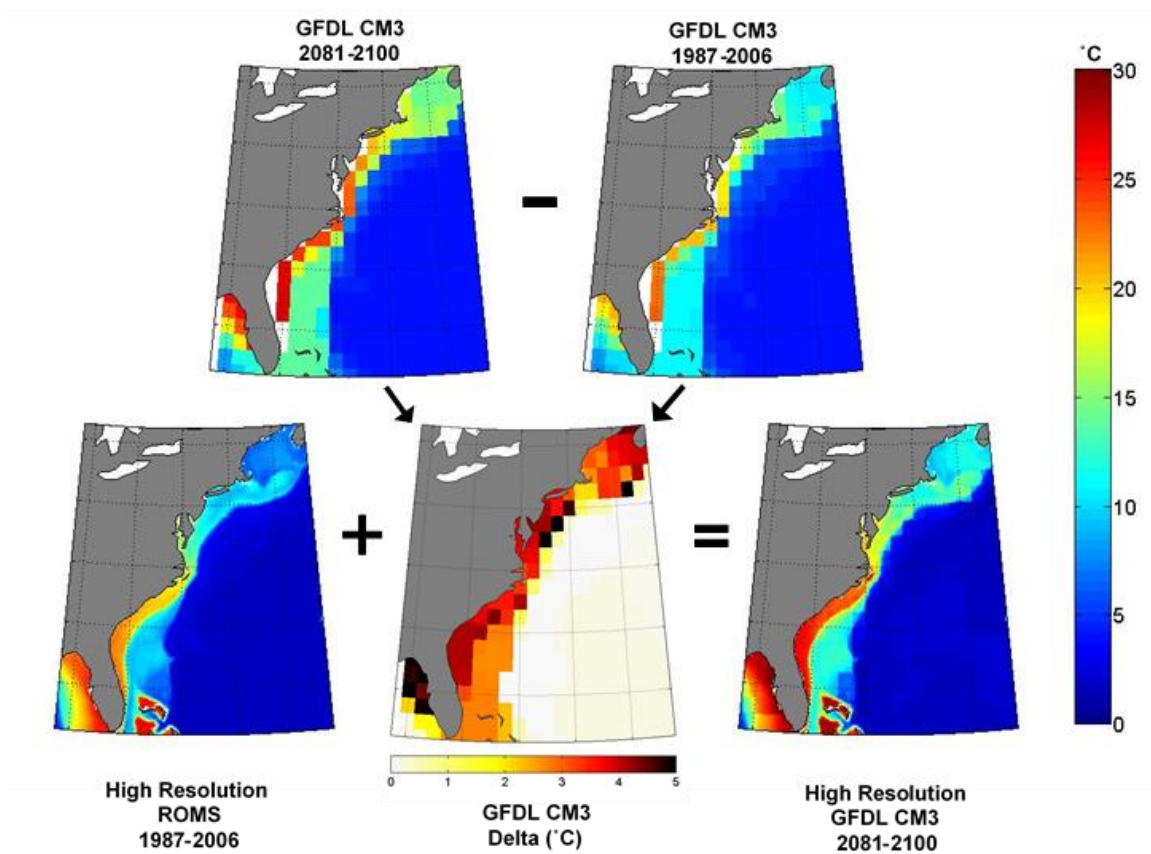


Figure 2.1: The delta method visualized for one model, NOAA-GFDL-CM3. In the top panels, the mean bottom-water temperature from the present period (1987-2006) is subtracted from the mean bottom-water temperature from the future period (2080-2100). This long-term difference is then interpolated using nearest neighbor and inverse-distance methods and added to the high-resolution (7-by-7 km) Regional Ocean Modeling System simulation of present-day temperatures (lower panels), giving a high-resolution estimate of future bottom-water temperatures.

number of days in each month, respectively. a is each 7-by-7 km region of the ROMS simulation.

Most BWT results are given as an average of all climate models used, as studies have shown that multi-model means are more accurate than single models alone (Randall *et al.*, 2007; Reichler & Kim, 2008). However, each model can also be considered as a trial, requiring a minimum threshold of agreement among the models to consider an area habitable (e.g. Wethey *et al.*, 2011). These analyses required inverse-distance interpolation of the delta before being added to the ROMS simulation.

Lionfish distributions

Lionfish are habitat generalists that can survive in a variety of biological conditions. Here, I assume that within the potential expansion range, there is suitable bottom habitat, ample prey, and no significant habitat limitation due to predation. Given the array of habitats in which lionfish have thrived (Barbour *et al.*, 2010; Jud *et al.*, 2011; Claydon *et al.*, 2012; Cure *et al.*, 2014) and the variety of food they have been found to consume (Morris & Akins, 2009; Muñoz *et al.*, 2011; Layman & Allgeier, 2012), I believe this to be reasonable assumption. As for physical conditions, lionfish are usually found at depths between 0.5-100 m (Meister *et al.*, 2005) depending on the habitat, but have been spotted beyond 300 m depth (Muñoz *et al.*, 2011). Previous work by others has noted a lack of correlation between presence of lionfish to rugosity, current speed, wave action, distance to freshwater sources, and proximity to other predators, including fellow lionfish (Cure *et al.*, 2014). Prolonged exposure to low salinity (~10‰) does not alter lionfish

behavior or physiology, but anything lower is fatal (Jud *et al.*, 2014). This is only important in estuaries, as salinities in the open ocean are much higher (~35‰) year-round.

Given the lack of significant limitations on non-estuarine lionfish distribution by predators, salinity, prey availability, and water depth, BWT is believed to be the primary factor influencing the fundamental niche of lionfish. Lionfish are a benthic species, and sea surface temperatures in relatively deep (>30 m) waters appear to have no impact on lionfish presence (Kimball *et al.*, 2004). Kimball *et al.* (2004) estimated that lionfish stop feeding at approximately 16°C and die at 10°C. It has not been experimentally determined how long lionfish can survive starvation, but Fishelson (1997) observed a group of adults that all survived three months in experimental aquaria without feeding before cessation of the experiment. Seasonally, adult lionfish have been found in areas that experience up to four months of suboptimal conditions (10°C-16°C).

A bioclimatic envelope model was created using the above parameters. Areas (7-by-7 km) were considered potentially habitable by lionfish as long as the present-day salinity always exceeded 10‰ (depth-resolved salinity was not available in climate models used) and the mean monthly temperature (MMT) minus one daily SD never fell below 10°C. If an area met the minimum criteria outlined above, I calculated suboptimal months as the number of months per year the MMT plus one SD was between 10°C and 16°C. These areas were compared with lionfish sightings reported to the United States Geological Survey Nonindigenous Aquatic Species database (Schofield, 2009) to investigate assumptions. Areas were labeled habitable year-round if they experience less

than 2 months per year of suboptimal conditions, seasonally habitable if 2-3 months exhibited suboptimal BWT conditions, and potentially habitable if 4 months had suboptimal BWT conditions. No more than 4 suboptimal months were considered as potential habitable areas. The bioclimatic envelope analysis was conducted using the multi-model mean BWT from all climate models, then repeated requiring at least 50% model agreement in order to consider an area habitable in any capacity.

Assessment of ROMS BWT accuracy

Present-day bottom-water temperatures in the ROMS simulation were compared with NOAA Winter, Spring, and Autumn Bottom Trawl Survey data from 2002-2006. In these surveys, bottom trawls were conducted throughout the Mid and North Atlantic Bights in February, March, April, September, and October in order to census fish abundance and diversity. Water temperature and depth data were obtained during each trawl using a CTD (conductivity, temperature, and depth) instrument. These data were obtained from Resource Survey Reports of each expedition from the NOAA Northeast Fisheries Science Center website.

Samples were matched to equivalent points in the ROMS simulation. For each point, the five year (2002-2006) monthly average bottom-water temperature from the ROMS simulation and bottom depth were recorded to develop an observed and modeled climatological series that could be compared. If there were multiple samples for each point across years, they were averaged together. If the depth of the sample and the depth represented in the model grid were not within 50 m of one another, they were discarded;

this usually 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 a 7-by-7 km grid spacing. The resulting monthly datasets were combined and analyzed using a non-parametric Wilcoxon Signed Ranks test for paired data ($\alpha = 0.05$), testing the null hypothesis that the model monthly mean BWT was not significantly different from the observed BWT. Data did not meet normality assumptions required for parametric statistics.

CHAPTER 3

RESULTS

Assessment of ROMS BWT accuracy

Over the 2002-2006 period of NOAA trawl surveys examined here, there were 2802 samples deemed suitable for comparison. Altogether, the ROMS model averages 0.06°C warmer than the samples, with some seasonal variation. According to a Wilcoxon Signed Ranks test, the observed BWTs are not significantly different than those in the model ($N = 2802$, $p = 0.13$), indicating that the ROMS simulation provides a suitable present-day representation of BWT on the continental shelf and is useful for examining potential changes in lionfish distribution in the region. The biases present (e.g., the model's maximum bias of 0.30°C cooler than observations in September) are rather small. A mean monthly BWT difference of 0.30°C is substantially less than the average daily SD of 1.41 in the SAB in September.

Bottom-water projections

Discernible warming of bottom-water is limited to the continental shelves and is more extreme in the polar regions. Under the RCP 8.5 scenario, winter-time BWTs in the SAB are expected to rise 2.37°C from the 1987-2006 average to 19.03°C in 2081-2100 (Figure 3.1). In the same region, RCP 4.5 shows a 1.35°C increase by the 2100 period, leading to an average BWT of 18.01°C (Table 3.1). In both scenarios, warming proceeds at

Table 3.1: Spatially-averaged bottom-water temperatures and total lionfish habitat in the South Atlantic Bight

| RCP 8.5 | SAB Temperature (°C) | Habitable Area (km ²) | Seasonal Area (km ²) | Extreme Area (km ²) |
|------------------|----------------------|-----------------------------------|----------------------------------|---------------------------------|
| 1987-2006 | 16.66° | 65,709 | 21,749 | 2,989 |
| 2040-2060 | 17.74° | 77,959 | 25,669 | 3,577 |
| 2080-2100 | 19.03° | 89,229 | 26,943 | 5,635 |
| Change | 2.37° | 23,520 | 5,194 | 2,646 |
| RCP 4.5 | | | | |
| 1987-2006 | 16.66° | 65,709 | 21,749 | 2,989 |
| 2040-2060 | 17.69° | 75,950 | 25,669 | 3,381 |
| 2080-2100 | 18.01° | 78,253 | 25,914 | 3,822 |
| Change | 1.35° | 12,544 | 4,165 | 833 |

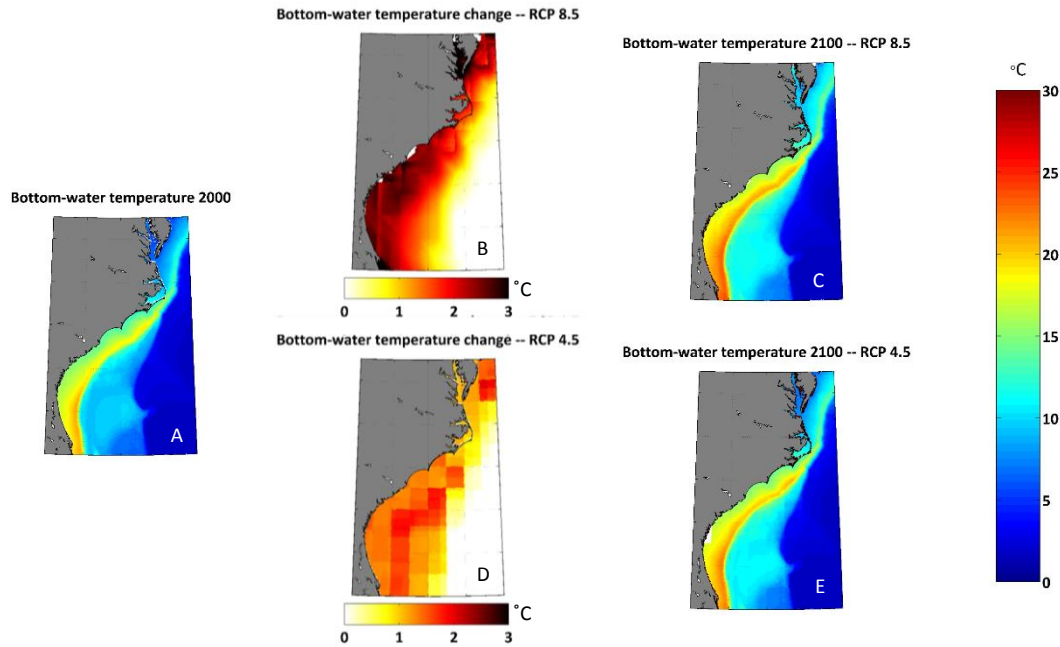


Figure 3.1: Bottom-water temperature projections and anomalies in the South Atlantic Bight. A) Present day period (1987-2006) from ROMS model. B) Anomaly between 2100 (2080-2100) and present day under RCP 8.5. C) 2100 period under the RCP 8.5 scenario. D) RCP 4.5 anomaly. E) 2100 period under RCP 4.5.

a similar pace through the 2040-2060 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 3.1).

Lionfish distributions

Most of the reported lionfish sightings are in areas that have one or fewer months of suboptimal temperature conditions (10°C - 16°C) per year (Figure 3.2). This year-round habitat covers ~65,700 km² of the SAB (Table 3.1). In present-day conditions, inshore areas off the coast of Georgia and the Carolinas, exhibiting 2-3 months per year of suboptimal conditions, are uninhabited by lionfish in the winter. However, lionfish have been found in these areas during summer months. These conditions cover ~21,700 km². Sightings at the extreme end of lionfish's physiological cold tolerance (4 suboptimal months per year) are rare (Table 3.1; Figure 3.2).

Under future scenarios of continued greenhouse-gas emissions, the number of suboptimal months for lionfish survival is expected to decrease throughout the inner continental shelf of the SAB, increasing the probability of successful lionfish invasion. Under the RCP 8.5 scenario, no suboptimal conditions are expected off Georgia and South Carolina at any point of the year by the last two decades of the 21st century (Figure 3.2). Suitable year-round habitat could increase by up to 23,500 km² by the same period – an increase of 35% over presently suitable habitat range on the continental shelf of the SAB (Table 3.1). The fundamental niche of year-round habitat in the 2100 period under RCP 4.5 is similar to the fundamental niche projected by RCP 8.5 in the 2050 period, increasing year-round habitat by 10,000 km²-12,000 km² over the current year-round habitat

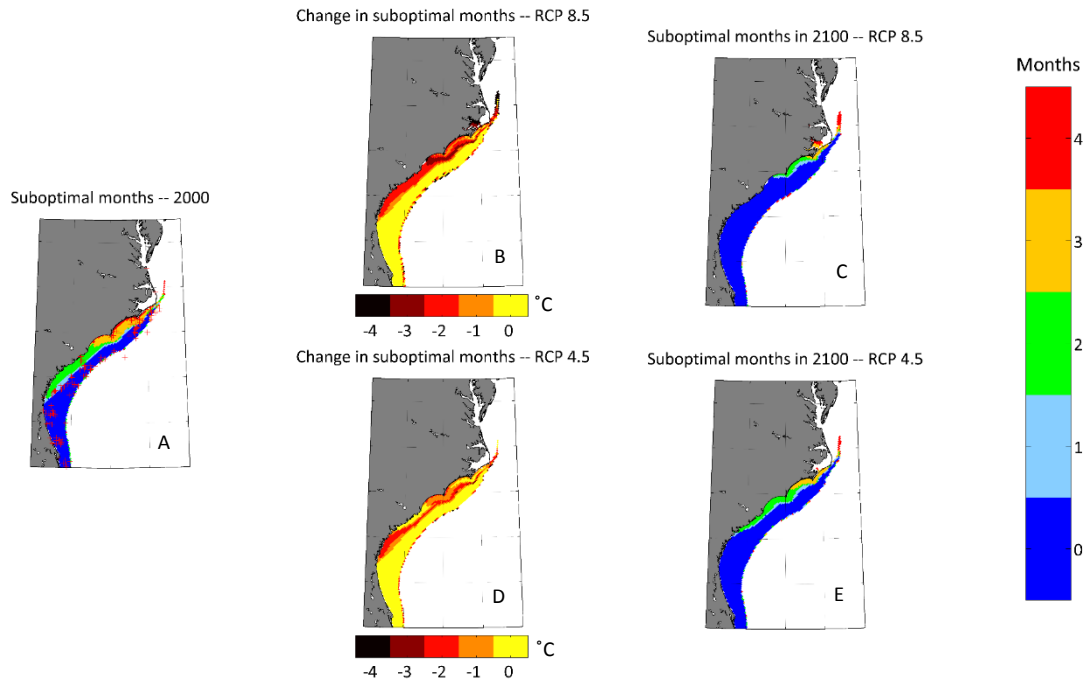


Figure 3.2: Number of suboptimal months (10°C - 16°C) per year in present and future time periods under different RCP scenarios. Less than two months is considered suitable habitat for lionfish year-round, 2-3 months may be vulnerable seasonally, and 4 months is the most a lionfish could survive. A) Present day (1987-2006) from ROMS model. Red crosses indicate confirmed lionfish sightings. B) Change between 2100 time period (2080-2100) and present day time period under RCP 8.5. C) 2100 time period under RCP 8.5. D) Change between present and 2100 period for RCP 4.5 E) 2100 period under RCP 4.5.

estimated by present-day BWT. Under RCP 4.5, the rate of increase of lionfish habitat drops off dramatically after 2040-2060, with RCP 4.5 gaining only 20% of the year-round habitable area that the region gains under RCP 8.5, despite having similar areas in 2050 (Table 3.1).

New regions throughout the SAB may face novel pressure of seasonal lionfish migration in the future under RCP 8.5, with seasonally suitable expansion up to 24%. These regions also face some of the sharpest decreases in suboptimal months per year, with portions of the inshore SAB losing 3 months of lionfish-detering cold water (Figure 3.2). This includes the southern fork of the Pamlico Sound, NC. RCP 4.5 showed similar results for seasonal habitat.

If lionfish are able to tolerate living at the extreme cold limits of their physiological tolerance (4 suboptimal months per year), RCP 8.5 projects the northern fork of the Pamlico Sound to be threatened by seasonal lionfish invasion. Also, lionfish could move approximately 100 km north in a deep branch of the Gulf Stream along the Outer Banks, almost reaching 37°N (Figure 3.2). However, expansion into these extreme conditions is minimal under RCP 4.5, with only ~800 km² being added in this scenario (Table 3.1).

The same analysis was conducted treating bioclimatic envelopes created by each model as a replicate instead of using the ensemble average. Using a threshold of 50% model agreement to define habitat area, I found that habitat expansion may be greater than that projected by the ensemble average; about 2000 km² of additional year-round habitat expansion is projected by using the median modeled habitat area in comparison

to the ensemble average BWT for RCP 8.5. A similar 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 relied on temperatures from few climate models. Most of the climate models agree that the majority of the SAB will be seasonally impacted by 2040-2060, although the suitable year-round habitat criteria showed a more steady progression between now and the 2100 period (Figure 3.3).

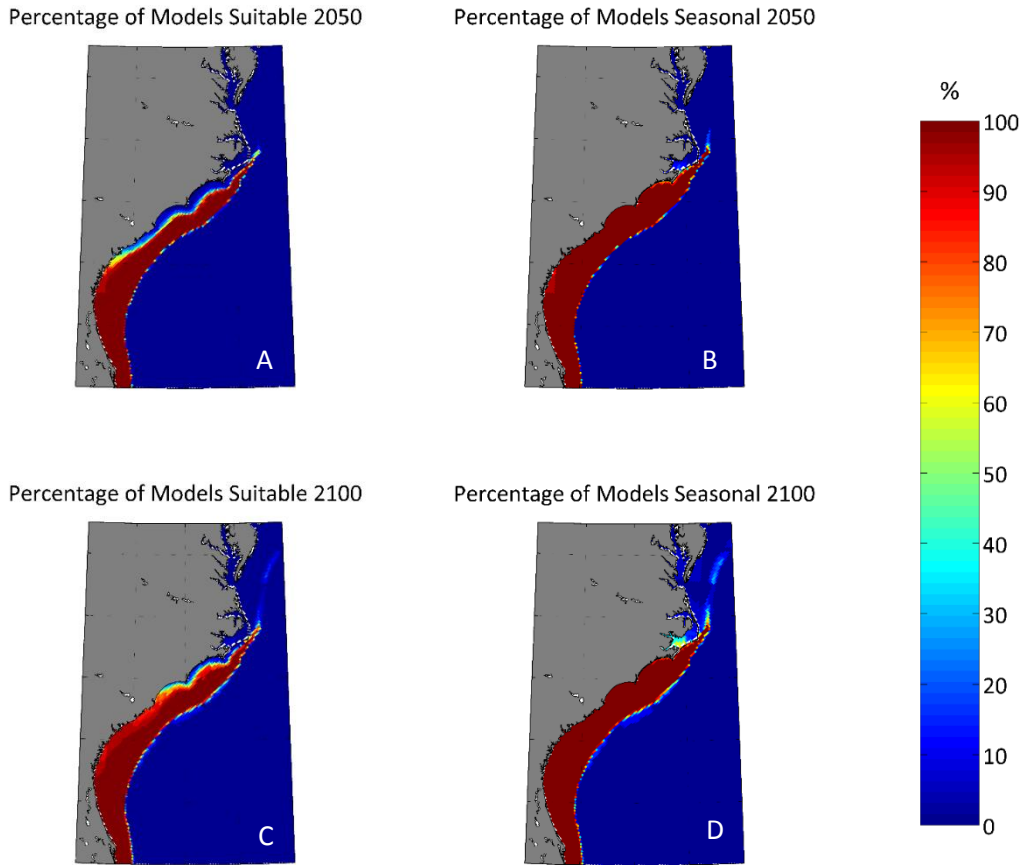


Figure 3.3: Percentage of RCP 8.5 models (out of 17) that project year-round (0-1 suboptimal months; A,C) and seasonal (2-3 suboptimal months; B,D) lionfish habitat for the 2050 (2040-2060; A,B) and 2100 (2080-2100; C,D) periods

CHAPTER 4

DISCUSSION

The aim of this investigation was to explore the expansion of lionfish thermal habitat associated with anthropogenic global warming as projected by an ensemble of IPCC-style climate models. Based on these models, I expect to see a substantial increase in potential lionfish habitat in the coming century. As expected, the RCP 4.5 scenario leads to a smaller BWT niche for lionfish, about 50% less increase in total areal extent by the end of the 21st century in comparison to the RCP 8.5 scenario. This is largely due to the decreased rate of expansion in the second half of the century. This is also expected, as the RCP 4.5 scenario caps emissions by 2050 (Meinshausen *et al.*, 2011; van Vuuren *et al.*, 2011). Under the RCP 8.5 scenario, lionfish's projected range will expand to include almost the entire SAB, with the remaining area susceptible to seasonal invasion by the species. This shoreward expansion of range is relatively unique among fishes, with most species distribution models projecting poleward shifts of marine fishes with climate change (Perry *et al.*, 2005; Cheung *et al.*, 2010; Hare *et al.*, 2012).

So far, the only effective management strategy against lionfish is regular culling of adults. This has been shown through both models (Arias-González *et al.*, 2011; Barbour *et al.*, 2011; Morris *et al.*, 2011) and experiments (Frazer *et al.*, 2012; Green *et al.*, 2014). Although complete eradication is almost certainly impossible, studies have shown that

partial eradication of adults can be extremely effective at reducing lionfish populations and restoring prey biomass (Morris *et al.*, 2011; Frazer *et al.*, 2012; Green *et al.*, 2014). However, these previous analyses were conducted for Bahamian populations of lionfish. Characteristics of the SAB may make the dynamics of invasion and management different than Bahamian reefs for a number of reasons. For instance, lionfish density is much lower in the SAB than it is in the Bahamas, averaging 21.2 lionfish per hectare and 393 lionfish per hectare, respectively (Whitfield *et al.*, 2007; Green & Côté, 2009). In theory, this would make controlling populations easier in the SAB. However, primary lionfish habitat is currently further offshore and in deeper water than the Bahamian reef system, requiring use of SCUBA to cull individuals rather than snorkeling or freediving. Additionally, limited visibility caused by increased turbidity on the SAB combined with fewer fish being easy to find may limit the efficiency of targeted culling efforts. These factors make culling in the SAB comparatively difficult and expensive, and could preclude many civilians from hunting lionfish recreationally.

The shoreward expansion of this voracious predator population is alarming. However, it is important to note the caveats of the techniques used here. I explored the BWT changes associated with two emissions scenarios, RCP 4.5 and RCP 8.5. The RCP 8.5 scenario is considered the “worst-case” (or “business as usual”) that anticipates increasing rates of emissions over time. The RCP 4.5 scenario is more moderate, and suggests a stabilization in radiative forcing by year 2100. Of course, the exact evolution of future emissions is unknown, and my projections of lionfish habitat are sensitive to assumptions regarding cumulative emissions of greenhouse gases in coming decades.

Note, however, that emissions during the recent five years have met or exceeded those expected under the RCP 8.5 scenario (Fuss *et al.*, 2014), and continued “business-as-usual” emissions seems increasingly likely.

In addition to assumptions regarding the future evolution of climate, my results have not considered future rapid change in lionfish physiology and behavior, nor the potential adaptability of larger piscivorous fishes and sharks in the region that may exert biological control on the population, particularly fish weakened by suboptimal physical conditions (Maljković *et al.*, 2008; Mumby *et al.*, 2011; Diller *et al.*, 2014). My results are also sensitive to the bioclimatic envelope parameters (i.e. that “suboptimal months” is a useful metric, lionfish behave similarly in cold-water habitats), suitability of new ranges (presence of appropriate bottom-habitat, available food), and even lionfish’s current range (wintertime surveys are rare). Planque *et al.* (2011) review other sources of uncertainty in distribution models, and the difficulties with this model are no exception.

Despite these caveats, I expect this information will be useful for fisheries managers and conservationists throughout the Southeastern United States as they consider the likelihood of lionfish invasion in coming years. Lionfish have already been found in estuaries (Jud *et al.*, 2011; Prakash *et al.*, 2012), which are valuable nursing grounds for many important species supporting the \$162 million commercial fishery of the SAB (National Marine Fisheries Service, 2013). Economically, much more is brought in by tourism and recreational fishermen as well. Georgia and the Carolinas are home to many ecologically and economically valuable estuaries and protected areas, and any

insight regarding the timing and likelihood of lionfish invasion would be vital for planning future eradication efforts and marine spatial planning.

Mechanistic species distribution models (SDM) – models using experimentally-derived physiological limits to simulate future distributions – are uncommon for fish species (but see Hare *et al.*, 2012). Nevertheless, similar methodology can be applied across species in a variety of different systems (Wetthey *et al.*, 2011; Glibert *et al.*, 2014; Overgaard *et al.*, 2014; Fly *et al.*, 2015). The more common approach for SDMs, called correlative SDMs, utilizes presence/absence data from established populations to statistically determine parameters relevant to their occurrence. These parameters are then used to estimate a species' range in currently unoccupied regions (Guisan & Zimmermann, 2000). However, this method can underestimate the impact of invasive species because the invader may be released from whatever biological interactions were responsible for confining expansion in its native range (Fitzpatrick *et al.*, 2006; Broennimann *et al.*, 2007). As a result, correlative SDMs may be more conservative for species in new habitats than mechanistic models (Buckley *et al.*, 2010). Similarly, research regarding species' range expansion under conditions associated with future climate change may benefit by considering both biotic and abiotic factors in defining niche space (Helmuth *et al.*, 2005; Buckley *et al.*, 2010; Woodin *et al.*, 2013).

In summary, the South Atlantic Bight is expected to warm substantially over the coming decades. With that warming, ranges will expand, contract, and move for most mobile and widely-dispersing species, likely leading to changes in the ecosystem; lionfish

are just one particularly damaging example. The magnitude of these changes can be mitigated by large-scale decreases in greenhouse gas emissions, continued lionfish culls, and increased education about invasive species.

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