

REGULAR ARTICLE

Climate variability hypothesis is partially supported in thermal limits of juvenile Northwest Atlantic coastal fishes

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Abstract

As ocean warming continues to impact marine species globally, there is a need to understand the mechanisms underlying shifts in abundance and distribution. There is growing evidence that upper and lower temperature tolerances rather than mean preferences explain range shifts, but the full thermal niche is unknown for many marine species and observational data are often ill-suited to estimate the upper and lower thermal tolerances. We quantified critical thermal maximum (CT_{max}) and critical thermal minimum (CT_{min}) using standard methods to quantify temperature limits and thermal ranges of 14 economically and ecologically important juvenile fish species on the US Atlantic coast. We then tested the climate variability hypothesis (CVH), which states that higher-latitude species should have a wider temperature tolerance due to higher climatic variability closer to the poles. Our findings generally support the CVH in the juvenile fishes that we evaluated. However, low-latitude species were not uniformly stenothermal. Rather, species with median occurrences across a wide range of latitudes had wide temperature tolerances, but only the tropical species we tested had more narrow ranges. These findings suggest that quantifying temperature tolerances may be used to predict which low-latitude species are most likely to shift in response to warming water and those that may be more sensitive to climate change in this region.

KEYWORDS

biogeography, climate change, climate variability hypothesis, CT_{max} , CT_{min} , temperature tolerance, thermal range, US Atlantic coast

1 | INTRODUCTION

The global redistribution of biodiversity in response to warming and other changes associated with climate change will change ecosystem productivity and challenge food security and overall human well-being (Pech et al., 2017; Poloczanska et al., 2013; Stock et al., 2017). Thus, it is critical to understand mechanisms underlying shifts in distribution and abundance of marine organisms upon which coastal communities depend. Temperature affects every physiological process in marine ectotherms including individual growth, consumption rates, and survival (Brett, 1956; Brett, 1970; Claireaux & Lefrançois, 2007; Fry, 1971;

Pörtner & Peck, 2010). Trade-offs between production, metabolism, and mortality can scale up to population and ecosystem-level processes (Barneche et al., 2014) with climate change predicted to decrease overall global marine biomass (Carozza et al., 2019). Furthermore, as ectotherms use temperature as a primary signal for critical life-stage events, warming will likely impact the timing of spawning, migration, and egg and larval transport (Pörtner & Peck, 2010). Changing environmental cues and conditions can result in a mismatch between resource requirements and availability (Durant et al., 2007).

Species have already started shifting their distribution in response to ocean warming (Nye et al., 2009; Perry et al., 2005; Pinsky

et al., 2013), and there is growing recognition that changes in temperature at the extremes of species range better explain historical range shifts than the mean temperature preference (Fredston et al., 2021; Lynch et al., 2014; Morley et al., 2017). Although many studies have focused on the temperature at which a species experiences their optimum growth rate, an organism's thermal limits have been demonstrated as a better indicator of a species' geographic range and population productivity (Lynch et al., 2014). For example, Rapoport's rule describes a phenomenon where species' geographical ranges, measured in degrees of latitude, tend to increase with latitude (Rapoport, 1975; Stevens, 1989). This observation forms the basis of the climate variability hypothesis (CVH) that postulates that stable climates select for narrower thermal tolerances among species that inhabit them, and more variable climates select for organisms with a large range of temperature tolerances (Dobzhansky, 1950; Gutiérrez-Pesquera et al., 2016; Shah et al., 2017; Stevens, 1989; Sunday et al., 2011). It is important to note that Rapoport's rule has been observed more frequently in terrestrial organisms than in marine organisms, perhaps because seasonal variation in environmental temperatures is generally much greater on land than in the ocean (Cohen, 1994; Pörtner & Peck, 2010). This discrepancy is demonstrated by studies that generally support Rapoport's rule in terrestrial settings where species at high latitudes possess the widest thermal tolerance range while studies in aquatic ecosystems often refute some or all aspects of the rule (Gutiérrez-Pesquera et al., 2016; Pintor et al., 2015; Sunday et al., 2011). Some studies have shown that aquatic species at higher latitudes display narrower thermal tolerances than those at lower latitudes (Pörtner & Peck, 2010; Shah et al., 2017).

To determine if there is a consistent pattern in species thermal limits and latitude of occurrence for marine fishes, we tested the CVH in common juvenile fish species across nine different families along the US East Coast. We measured the critical thermal minimum (CT_{min}) and critical thermal maximum (CT_{max}) of 14 species of North Atlantic fishes found near Cape Hatteras, NC, a major biogeographic barrier separating distinct subtropical and temperate species (Briggs, 1974; Briggs & Bowen, 2012; Floeter et al., 2008). We hypothesized that CT_{min} would be more highly correlated to their center of occurrence than CT_{max} . We also hypothesized that their temperature range, the difference between CT_{min} and CT_{max} , would increase with the median latitude of occurrence. We hypothesized that CVH would be supported, with fish species whose center of occurrence occurred at mid-latitudes having a larger thermal range than tropical species.

2 | METHODS

2.1 | Study site

Our study region encompasses seven estuarine and one offshore locations in North Carolina, USA (Figure 1). This region is located just south of the biogeographic barrier at Cape Hatteras, NC, the

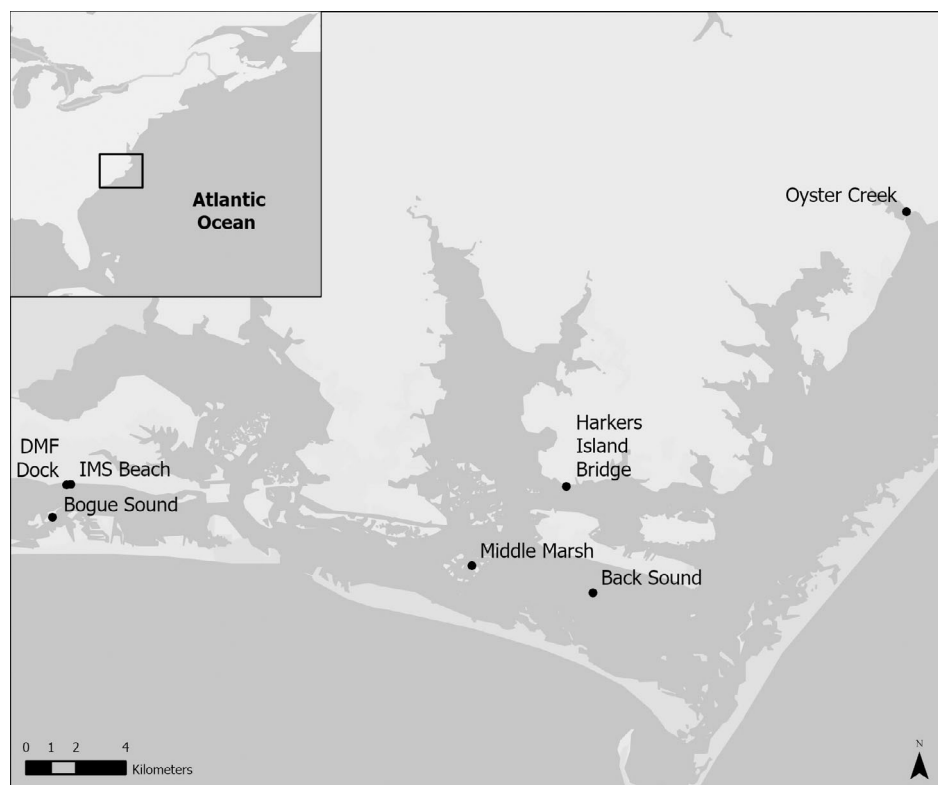
narrowest region of the continental shelf that separates the South Atlantic Bight from the Mid-Atlantic Bight to the north. As there is cold water above the barrier and warm subtropical water below because of Gulf Stream redirection (Briggs & Bowen, 2012), both subtropical and temperate species reside here. To obtain a diverse assemblage of species, a variety of collection methods were used, including trawls, traps, and cast-nets from September 2020 to October 2022. We collected 1179 samples of various juvenile species from nine different families. After fish were collected, they were acclimated to one of three acclimation temperatures, 15°, 20°, and 25°C. We selected these temperatures because they were within the range of temperatures that fish in this region frequently experience. Water temperature was adjusted by no more than one degree per day to reach the acclimation temperature. The fish were kept at their respective acclimation temperature for at least 7 days before we tested for critical thermal values. They were fed at least once each day before the trials. On the day before each trial, one fish was placed into an individual experimental tank to allow it to acclimate for at least 24 h. The tanks were kept at the fish's respective acclimation temperature using a water-bath and/or small tank heaters before the start of the experiment. Fish were not fed within 24 h of the experiment. All biotic samples were collected and processed in accordance with the University of North Carolina's Institutional Animal Care and Use Committee protocol (IACUC permits: #20-207.0 and #22-106.0).

2.2 | Critical thermal method

To test thermal range limits of these coastal fish species, we utilized previously established methods for CT_{max} and CT_{min} . CT_{max} and CT_{min} is a common and accepted method of quantifying temperature tolerance in both terrestrial and marine organisms (Becker & Genoway, 1979; Cox et al., 1974; Morgan et al., 2018). Both endpoints are defined as the temperature at which an organism's locomotion becomes disorganized and weakened in response to rapid temperature change (Morgan et al., 2018). In fish specifically, this is usually observed as an inability to maintain an upright position and leaning heavily or flipping briefly upside down while attempting to swim in the water. The use of CT_{max} and CT_{min} was chosen for this experiment because it allowed for trials of a wide variety of individuals to be completed in a relatively short period of time, allowing greater sample sizes (Table 1) and a higher degree of confidence in the results.

Acclimation temperature plays an important role in these critical thermal values. Higher acclimation temperatures have been documented to increase critical thermal values in marine fish, whereas lower acclimation temperatures have been shown to decrease them (Barker et al., 2018; Pörtner & Peck, 2010; Zhang & Kieffer, 2014). We report and confirm that acclimation temperature had an effect on critical thermal values, so we only compared thermal temperature range at an acclimation temperature of 20°C. After CT_{max} and CT_{min} was tested on fish in the lab, the fish were euthanized with a lethal dosage of MS-222 dissolved in the salt-water. The fish was then measured for

FIGURE 1 Estuarine and offshore collection sites in North Carolina. Inset shows the location of sample sites within the broader Northwest Atlantic Ocean.



both total length, standard length, and mass (grams) to determine if size affected CT_{max} and CT_{min} .

To test CT_{max} , we based our experimental setup on a previous study (Morgan et al., 2018). Each fish was placed in a 9.5-L glass tank each with a pump fed into a vertical PVC pipe; larger fish were placed in a 29.5-L tank. A 300-W coil heater was used to warm the water and clipped to the top opening of the PVC pipe. Holes were drilled along the bottom of the pipe to allow even heating throughout the surrounding tank. The pump and heater were separated by a mesh panel to prevent reef-associated fish from laying against those structures, which would alter their body temperature and make it difficult to determine loss of equilibrium. A proportional integral derivative (PID) controller was connected to the coil heater and a temperature sensor to maintain the rate of warming, that is, 0.3°C per minute or 18°C per hour. This ramping rate is a widely accepted rate for use in CT_{max} experiments (Becker & Genoway, 1979; Cox et al., 1974), and slower warming rates may result in more variable and/or lower CT_{max} values (Mora & Maya, 2006; Moyano et al., 2017).

The temperature was ramped in one tank at a time, and the fish in this tank was monitored continuously during this ramping period. As soon as it displayed clear weakening of orientation or motor control—usually defined as leaning during swimming and/or briefly flipping upside down—the fish was removed from the tank and the ramping process ceased. The temperature at which this behavior was observed was recorded as CT_{max} .

Similar to CT_{max} experiments, to determine CT_{min} , an individual fish was placed in each of several 29.5-L glass tanks 1 day before testing. A separate holding tank of water approximately 4°C was chilled,

and the PID controller activated a submersible pump that delivered cold water to the experimental tank to achieve the desired cooling rate of -0.3°C per minute. As with the CT_{max} tests, fishes in the tank were monitored until signs of motor control loss were detected after which the temperature value recorded as the CT_{min} and length and weight measurements were taken.

For each species with at least seven replicates in our critical thermal value trials at 20°C , a linear model was used to determine if a relationship existed between mass and critical thermal values. The number of individuals tested for CT_{max} and CT_{min} and then used in the statistical analysis is given in Table 1. We selected this acclimation temperature as it contained the largest sample of juvenile fish for the majority of our species. To perform multiple comparisons between critical thermal values and mass between each species, we conservatively used a Bonferroni correction that changed the significance values as follows for CT_{max} ($p\text{-value} = \frac{0.05}{15} = 0.00333$) and CT_{min} ($p\text{-value} = \frac{0.05}{14} = 0.00357$).

2.3 | Climate variability hypothesis

We used species distribution models produced by AquaMaps (Kaschner et al., 2019) to assign a median latitude of occurrence to each species. Aquamaps uses freely available presence-only data to make species distribution maps for many species globally. The maps have been validated with independent observation, and the models perform well (Anderson et al., 2003; Phillips et al., 2006; Ready et al., 2010). We estimated median latitude using (1) latitudes of grid

TABLE 1 Species evaluated for CT_{max} (a) and CT_{min} and sample size at each of three acclimation temperatures (15, 20, and 25°C).

Species	CT _{max}			CT _{min}		
	Acclimation temperature (°C)					
	15	20	25	15	20	25
Family Carangidae						
Crevalle Jack <i>Caranx hippos</i>		7			7	
Pompano <i>Trachinotus carolinus</i>		25 (24)	25		26 (25)	20
Permit <i>Trachinotus falcatus</i>		34 (32)			31	
Family Clupeidae						
Atlantic thread herring <i>Opisthonema oglinum</i>		20			14	4
Family Monacanthidae						
Planehead filefish <i>Stephanolepis hispidus</i>	25	25 (24)	13	25	25	12
Family Serranidae						
Black sea bass <i>Centropristis striata</i>		31 (9)	12	21	40 (16)	16
Gag grouper <i>Mycteroperca microlepis</i>		26	17		26 (25)	25
Family Paralichthyidae						
Gulf flounder <i>Paralichthys albigutta</i>		23	21		25 (23)	15
Family Lutjanidae						
Gray snapper <i>Lutjanus griseus</i>	25	26	25	25	25	25
Lane snapper <i>Lutjanus synagris</i>		10 (9)	8		1	
Mutton snapper <i>Lutjanus analis</i>		7	8		2	
Family Sparidae						
Pinfish <i>Lagodon rhomboides</i>	15	28 (22)		34	26 (20)	
Sheepshead <i>Archosargus probatocephalus</i>		25	24	4	25/14	13
Family Sciaenidae						
Southern kingfish <i>Menticirrhus americanus</i>		19			21	
Spot <i>Leiostomus xanthurus</i>	16	19		19	20 (19)	
Spotted sea trout <i>Cynoscion nebulosus</i>		11			10	
Family Labridae						
Tautog <i>Tautoga onitis</i>		9			11 (10)	

Note: Shaded columns indicate the acclimation temperature used to test latitude of occurrence and thermal tolerances. Numbers in parentheses indicate sample sizes once sizes were restricted to <80 g and outliers were removed.

cells that Aquamaps predicted 90% probability of occurrence or higher, and (2) latitudes of grid cells at which at least a 50% or higher probability of occurrence. Our results were qualitatively the same, so we used the values estimated using the 50% or higher occurrence threshold to better capture that species' core habitat.

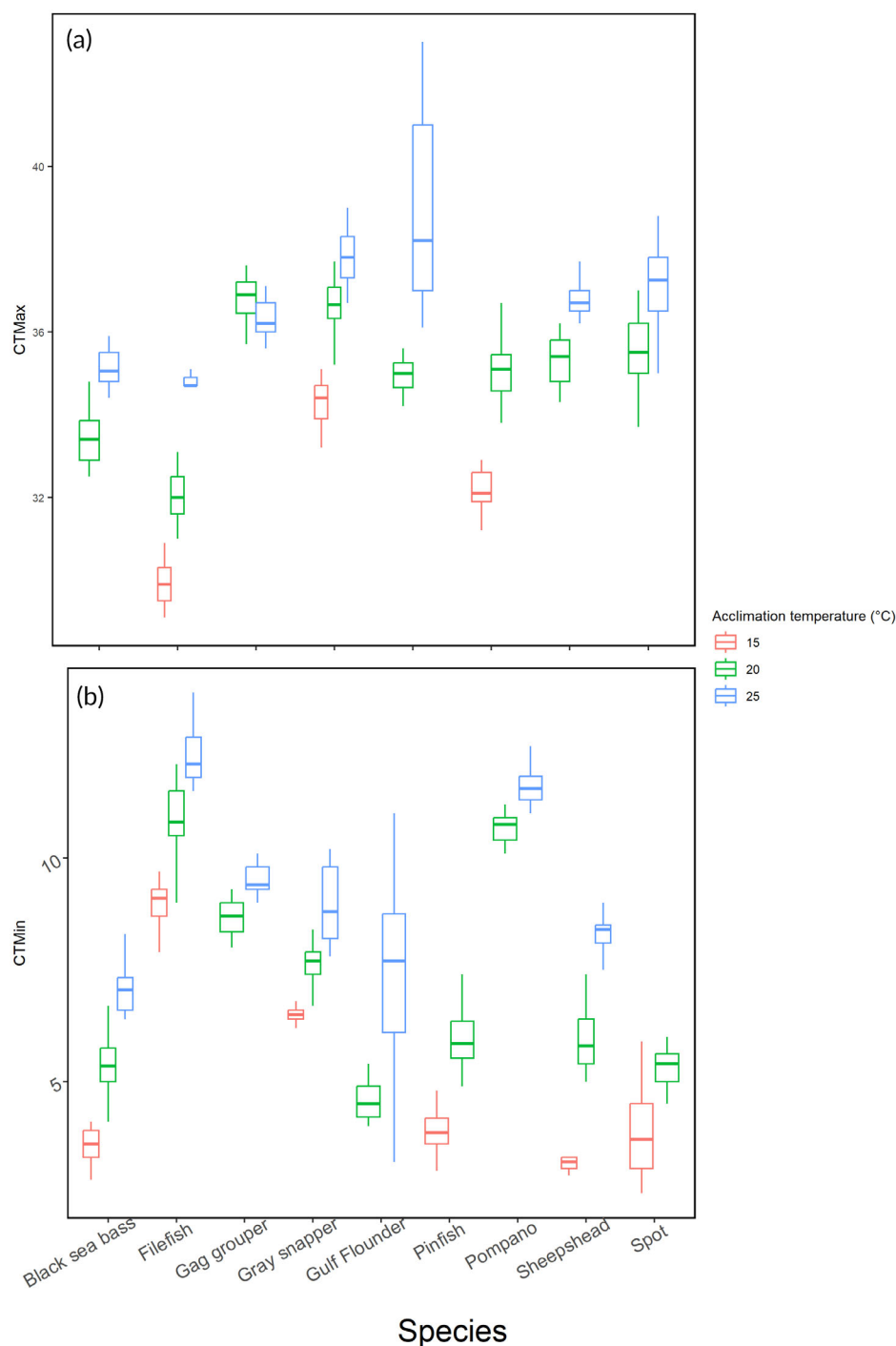
The median latitude of occurrence for each species was plotted against CT_{min} and CT_{max} values for each species (using only 20°C acclimation trials) to determine if critical thermal values changed with the median latitude of occurrence. To directly test the CVH, we calculated critical thermal range (CT_{range}) by subtracting each species average CT_{min} from their average CT_{max} for species that had seven samples in both our CT_{min} and CT_{max} trials (Table 1). Species latitude was plotted against CT_{range} , and a linear model was created to test if thermal tolerance range was a function of species latitude. An ANOVA test was performed on the linear model after fitting to analyse the validity of the model using the standard significance value of $p < 0.05$.

3 | RESULTS

3.1 | Critical thermal values and acclimation temperature

We ran experiments on 561 samples of juvenile fish species for CT_{max} and 590 samples for CT_{min} (Table 1). For the nine species for which we had at least two acclimation temperatures, acclimation temperature affected both CT_{max} and CT_{min} (Figure 2a). For some species, the effect of acclimation temperature did not appear to affect CT_{max} greatly such as Gag grouper, *Mycteroperca microlepis* (Goode & Bean, 1879). However, for CT_{min} experiments, nearly all species displayed visual differences in CT_{min} between different acclimation temperature groups (Figure 2b). For CT_{max} in particular, the difference in critical thermal values between fish acclimated at 15 and 20°C was larger than the difference between fish acclimated at 20 and 25°C

FIGURE 2 Critical thermal values by acclimation temperature. Effect of acclimation temperature on (a) critical thermal maximum (CT_{max}) and (b) critical thermal minimum (CT_{min}) for nine fish species examined. Only species for which we had at two or more acclimation temperatures are shown.



(Figure 2a). For the remainder of the analysis, we use only the trials that occurred at 20°C.

3.2 | Critical thermal values and species mass

Out of the 15 species examined, only spot *Leiostomus xanthurus* (Lacepède, 1802) and black sea bass *Centropristis striata* (Linnaeus, 1758) had a significant trend between CT_{max} and weight of the 15 species examined ($F_{1,17} = 22.38$, $p < 0.001$, $F_{1,29} = 27.69$, $p < 0.001$,

respectively). Spotted seatrout *Cynoscion nebulosus* (Cuvier, 1830) was the only species that displayed a significant trend between CT_{min} and weight out of 14 species examined ($F_{1,8} = 18.64$, $p = 0.00255$). Black sea bass was one of the few species for which we had a large size range so when we excluded older fish >80 g, the effect of size was no longer significant. Similarly, when outliers, defined as three standard deviations from the mean (Howell et al., 1998), were removed from each individual species, there was no effect of size. We used this reduced dataset for the remainder of the analysis (Figure 3; Table 1).

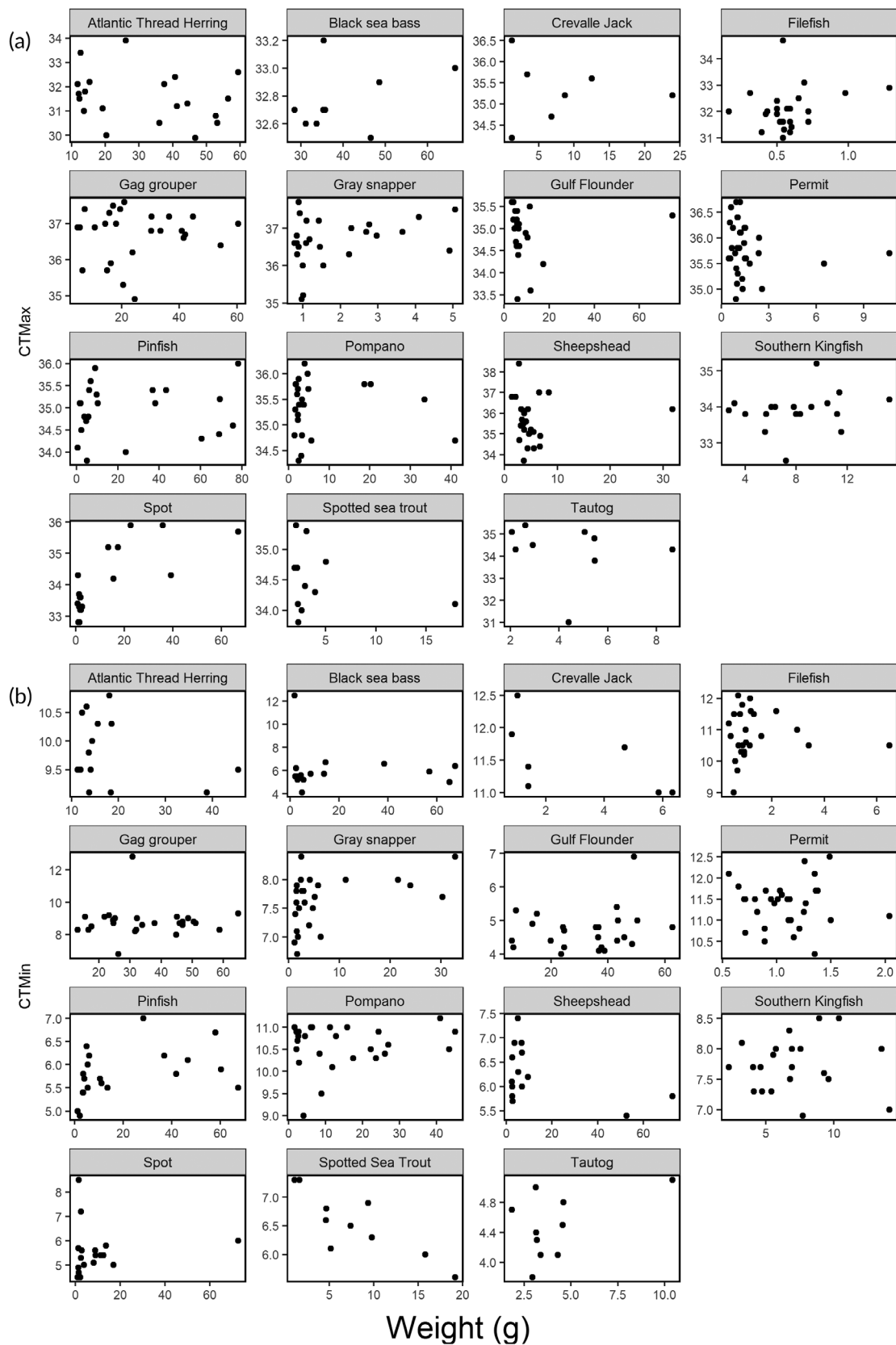


FIGURE 3 Critical thermal values by weight. Relationship of (a) critical thermal maximum and (b) critical thermal minimum versus weight for all individuals weighing less than 80 g by species.

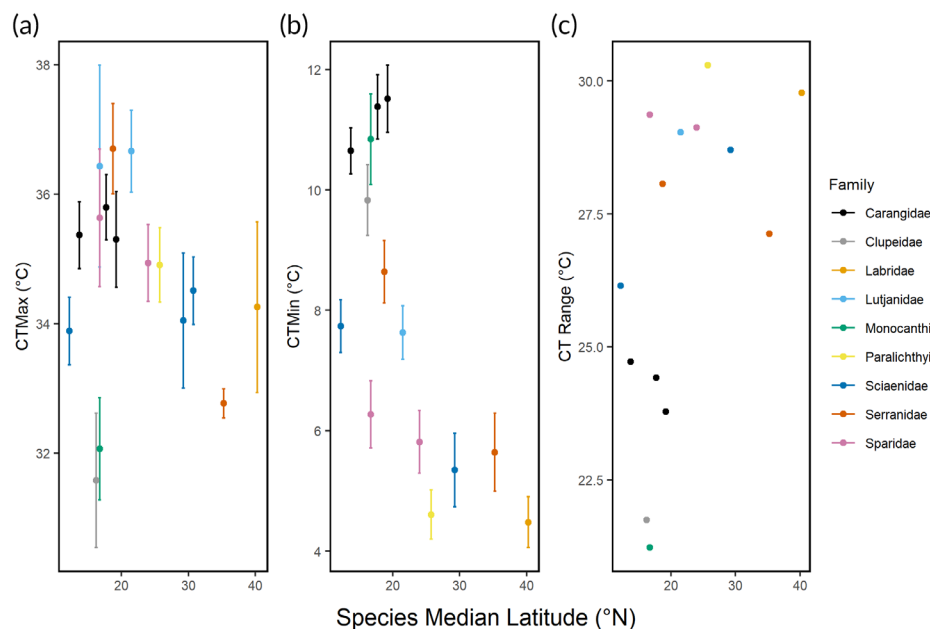


FIGURE 4 Critical thermal values versus median latitude of occurrence by species. Plots of mean and standard deviation of (a) critical thermal maximum (CT_{max}), (b) critical thermal minimum (CT_{min}), (c) scatterplot of CT_{range} ($CT_{max} - CT_{min}$) versus species' median latitude of occurrence. Visually, CT_{min} displayed a trend of greater magnitude than CT_{max} and decreased as median latitude of occurrence increased. For CT_{range} both linear ($F_{1,12} = 5.538$, $p = 0.03649$) and logarithmic ($F_{1,12} = 6.358$, $p = 0.02683$) models were fitted to the data as both were equally good fits to the data according to a comparison of their AIC values. Due to neither CT_{max} or CT_{min} values being normally distributed, a linear model was not plotted for these data.

TABLE 2 Comparison of linear and lognormal models of thermal range as a function of species median center of occurrence.

Model	F-statistic	Adjusted R^2	AIC	ΔAIC	Shapiro Wilk
Linear	$F_{1,12} = 5.31$ $p = 0.039$	0.25	71.02	0.42	$W = 0.95$ ($p = 0.61$)
Lognormal	$F_{1,12} = 4.79$ $p = 0.049$	0.23	20.59	0	$W = 0.94$ ($p = 0.48$)

3.3 | Critical thermal values and species latitude

No statistically significant relationship was observed between CT_{max} and species latitude after accounting for the effect of species ($F_{13,1} = 0.969$, $p = 0.343$, Figure 4a). These data were normally distributed only after accounting for the error and different number of replicates for each species within a nested ANOVA (Shapiro Wilk $W = 0.94666$, $p = 0.51$). Among species, there was considerable overlap in the distribution of CT_{max} values, with averages ranging from $\sim 30^\circ\text{C}$ to slightly above 38°C . Most of the species had values of CT_{max} lying between 33°C to just under 38°C (Figure 4a). Despite the tropical distribution of filefish *Stephanolepis hispidus* (Linnaeus 1766) and Atlantic thread herring *Opisthonema oglinum* (Lesueur 1818), their CT_{max} values were below the overall distribution (32.0 and 31.7°C , respectively).

An inverse relationship was observed between CT_{min} and species latitude (Figure 4b). Compared to CT_{max} , there was greater range in observed average values of CT_{min} , from 3°C to over 12.5°C (Figure 4b). The CT_{min} data had a bimodal distribution and was not normally distributed, so an ANOVA was not performed on the

relationship between latitude and CT_{min} values. However, there was a clear negative trend in CT_{min} as latitude increased from tropical to temperate (Figure 4b).

There was a positive relationship between CT_{range} and species latitude (Figure 4c). We fitted two possible models to the data, linear and logarithmic models, and calculated AIC values for each model to select which model best represented the data (Guthery et al., 2003). The AIC values suggested that both the logarithmic and linear model were equally effective at modeling the data (Table 2). Both models were plotted over our data points and provided further evidence for the observed trend in the data (Logarithmic: $F_{1,12} = 5.437$, $p = 0.03795$; Linear: $F_{1,12} = 5.91$, $p = 0.03167$). All residuals were normal and homoscedastic.

At all median latitude of occurrences, we observed wide ranges in temperature tolerance, spanning 26 degrees of temperature or more. However, we only estimated narrow ranges of temperature tolerance of 25 degrees of temperature or less in tropical or subtropical species, those species whose median latitude of occurrence was less than 25°N .

4 | DISCUSSION

Our results support the CVH in that thermal tolerance range generally decreased with latitude. However, upper and lower thermal tolerances did not decrease linearly with latitude in parallel. Rather, some tropical or subtropical species, those species whose center of occurrence was equatorward of 25°C clustered at higher CT_{min} and lower CT_{max} values. Our results suggest that species with wide thermal ranges (26 degrees of temperature or more) have center of occurrences across a wide range of latitudes, including some tropical or subtropical in distribution. However, we only estimated narrow temperature tolerances in low-latitude species. These results suggest that we cannot assume that all tropical or subtropical species have a narrow temperature tolerance and that there are low-latitude species with wide temperature tolerances that may be able to shift their distribution more readily than those with narrow temperature tolerance. Quantifying temperature tolerances for a wider variety of species would allow us to understand the generality of this observation.

The results of our CT_{range} data demonstrated that coastal marine species on the North Carolina coast provided evidence for the CVH, although the relationship observed in these marine fishes was different from the generally positive linear relationship between thermal range and latitude observed in terrestrial systems (Gutiérrez-Pesquera et al., 2016; Sunday et al., 2011). In this study, thermal range seemed to plateau at mid-latitudes and decreased as their distribution moved toward the equator, as has been observed in other studies (Pörtner & Peck, 2010; Shah et al., 2017). We were unable to test high-latitude species and cannot determine if thermal ranges increase monotonically with latitude as they do on land. However, we suspect that this relationship would eventually become parabolic to match observations in marine fishes where polar species had the lowest thermal tolerance range of all the species examined (Pörtner & Peck, 2010). The vaguely logarithmic shape of the trend in our study also supports this hypothesis. Similar to previous studies in aquatic and marine ecosystems, our results suggest that Rapoport's rule does not hold for marine systems, but that does not mean that the CVH is not supported. In marine systems, the highest variability in temperature is at mid-latitudes and the lowest temperature variability is at the poles and the tropics (Laing & Evans, 2010; Sunday et al., 2011). This suspected parabolic relationship between latitude, seasonality, and thermal range may explain some studies in which diversity in some taxa peaked at mid-latitudes in marine systems (Chaudhary et al., 2021; Rutherford et al., 1999).

For coastal North Carolina fish species, CT_{max} values provided little indication of the distribution of fish species and was relatively constant between all species examined. A notable exception to this was the much lower CT_{max} values found in *O. oglinum* and *S. hispidus*, especially unusual given that they are among the most tropical fish species examined in this study. These two species had high CT_{min} values, as was expected for low-latitude species. The combined values of low CT_{max} and high CT_{min} resulted in the lowest range limits. Interestingly, the three Carangid species we tested had high CT_{min} values as expected for low-latitude species, but their CT_{max} values were also

much lower than expected. That these species within a single family had similar upper and lower temperature tolerances illustrates the importance of phylogeny in temperature tolerances in addition to latitude of occurrence and latitude of origin.

The geographic location of where we collected the fish species in this study may be important to consider. Our study site is near where the Gulf Stream bifurcates from the North American East Coast. The warm water that the Gulf Stream brings to the US East Coast allows for a wide distribution of subtropical and temperate species that is not representative of other areas of similar latitude. There is also a sharp temperature gradient between the Mid-Atlantic and South Atlantic Bight (Savidge & Austin, 2007). This combination allows for the sampling of both tropical and mid-latitude fish species, which experience similar temperatures. Thus, many of the low-latitude species that we examined may have higher temperature ranges than most tropical species because of the distribution near a thermally dynamic region.

We did not find evidence of a relationship between critical thermal values and species mass for 12 out of the 15 species examined in this study. This may seem in contrast to other studies that found that thermal tolerance was heavily dependent on size (Zhang & Kieffer, 2014; Pörtner et al., 2008) and ontogeny (Dahlke et al., 2020). However, other studies did not observe a relationship between CT_{max} and mass across juveniles and adults (Ospina & Mora, 2004). Our focus on juveniles is likely the reason why species mass and critical thermal values were uncorrelated, as size range of our samples ranged from 1 to 80 g. Only when we included fish up to 200 g did we see an effect of size in some species like black sea bass. It is likely that a relationship between size and thermal tolerances could have been observed if the size range of fish samples in our study was much larger (Dahlke et al., 2020). However, we deliberately limited our analysis to juveniles to exclude variables that would have potentially complicated our test of the CVH. Future studies should use similar techniques to determine CT_{max} and CT_{min} values on multiple life stages to determine if the CVH is more strongly supported for different life stages.

The plots of critical thermal values versus latitude identified by our study for juvenile species are in some ways reflective of the findings in previous studies. In particular, the lack of any statistically significant trend in CT_{max} values in species from the equator to 40° N latitude aligns with the conclusion in another recent study on temperature limits of fish species that found a much stronger trend in thermal minimums versus latitude over the same latitudinal range (Dahlke et al., 2020). This observation is likely due to how annual ocean temperature profiles change moving from the equator north to the poles. Fish species living at the equator versus species at 40° N experience similar temperature maximums over an annual period, but species further north experience much colder annual minimum temperatures than those at more stable equatorial latitudes.

Another confounding factor in testing the CVH is the fact that temperature tolerance has a genetic basis, and, as such, the temperature variability in which the species evolved may be more important in determining its temperature tolerances than the temperature range it

currently experiences. Species of similar evolutionary history often have similar physiological preferences (Hasnain et al., 2018); the classic example being the Nototheniid fishes that have very narrow temperature tolerances (Pörtner & Peck, 2010), having evolved adaptations to very low, but very stable temperatures in Antarctic waters (Beers et al., 2015). Consider an example of a species of fish which currently inhabits a range of latitude from the equator to 25° N/S. It currently lives in a relatively stable temperature regime that changes little throughout the year, but may have evolved at a time when temperature was more variable. Furthermore, its current distribution may be limited by other factors such as habitat availability. Habitat destruction may have caused its range to shrink from limits at 35° N/S to where it lies presently, but the temperature tolerance the species would require to survive in its historical range has persisted through the time period since this habitat destruction occurred. This would mean that this species would potentially have very different thermal limits compared to another species despite both presently occupying the same latitudinal range, which would appear contrary to the CVH. This illustrates that the climate in which a species evolved is an important consideration when evaluating experimental evidence of the CVH. For example, reef fishes are thought to be relatively stenothermal, but many reef fishes have large latitudinal ranges and have exhibited high acclimation capacity when exposed to temperature increases well above the maximum temperatures projected for climate change (Munday et al., 2008, Burt et al., 2011, Rummer & Munday, 2017).

Previous studies on critical thermal values use data obtained through different sampling designs. Environmental history, local population differences, and acclimation temperatures can greatly affect maximum and minimum temperature thresholds (Barker et al., 2018; Pörtner & Peck, 2010). This can make direct comparisons between critical thermal limits from different studies difficult; although provided that the methods used in the studies are sound, the qualitative trend of critical thermal values with latitude can be compared between studies to see if similar patterns are observed.

It is important to note that our results for critical thermal maxima, minima, and range as a function of latitude are all for juveniles of specific US Atlantic Coast species. Future research is needed to evaluate critical thermal values for other species in a diverse range of latitudes, sizes, and ontogenetic stages to provide more conclusive evidence for the CVH and the trend between latitude and CT_{range} discussed in this study. Further studies of CT_{min} and CT_{max} versus latitude at latitudes outside of the 0–40° N/S range would be of particular interest to discover if the significance of CT_{min} versus latitude compared to CT_{max} is maintained even through higher latitudes, or if CT_{max} becomes a better predictor of species' latitude at higher latitudes as we would anticipate.

If the CVH provides a significant explanation for the latitudinal distribution of fish species as our study and others have suggested, it provides an important framework for which to view how climate change may impact the north/south distributions of fish species. Recognizing these changes may help managers better anticipate shifts of new organisms into their management areas from lower latitudes as the oceans warm. It may also help managers prioritize the

conservation of species that may be unable to relocate in response to climate change due to their current latitudinal distribution. The CVH driving latitudinal changes in the distribution of fish species also means that climatic pulse disturbances are of particular concern to species at low and high latitudes, which generally have narrow temperature tolerance ranges and are therefore more susceptible to extreme weather events than species with higher temperature tolerances (Harris et al., 2018; Mills et al., 2013).

AUTHOR CONTRIBUTIONS

Janet A. Nye conceived the study, developed methods, obtained funding and supervised research. Ryan N. Strader developed methods, led statistical analysis and led manuscript preparation. Sally C. Dowd, Camryn Blawas, Richard D. Mahoney, Natalie C. Patetta, and Jaelyn Leslie collected samples, contributed to experimental protocols, assisted with statistical analysis and made significant edits to the manuscript.

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