



Distinct temperature stressors acting on multiple ontogenetic stages influence the biogeography of Atlantic blue crabs

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ABSTRACT: To understand and predict shifts in species distribution in a changing climate, it is important to consider the exposure and sensitivity of multiple life history stages, particularly for marine species with complex life cycles. In this study, we examined spatio-temporal trends in the abundance of the blue crab *Callinectes sapidus* and how different temperature stressors acting on multiple ontogenetic stages may affect the species' current and future distribution across the Atlantic coast of the USA. Since 1975, crab abundance has remained constant or increased in the northeast and northern mid-Atlantic regions but declined in the southern mid-Atlantic and southeast. In the northeast, abundance changes and the location of the northern range boundary appear to be dictated primarily by lower thermal constraints on summer larval stages and may be reinforced by chronic winter cold stress on juveniles and adults. In the mid-Atlantic, acute winter cold stress on juveniles and adults may regulate crab abundance, whereas in the southeast, temperature stress is likely not limiting or directly driving abundance declines. Temperature projections suggest a potential for northward range expansion and increased abundance in the northeast. In the northern mid-Atlantic, however, changes in the duration, magnitude, and phenology of summer temperatures may have complex effects on crab reproduction. Our results highlight how past and future changes in environmental suitability can vary non-uniformly both within and beyond a species' current range, and the value of examining multiple life history stages and aspects of temperature stress.

KEY WORDS: Range shifts · *Callinectes sapidus* · Life history · Thermal performance · Species distribution model

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1. INTRODUCTION

Poleward range expansions of species in response to climatic warming are now well documented (Parmesan & Yohe 2003, Perry et al. 2005, Poloczanska et al. 2013). Studies are also beginning to show that in addition to shifts in range boundaries, changes in local abundance, growth, and survival are occurring well within range limits, potentially in response to environmental mosaics (Ackerly et al. 2015, Carroll et al. 2016). Understanding current spatial distribu-

tion patterns and predicting future distributional shifts will require identification of the factors limiting occurrence and abundance across a broad geographic range (Sexton et al. 2009).

For species with complex life cycles, where any one of several stages may act as a potential bottleneck, consideration of multiple ontogenetic stages is key in evaluating range expansion potential and climate change vulnerability (Rijnsdorp et al. 2009, Dahlke et al. 2020, Dudley et al. 2021). Since distinct life stages may have different habitat usage and

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physiological constraints (Pörtner & Peck 2010, Russell et al. 2012, Sinclair et al. 2016), the life cycle must be considered in order to identify the relevant environmental variables in space and time that affect a species' distribution and abundance. In addition, multiple aspects of a single environmental driver such as temperature can play a role in determining distribution patterns. These aspects include not just the mean, but also minimum and maximum values, phenology (Burrows et al. 2011, Crickenberger & Wethey 2018), and both the intensity and duration of exposure to lethal and sublethal extremes (Rezende et al. 2014). For instance, poleward distributional limits may be set either by short-term exposure to temperatures below the lower lethal temperature (LT_{min}) or by chronic exposure to temperatures below the lower critical temperature (CT_{min}). CT_{min} is the temperature $\geq LT_{min}$ below which physiological performance is zero but at which there is no acute mortality (Woodin et al. 2013). The aspects of temperature which regulate populations and the affected life history stages may vary across the range of the species and at different spatial scales (Woodin et al. 2013, Seabra et al. 2015). Thus, improved understanding and prediction of biogeographic shifts can be gained by examining how different aspects of the environment constrain multiple life history stages both within and beyond species ranges.

Mechanistic species distribution models have the ability to explicitly incorporate physiology, ecology, and life history (Kearney et al. 2008, Levy et al. 2015); make projections under current and future climate conditions (Crozier & Dwyer 2006, Hare et al. 2010, Régnière et al. 2012); and identify where physiological tolerances (as opposed to dispersal limitation or biotic interactions) may constrain species ranges (Buckley 2008, Kearney & Porter 2009). However, these models often require more data and information than are available for most species and are time-consuming to develop. Another, more easily implemented approach is to use physiological thresholds for a particular life stage (hypothesized to be critical) with temperature projections to predict distributional shifts (Hare et al. 2012, Levy et al. 2015). In

this study, we expand upon this approach by evaluating exposure and sensitivity of multiple life history stages to several different aspects of temperature stress across a species' geographic range, identifying constraints (including life history bottlenecks), and making spatially explicit projections under future climate conditions. We used Atlantic blue crabs *Callinectes sapidus* as our focal species.

Blue crabs are an ecologically and economically important species with a broad geographic range. Their native range in the Northern Hemisphere extends from the northeast coast of the USA through the Gulf of Mexico and Caribbean to Venezuela, and in the Southern Hemisphere from Brazil to Argentina. In the USA, the crabs are the basis of a major commercial and recreational fishery as well as being important benthic predators in their estuarine communities (Hines et al. 1990, Silliman & Bertness 2002). In this study, we focused on crab populations along the US Atlantic coast (Fig. 1). This coastline

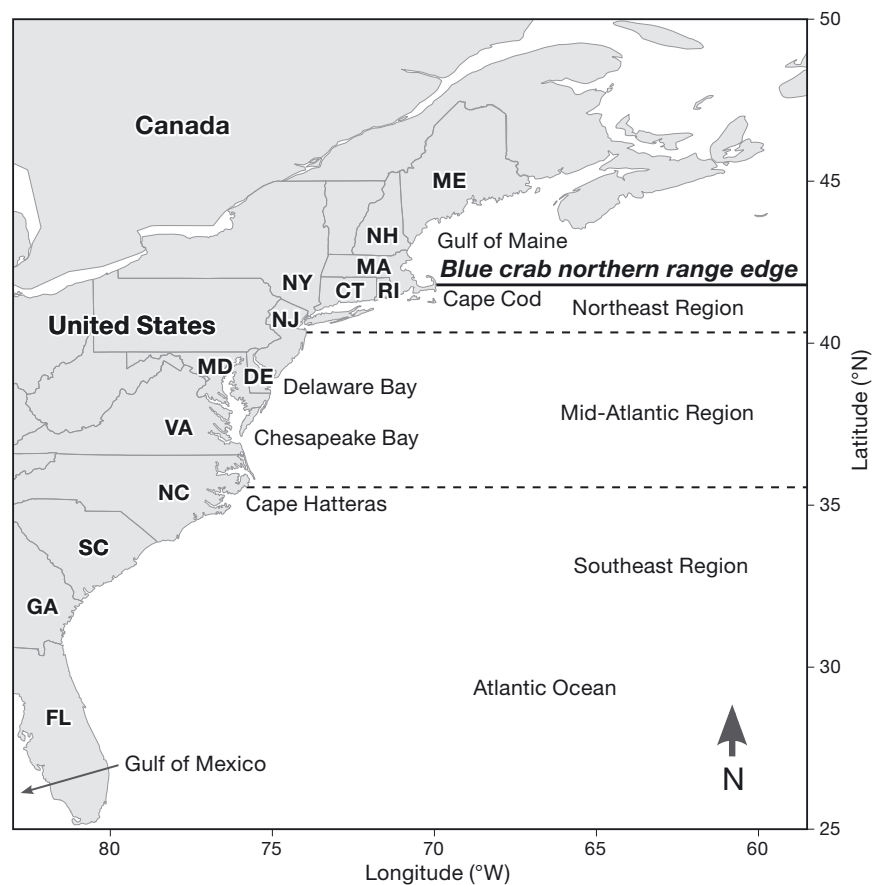


Fig. 1. Focal region (US Atlantic coastline) indicating location of blue crab northern range edge and landmarks and regions referenced in the paper. ME: Maine; NH: New Hampshire; MA: Massachusetts; RI: Rhode Island; CT: Connecticut; NY: New York; NJ: New Jersey; DE: Delaware; MD: Maryland; VA: Virginia; NC: North Carolina; SC: South Carolina; GA: Georgia; FL: Florida

has one of the world's steepest latitudinal thermal gradients (Baumann & Doherty 2013) and represents the central and high latitude (leading edge) portions of the blue crab's range in the Northern Hemisphere. The northernmost permanent populations of crabs in this region occur along the southern and outer eastern shores of Cape Cod, Massachusetts (41.8°N). Recent reports (Johnson 2015) and historical observations (Williams 1973) of blue crabs north of Cape Cod during warm periods suggest that temperature may control the northern high latitude range boundary, and there is potential for a range shift in response to regionally warming seas (Nye et al. 2009, Pershing et al. 2015). Blue crab abundance and environmental suitability may also change within the species' current range. Climate vulnerability assessments for the Northeast US shelf classified blue crabs as having 'very high' overall vulnerability and 'high' species distribution change potential, albeit with low certainty (Hare et al. 2016). Although potential climate impacts on blue crabs have been evaluated in more detail for individual estuaries in this region (e.g. Hines et al. 2011), range-edge populations have received much less attention, and studies have yet to examine population trends from a biogeographic perspective.

Blue crabs have a well-described, complex life cycle (Millikin & Williams 1984, Epifanio 1995) consisting of both planktonic larval stages (residing in offshore surface waters) and juvenile/adult crabs (residing in coastal estuaries). Blue crabs mate in low-salinity waters and then females migrate to the mouths of estuaries to release their larvae. The planktonic larvae (zoea) develop in offshore surface waters over the course of approximately 1 mo (Costlow & Brookhout 1959). In the mid-Atlantic region, peak spawning occurs in July and August, with larval abundance peaking in August and September (Epifanio et al. 1984, Rittschof et al. 2010). In the northeast region, the blue crab life cycle (including breeding phenology) is less well studied, but recent work suggests it is similar to the mid-Atlantic (Weiss & Downs 2020). In the southeast region and Gulf of Mexico, the larval period was thought to be bimodal, with most spawning in spring (January–June), and a smaller peak in late summer–early fall (references in Criales et al. 2019); however, more recent evidence suggests peak spawning may also occur in mid-summer (Gelpi et al. 2009, Ogburn & Habegger 2015, Kemberling & Darnell 2020). The post-larval stages (megalopae) then return to an estuary, primarily through wind-driven surface currents (Epifanio & Garvine 2001), where they settle in benthic habitats and metamorphose into juvenile crabs.

Depending on oceanographic conditions, blue crab larvae may return to their parent estuary or be transported among estuaries (Epifanio et al. 1989, Johnson & Hess 1990), and studies suggest that high gene flow occurs among neighboring estuaries (McMillen-Jackson et al. 1994, McMillen-Jackson & Bert 2004, Alaniz Rodrigues et al. 2017). On the Atlantic coast, blue crabs apparently do not move among estuaries after settlement (McMillen-Jackson & Bert 2004), so dispersal occurs primarily during larval stages. Settled juveniles migrate to lower salinity waters, where they grow to maturity. In the mid-Atlantic and northeast regions (north of Cape Hatteras, 35.3°N), adult and juvenile crabs hibernate during the winter months, buried in sediment and deep channels. In the southeast region and Gulf of Mexico, the crabs are active year-round.

The life history stages of blue crabs (eggs, zoea, megalopae, juveniles, adults) are subject to different environmental conditions (e.g. estuaries vs. offshore) and have different environmental tolerances that have been documented in laboratory studies. Thus, they may be differentially affected by environmental change, and different life stages may be limiting in different areas. There is some evidence that winter severity can regulate survival of adult and juvenile blue crabs (Rome et al. 2005, Bauer & Miller 2010a, Weiss & Downs 2020), but constraints on early life history stages have not been examined. In terms of understanding range expansion potential, studies on other crab species have typically used temperature projections in combination with correlative species distribution models such as MaxEnt (Compton et al. 2010, de Rivera et al. 2011, Neumann et al. 2013, Murphy 2020) that do not incorporate known aspects of life history and physiology. Other studies have quantified temperature thresholds for multiple life history stages and identified bottlenecks using historical temperature data (Sanford et al. 2006, de Rivera et al. 2007) but have not used this information to make projections.

In this study, we (1) investigated how the multiple life stages of blue crabs are constrained by multiple aspects of temperature stress, (2) related these constraints to current abundance trends and spatial distribution, and (3) projected these constraints into the future to identify how abundance and distribution might shift under climate change. To achieve these goals, we first examined historical trends in blue crab abundance across the US Atlantic coastline to identify spatial patterns in abundance change with the crabs' current range. We then compared the lower and upper thermal tolerances of all life history stages, ob-

tained from a thorough literature review, to ecologically relevant aspects of water temperature across the coastline to identify bottlenecks. Finally, we evaluated how projected changes in ecologically relevant aspects of water temperature may affect thermal constraints on crabs in different regions of the coastline.

2. METHODS

2.1. Trends in blue crab abundance

To provide context for our analysis of physiological constraints, we first examined spatial variation in blue crab abundance trends across the Atlantic coastline. We quantified the linear trend in annual blue crab abundance indices (log catch-per-unit effort) from fishery-independent surveys from 9 states which had at least 25 yr of data (Table S1 in the Supplement at www.int-res.com/articles/suppl/m690p097_supp.pdf). These surveys sampled adult and juvenile crabs (there is, unfortunately, no coastwide long-term monitoring of blue crab larval stages). If a state had multiple survey indices, these were averaged with equal weighting. Start years ranged from 1975–1988, and the time series ended in 2015. To expand the spatial and temporal extent of this analysis, we also quantified trends in annual commercial blue crab landings (harvest of legal-sized adults) for 10 states over the same time period (Table S1). These data are less reliable, however, as changes in landings can also be influenced by changes in fishing effort and reporting. The abundance indices and landings data were standardized by computing their Z-scores (i.e. subtracting the mean and dividing by the standard deviation) to allow for comparison of slopes across states. To account for autocorrelation of

residuals, generalized least squares models with AR(1) correlation structures were used.

2.2. Physiological constraints by life stage

To examine physiological constraints on blue crabs, as well as the life history stages acting as potential population bottlenecks, we first obtained lower and upper thermal tolerances for all blue crab developmental stages (egg, zoea, megalops, juvenile, and adult) from the literature (Table 1). All estimates came from experimental laboratory studies. We considered both upper and lower lethal (LT_{\min} , LT_{\max}) and critical (CT_{\min} , CT_{\max}) temperature thresholds where information was available. Since temperature tolerance estimates varied among studies, ranges are presented for each life history stage. A summary of the methods and results of each literature study, which we used to identify these ranges, are presented in Table S2. Since our study region encompassed the central and poleward edge of the species' range, we suspected that lower tolerances would be more limiting than upper tolerances, but analyzed both for completeness.

2.2.1. Juvenile/adult crabs

For juvenile and adult blue crabs, we defined CT_{\min} as the temperature at which feeding and growth (ecdysis) cease and winter hibernation is induced. Protracted periods below this threshold would inhibit growth and reproduction, preventing population establishment. CT_{\min} estimates ranged from 9–15°C. For our main analysis, we used the value of 12.2°C, a mean of previously reported values that was used by

Table 1. Lower and upper temperature thresholds (LT: lethal; CT: critical) of blue crabs at different life stages. For details on the methods and results for each reference, see Table S1

Life stage	Threshold	Temp. (°C)	References
Juvenile/adult	LT_{\min}	0–5	Tagatz (1969), Rome et al. (2005), Bauer & Miller (2010b)
	LT_{\max}	37–39	Tagatz (1969), Holland (1971)
	CT_{\min}	9–15	Churchill (1919), Leffler (1972), Smith (1997), Brylawski & Miller (2006)
	CT_{\max}	33–34	Holland (1971), Leffler (1972)
Megalops	CT_{\min}	15–20	Costlow & Brookhout (1959), Costlow (1967)
	CT_{\max}	30	Costlow (1967)
Zoea	CT_{\min}	20–25	Sandoz & Rogers (1944), Costlow & Brookhout (1959)
	CT_{\max}	29	Sandoz & Rogers (1944), Costlow & Brookhout (1959)
Egg	CT_{\min}	16–19	Sandoz & Rogers (1944), Amsler & George (1984)
	CT_{\max}	29	Sandoz & Rogers (1944)

Darnell et al. (2009). We defined LT_{min} for adult/juvenile crabs as the temperature below which mortality is observed during hibernation. Estimates for LT_{min} ranged from 0–5°C. All studies found an increased risk of mortality at temperatures below 3°C, which is the value we used for our main analysis. Mortality rates below this threshold depended on a variety of factors, including acclimation temperature, salinity, body size, and duration of the cold stress. For upper thresholds, we used 33°C for CT_{max} and 37°C for LT_{max} , which were based on mortality measures under conditions of acute and chronic heat stress.

Surveys indicate that juvenile and adult crabs overwinter in the deeper parts of estuaries, with some variation in exact location depending on age and sex, and it is during this time period that cold-induced mortality is reported (Rome et al. 2005, Bauer & Miller 2010a). There are no reports of heat-induced mortality for Atlantic blue crabs at other times of the year (e.g. during mating or spawning aggregations), but for completeness, we assume the deeper parts of the estuary also reflect the coolest environments available to crabs during summer. Therefore, we used time series of estuarine bottom water temperatures to examine thermal suitability across the Atlantic coastline. We specifically examined (1) the number of days per year with temperatures suitable for blue crab growth (above CT_{min} and below CT_{max}) and (2) the number of days per year with temperatures that were acutely stressful (below LT_{min} and above LT_{max}). As a data

source, we used daily mean bottom water temperatures from 10 estuaries (NOAA National Estuarine Research Reserve System 2016) spanning the US Atlantic coast (Fig. 2a, Table S1). Start dates ranged from 1994–2002, and the time series ended in 2015. Gaps in the time series of less than 30 d were linearly interpolated. If, after this interpolation, a year still contained missing summer values (between May and September), that year was excluded from the analysis of days above CT_{min} , above LT_{max} , and below CT_{max} (calculated by subtracting the number of days above CT_{max} from the number of days in the year). If a year still contained missing values between January and March, it was excluded from days below LT_{min} . Many years from northern sites were excluded due to missing data during winter months. In addition to the values used in our main analysis, we also conducted a sensitivity analysis using the minimum and maximum estimates of each temperature tolerance. Due to the shortness of the time series and missing data, we were unable to examine temporal trends in suitability.

2.2.2. Larval crabs

For blue crab early life history stages (eggs and larvae), information was available only on CT_{min} and CT_{max} , the temperatures below/above which development does not progress. Eggs and megalopae tolerated temperatures as low as 16 and 15°C, respec-

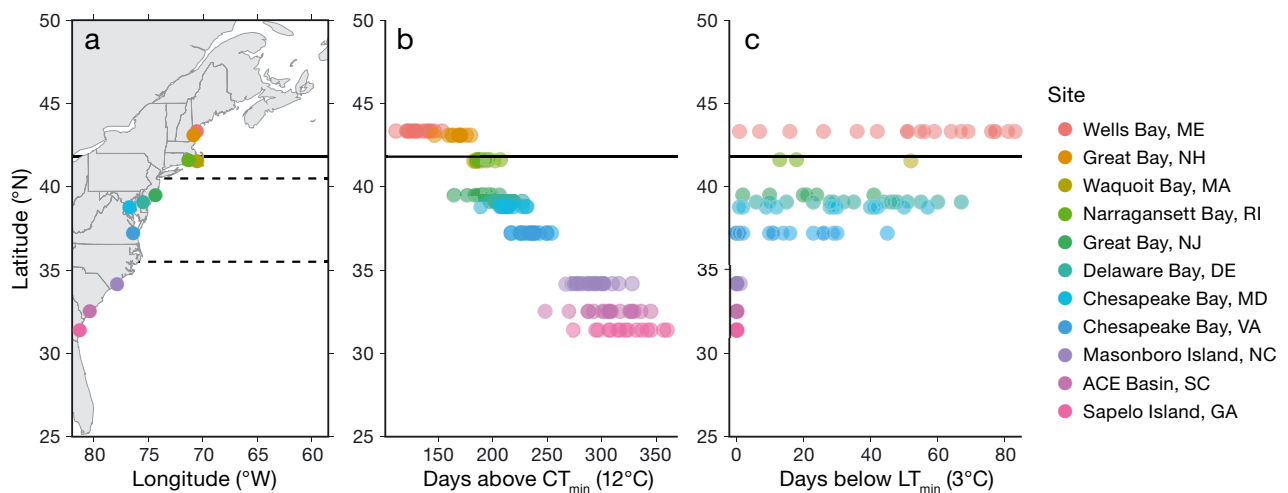


Fig. 2. Temperature conditions in relation to blue crab adult/juvenile lower temperature tolerances. (a) Points from which water temperature data were obtained; (b) days above 12°C (lower critical temperature; CT_{min}); (c) days below 3°C (lower lethal temperature; LT_{min}). Horizontal black line (all panels): historical blue crab northern range limit; dashed lines (panel a): divisions of northeastern, mid-Atlantic, and southeastern regions. Data are from NOAA National Estuarine Research Reserve System (NERRS) water quality monitoring stations (specific stations given in Table S1). State abbreviations as in Fig. 1. For sensitivity analysis, see Fig. S2

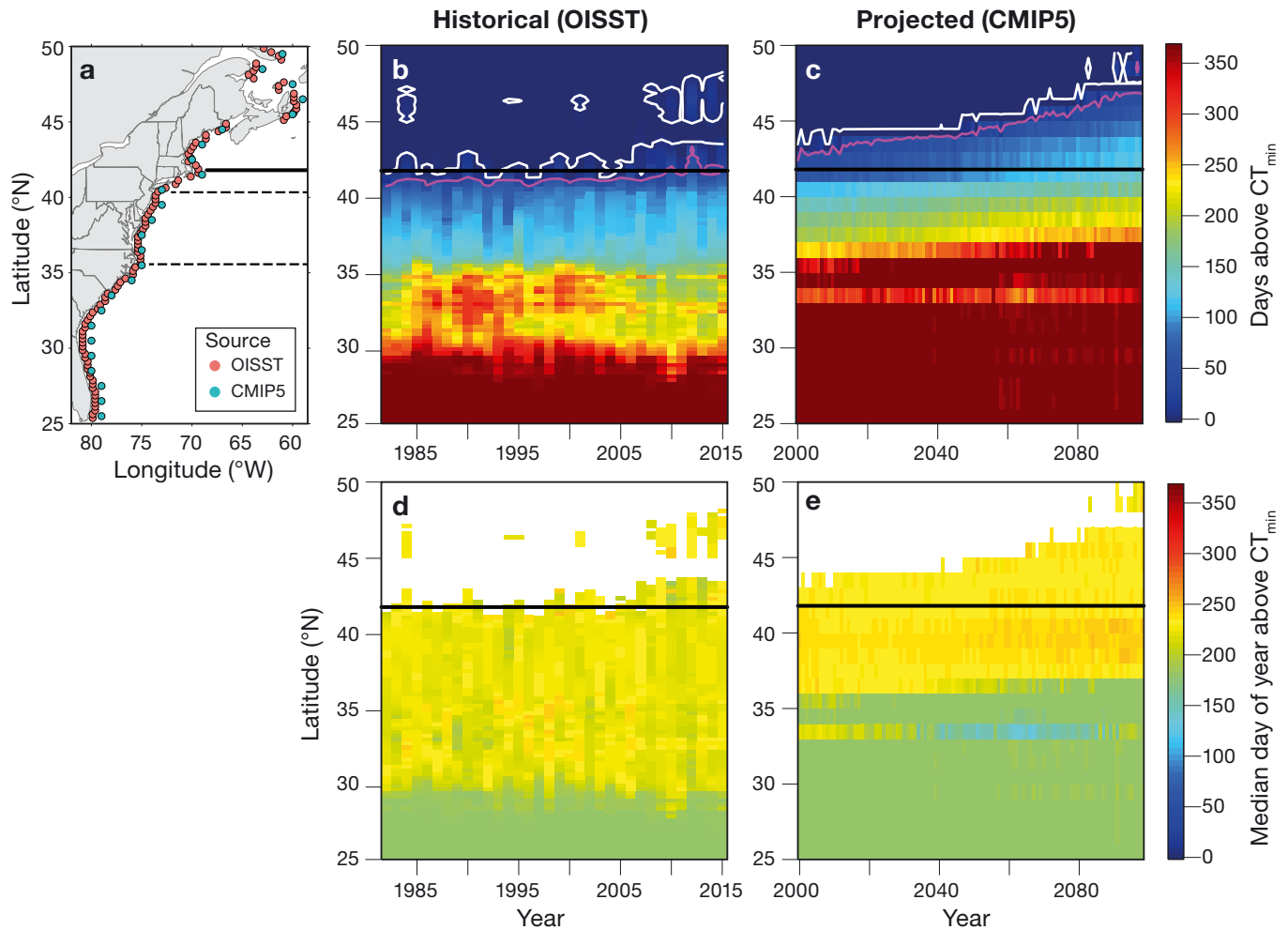


Fig. 3. Historical and projected temperature conditions in relation to blue crab larval (zoeal) lower temperature tolerances. (a) Points from which water temperature data were obtained. OISST: Optimum Interpolation Sea Surface Temperature; CMIP5: IPCC Coupled Model Intercomparison Project. (b,c) Number of days above lower critical temperature (CT_{min} ; 20°C). Contour for 0 days is in white; 30 days is pink. (d,e) Median day of the year (days after January 1) above CT_{min} . White areas are locations/years with no days above CT_{min} . Horizontal black line (all panels): historical blue crab northern range limit; dashed lines (panel a): divisions of northeastern, mid-Atlantic, and southeastern regions

tively, but with delayed development. Zoeae, which failed to develop at temperatures below 20°C , were the least cold-tolerant of the early life history stages. Thus, we focused our analysis on zoeal stages and used 20°C as CT_{min} . CT_{max} was similar for eggs, zoea, and megalopae, around 29°C .

Surveys indicate that blue crab larvae occur in surface waters over the continental shelf during summer (Epifanio & Garvine 2001). Therefore, we used time series of sea surface temperature (SST) from this region of space and time to examine thermal suitability across the Atlantic coastline as well as temporal trends in suitability. We specifically examined (1) the number of days per year with temperatures above CT_{min} and below CT_{max} , (2) the median day of the

year with temperatures above CT_{min} and the median day of the year with temperatures above the 80% quantile (to examine changes in phenology during the larval period), and (3) the suitability of mean August and September SSTs for larval development, using a double logistic model for larval survival probability (with survival rate equal to 0.01 at CT_{min} and CT_{max}). As a data source, we used daily SST measurements from the Optimum Interpolation Sea Surface Temperature data set (OISST v2; Reynolds et al. 2007) from 1982–2015 (Table S1). We obtained temperatures for points spanning the Atlantic coast, at each 0.25° of latitude (the available grid size), located 0.5° from shore (Figs. 3a & 4a). We conducted a sensitivity analysis using 3 versions of the logistic model,

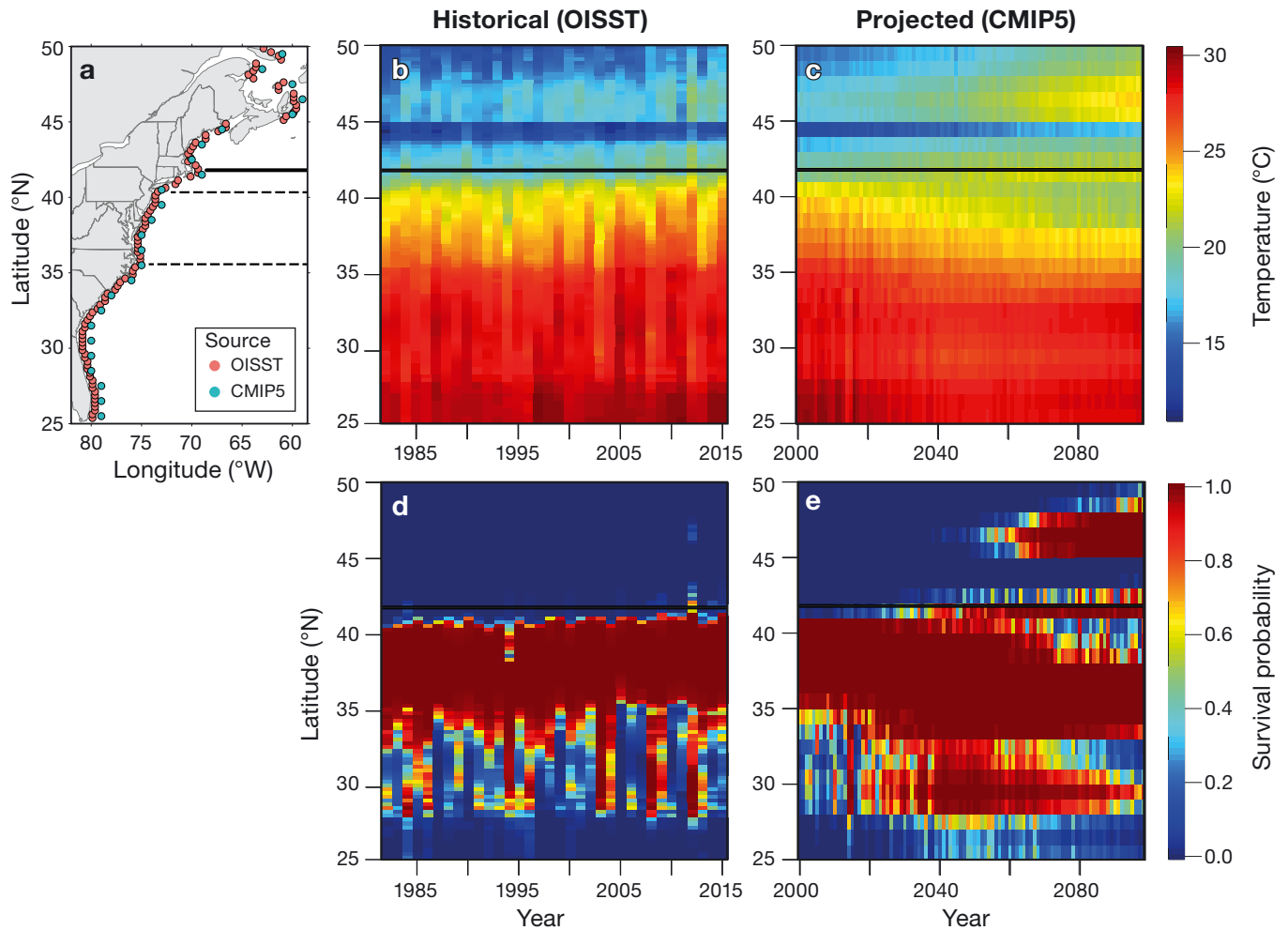


Fig. 4. Historical and projected temperature conditions in relation to blue crab larval (zoal) temperature tolerances. (a) Points from which water temperature data were obtained; (b,c) mean August water temperature; (d,e) suitability for larval survival given mean August water temperatures. Horizontal black line (all panels): historical blue crab northern range limit; dashed lines (panel a): divisions of northeastern, mid-Atlantic, and southeastern regions. See Fig. 3 for abbreviations; for sensitivity analysis, see Fig. S4

which varied in the ‘slope’ at which survival probability increased above CT_{\min} and below CT_{\max} (50% survival probability at 0.5, 1.0, and 1.5°C above/below CT_{\min}/CT_{\max}).

2.2.3. Temperature projections

We repeated the analysis for larval (zoal) stages using daily SST projections from the IPCC Coupled Model Intercomparison Project (CMIP5; Taylor et al. 2012) from 2000–2098, using the business-as-usual Representative Concentration Pathway scenario (RCP8.5). We obtained multimodel mean temperatures (from 19 models; Table S3) for points spanning

the Atlantic coast, at each 1° of latitude (the available grid size), located 1° from shore (Figs. 3a & 4a). The analysis assessing larval survival probability using mean August and September water temperatures was conducted using both the direct (uncorrected) model output and the model output that was bias-corrected at each latitude by subtracting the mean difference between the CMIP5 and OISST data during the period of overlap (2000–2015) following the methods in Wethey et al. (2016). In addition, we calculated the mean and variance of survival probability across each of the 19 models, bias-corrected individually, to assess inter-model agreement and uncertainty. All analyses were performed in R v.3.6.2 (R Core Team 2019).

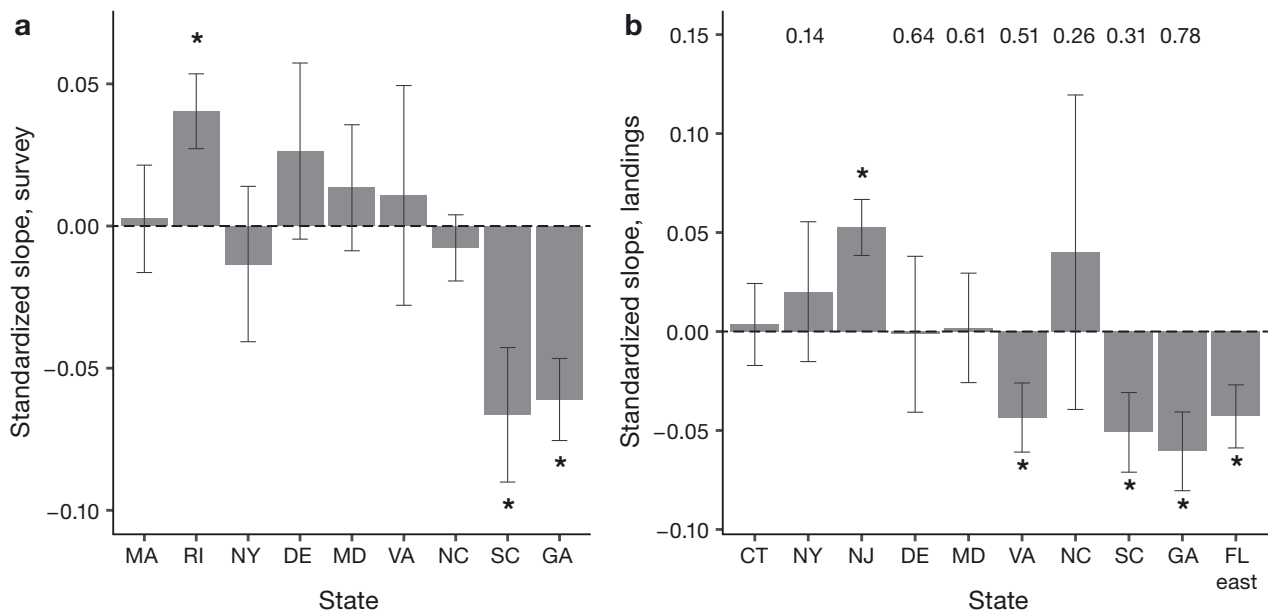


Fig. 5. (a) Linear trend in blue crab abundance indices from fishery-independent surveys (data within states scaled to mean = 0, SD = 1). Start years range from 1975–1988; end year for all is 2015. Slopes are from a generalized least squares model with AR(1) correlation structure. Error bars: ± 1 SE. Asterisks indicate slopes significantly different from 0 ($p < 0.05$). (b) Same as (a) but using blue crab landings from 1975–2015. Numbers at top are Pearson correlations between abundance indices and landings for states which have both. State abbreviations as in Fig. 1. Time series are shown in Fig. S1. Data sources are listed in Table S1

3. RESULTS

3.1. Trends in blue crab abundance

Blue crab abundance indices did not show a significant linear trend in most states, but did show a decreasing trend in the 2 southernmost states (Georgia and South Carolina) and an increasing trend in Rhode Island, in the northeast region (Fig. 5a). Blue crab landings showed similar patterns, with a decreasing trend in 4 of the 5 southernmost states and an increasing trend in New Jersey (Fig. 5b). Correlations between the fishery-independent abundance indices and landings by state ranged from 0.13 to 0.78. Time series of the abundance indices and landings are presented in Fig. S1.

3.2. Physiological constraints by life stage

3.2.1. Adult/juvenile crabs

The length of the 'growing season' for blue crabs (days per year with temperatures suitable for growth) varied spatially but was at least 3 mo in all estuaries (Fig. 2b). In the northeast region, locations

north and south of the range boundary (Cape Cod) had 100–175 and 175–200 d, respectively, above CT_{min} (12°C). The mid-Atlantic and southeast regions had 150–250 and 250–365 d, respectively, above CT_{min} . Across the entire coastline, days were very rarely above CT_{max} . Over the time period for which we had data, CT_{max} was exceeded for only 1 day of 1 year in Rhode Island and 15 days of 1 year in Georgia.

Acute temperature stress, specifically cold stress, was experienced only in the mid-Atlantic and northeast regions (Fig. 2c). During winter months, estuarine locations north and south of the current range boundary both contained an appreciable number of days (>20) below LT_{min} (3°C). In the southeast region, few to no days were below LT_{min} . Across the entire coastline, LT_{max} was not exceeded except for only 4 days of 1 year in Georgia.

Using the minimum estimates for LT_{min} (0°C) and CT_{min} (9°C) did not have a strong impact on the degree to which sites overlapped in the number of days above/below thresholds (Fig. S2). When using the maximum estimates for LT_{min} (5°C) and CT_{min} (15°C), the number of days above/below thresholds for the northernmost site (Maine) overlapped less with other sites in the northeast region (Fig. S2).

3.2.2. Larval crabs

South of the current range boundary, historical summer SSTs were nearly always above CT_{\min} for zoeae (20°C) for at least 30 d, but north of the boundary, the number of days dropped sharply to 0 (Fig. 3b). Only since 2007 have SSTs north of the boundary regularly exceeded 20°C. SSTs exceeded CT_{\max} only in the southeast region; however, most of the year was below this threshold. On average, 8 d yr^{-1} were above CT_{\max} between 28° and 35°N, and 55 d yr^{-1} were above CT_{\max} south of 28°N (the southern half of Florida).

The median date above CT_{\min} tended to be in mid-August (around calendar day 225), and there were no clear phenological shifts over the historical period (Fig. 3d). The highest temperatures of the year also occurred around this same time, as measured by the median date at which temperatures were above the 80th percentile (Fig. S3a).

Using historical mean August temperatures (Fig. 4b), the double logistic model for larval survival (with 50% survival probability at 1.0°C above CT_{\min} and below CT_{\max} ; Model 2 in Fig. S4) indicated a drop-off in larval survival north of ~41°N (just south of the current range boundary; Fig. 4d). The model also indicated that the southeast region is intermittently unsuitable for larval development in August due to temperatures exceeding CT_{\max} . The use of alternative logistic models did not qualitatively change the results (Fig. S4).

3.2.3. Temperature projections

Model projections indicate a rise in the number of days above larval CT_{\min} in the northeast and mid-Atlantic regions, including north of the current range boundary, which is particularly pronounced at the end of the century (Fig. 3c). During the period of overlap with the historical data, the projections tended to overestimate the number of days in the southeast region between 30° and 36°N but had low to moderate bias between 36° and 42°N and low bias at latitudes above 42°N and below 30°N (Fig. S5).

The projections also suggest that the median date above CT_{\min} may shift later in the year in the mid-Atlantic and northeast regions south of the range boundary (36°–40°N; Fig. 3e). The highest temperatures of the year were also projected to shift later in the year for latitudes between 38° and 40°N (Fig. S3b). Phenological trends in maximum temper-

atures were not as clear at lower latitudes, perhaps due to lower seasonality.

Projected mean August temperatures (bias-corrected) and the double logistic model suggest that conditions may become less suitable for larval development between 38° and 41°N, in line with projected decreases in August SSTs at these latitudes (Fig. 4c,e); however, there was high variability among climate models as to projected larval suitability in this region (Fig. S6). At the same time, more suitable conditions were predicted at the range boundary (41°–42°N) and above 45°N, in line with projected increases in August SSTs in this region. When a steeper increase in survival probability above CT_{\min} was used, range expansion occurred more quickly (Fig. S4). Results were similar whether we used bias-corrected multimodel mean temperature, multimodel mean bias-corrected temperature, or multimodel mean survival probability based on bias-corrected temperature (Fig. S6). Results with uncorrected temperature projections were likely inaccurate since the CMIP5 model mean tended to underestimate August SSTs during the period of overlap with the historical data (Fig. S4). Results using September temperatures were similar to those using August temperatures.

4. DISCUSSION

Our results indicate heterogeneous changes in historical and projected thermally suitable conditions for blue crabs across the US Atlantic coast. These patterns suggest that the location of the northern high latitude range boundary is dictated primarily by lower thermal constraints on early life history stages. We obtained these insights through examination of multiple aspects of temperature stress and multiple life history stages across a large region of the species' range.

Summer temperature conditions suitable for blue crab larvae dropped off sharply north of Cape Cod, suggesting that cold conditions during summer larval stages prevent development north of this range limit, and are thus most important in dictating the northern boundary. For any juvenile crabs that do settle north of the current boundary, sublethal (but not lethal) cold stress may further inhibit their establishment. While acute cold stress for juvenile and adult crabs (number of days below LT_{\min}) did not differ appreciably between the north and south side of the range boundary, the average duration of the 'growing season' (number of days above CT_{\min}) was lower north of Cape Cod and may hinder growth to maturity. How-

ever, since the range of durations north of the boundary overlapped with those of sites in the mid-Atlantic, we infer that larval stages are the more likely bottleneck. Larvae are often less stress-tolerant than adults (Andronikov 1975), and the dictation of range limits by cold-temperature effects on larval stages is consistent with results found for other crab species (Sanford et al. 2006, de Rivera et al. 2007). In a large analysis of marine and freshwater fishes, Dahlke et al. (2020) also found that spawners and embryos were the most temperature-sensitive life history stages, and projected that changes in thermal safety margins differed when considering only adults vs. the most sensitive life history stage. Although it does not appear to be the case for blue crabs, there are examples among invertebrates (Crickenberger 2016, Crickenberger et al. 2017) and fish (Hare et al. 2012), where poleward range limits appear to be set by overwinter juvenile or adult survival rather than by larval development.

Our results also provide insight about the role of cold stress within the species' current range. In the mid-Atlantic, the number of days of acute cold stress was highly variable and relatively high in some years. This clearly does not lead to local extinction but is consistent with findings that winter severity can regulate the overwinter survival of hibernating adult/juvenile blue crabs in the mid-Atlantic (Rome et al. 2005, Bauer & Miller 2010a) as well as the northeast, where the number of degree-days below CT_{min} the previous winter was found to show a relationship with crab abundance over a 7 yr period (Weiss & Downs 2020). Indeed, some studies predict that higher winter temperatures under climate change will increase overwinter survival of blue crabs in the Chesapeake Bay area (Glandon et al. 2019). In the southeast region, temperature conditions were suitable for growth (between CT_{min} and CT_{max}) for nearly the entire year. This is consistent with the lack of hibernation in blue crabs in this region and suggests these populations do not experience cold-induced mortality. Heat stress did not appear to be constraining for adult and juvenile crabs anywhere in the Atlantic, which is consistent with the fact that the blue crab range extends much farther south, into the Gulf of Mexico and Caribbean. Heat stress on larvae, however, may be constraining for populations in the southeast if spawning does indeed occur during the peak of summer. Whether crabs might compensate for this through adjustments or variation in spawning time is unknown. It is also unclear whether declines in historical abundance in the southern mid-Atlantic and southeast are related

to intermittently unsuitable conditions for larvae. These declines could be related to a variety of factors other than direct temperature stress (e.g. estuary/habitat size, predation, disease, harvest).

At and north of Cape Cod, past trends and projections in temperature suggest increasingly suitable thermal conditions for larval stages. Both August temperature and days above the larval development threshold (CT_{min}) have increased and are projected to increase in this region as a result of increases in both maximum and minimum temperatures. Thus, populations at the current range edge may increase in abundance due to increased recruitment and survival, and there is the potential for crabs to expand their range into the Gulf of Maine and Atlantic Canada by approximately 2050. This prediction is consistent with observed increases in blue crab abundance in northern states and with recent sightings in the Gulf of Maine (Johnson 2015), which is warming at a very rapid rate (Pershing et al. 2015). It appears that areas in the northern Gulf of Maine may always be too cold for blue crab larvae and may create a range discontinuity, although this assumes future spatial patterns in temperature will reflect current ones. If range expansion occurs, we speculate that blue crabs are also likely to appear on the eastern edge of Cape Cod Bay, which has some of the warmest SSTs north of Cape Cod and is where 2 other southern crab species with greater cold tolerance than blue crabs (fiddler crabs *Uca* spp. and purple marsh crabs *Sesarma reticulatum*) have their northernmost sizeable populations (Miller & Vernberg 1968, Sanford et al. 2006, Smith et al. 2012). Blue crab populations currently present in the Pleasant Bay and Nauset systems on the outer eastern shore of Cape Cod, where their presence and abundance has fluctuated directly with historical fluctuations in temperature (Richardson 1947, Able et al. 2002, Friedland & Hare 2007), may also increase. Currently, relatively persistent populations of blue crabs in Great Bay, New Hampshire (W. Watson pers. comm.) and Kejimikujik, Nova Scotia (Woodward 2015) may also act as refugia that could facilitate discontinuous range expansion (Hannah et al. 2014) through rescue effects (Eriksson et al. 2014).

In the northern mid-Atlantic, long-term changes in the duration, magnitude, and phenology of summer temperatures may have complex and less predictable effects on blue crab reproduction. In this region, mean August temperatures were projected to decrease, but the number of days above the larval development threshold were projected to increase. These results were due to a decrease in temporal variability at these locations (decreases in annual

maxima and increases in annual minima), which produced conflicting predictions in terms of larval suitability. An approach which integrates both the magnitude and duration of suitable thermal conditions (e.g. a degree-days requirement based on the relationship between temperature and development time, which is currently unknown for larval blue crabs) is likely to be most promising for resolving whether larval survival will ultimately increase or decrease. In this region, there were also projected phenological shifts in summer temperatures. Maximum temperatures were projected to occur later in the calendar year, and the projected increase in the number of days above larval CT_{min} appeared to result from additional days later in the calendar year. A longer developmental season may enhance reproduction if spawning behavior is plastic but could potentially lead to mismatches (e.g. in prey availability for larvae) if spawning cannot track shifts in peak temperatures. Since there was some disagreement among climate models as to long-term changes in the northern mid-Atlantic (Fig. S6), we cannot be highly confident in these projections; however, they provide an example of how multiple aspects of temperature and phenological changes may interact with physiological tolerances in complex ways to regulate populations within the current range of a species.

Trends in blue crab landings were generally correlated with trends in abundance indices, although the strength of this relationship varied by state. Thus, at least some variation in landings may be due to changes in abundance as opposed to effort. If this is true in other species, imperfect abundance proxies such as harvest (Pauly et al. 2013) could be a valuable tool for detecting biogeographic shifts in the absence of fishery-independent data, and rising catches near the range boundary could be indicative to managers of impending range shifts (Pinsky & Fogarty 2012). However, harvest could change for many reasons unrelated to abundance that need to be kept in mind (e.g. changes in preferred target species, improvements to fishing methods, changes in regulations). For blue crabs, our overall findings also underscore the need for more studies of blue crab biology and population dynamics north of Delaware Bay, where relatively little blue crab research has been done, the fishery has the potential to increase in size and value, and blue crab stock assessments currently do not exist. Further research on the exact drivers influencing abundance trends within the species' range, which may involve complex interactions between temperature and life stage, are also needed.

Although our results suggest that physiological thresholds maintain the northern range boundary of blue crabs, there are several other important factors to consider, including the potential effects of dispersal limitation (Gaylord & Gaines 2000). Cape Cod is a known biogeographic boundary (Engle & Summers 1999), with currents in this region flowing primarily southward (Pringle et al. 2011). Given that transport and recruitment in blue crabs and other Atlantic species are affected by wind and currents (Epifanio 1995, Epifanio & Garvine 2001), it is certainly possible that flow-induced dispersal barriers, rather than temperature, might also limit the northern range of blue crabs. However, given that other crab species with similar life histories, such as the introduced Asian shore crab *Hemigrapsus sanguineus* and European green crab *Carcinus maenas*, expanded rapidly from southern New England into the Gulf of Maine (Epifanio 2013) and several native crab species such as fiddler crabs occur in both regions (Sanford et al. 2006), Cape Cod is likely not an unbreachable barrier in terms of larval transport. Lack of suitable habitat is also unlikely to be an issue, as there are numerous estuaries north of Cape Cod similar to those inhabited by blue crabs farther south.

Multiple stressors may also further constrain the range of suitable thermal habitat. For instance, many studies show that temperature tolerance in blue crabs decreases at lower salinities (Table S2), and temperature can also affect tolerance to hypoxia (García-Rueda et al. 2021). Species interactions can also influence species distribution, abundance, and range limits (Araújo & Luoto 2007, Gotelli et al. 2010, Staniczenko et al. 2017). Blue crabs are known to interact with invasive green crabs, which are abundant in New England (de Rivera et al. 2005). Experimental and modeling results suggest that blue crabs can be outcompeted by green crabs at cold temperatures (16°C), which are typical of current summer conditions north of Cape Cod (Rogers et al. 2018). However, if dispersing larval crabs are unable to develop and settle north of Cape Cod and if the offspring of any crabs that do settle are unable to survive, this mechanism may not be relevant. Future increases in overall summer temperatures, in addition to allowing larval settlement, may act to reduce or reverse competitive interactions between blue and green crabs and increase consumption of green crabs by blue crabs (Rogers et al. 2018). Thus, the community-level effects of a blue crab range expansion are likely to include suppression of green crab populations, as is currently seen in assemblages south of Cape Cod. It is important to remember that climate

change will affect the distribution and abundance of not just individual species but of entire communities of species across the landscape (Lucey & Nye 2010).

Finally, geographic variation in thermal tolerance and local adaptation are other possible complications we did not consider here (Sanford & Kelly 2011). An important caveat in this study is that the lower temperature tolerance limits we obtained from the literature were for blue crabs from Chesapeake Bay and North Carolina, which are where the vast majority of blue crab studies have been conducted. Although gene flow rates for blue crabs are estimated to be relatively high (McMillen-Jackson et al. 1994, McMillen-Jackson & Bert 2004), it is possible that populations near the northern range limit may be more cold-tolerant due to local selection. It would be very informative for future studies to examine the temperature tolerance of blue crab life stages from more northern locations—to date, the only study to do so suggests that juvenile and adult blue crabs in New York are actually less cold-tolerant (in terms of acute temperature stress) than crabs from Chesapeake Bay (Molina et al. 2021). With consideration of the potential for regional differences, our methodology could easily be applied to other regions of the blue crab's range beyond the US Atlantic coastline (e.g. Gulf of Mexico, South America, invasive range in Europe). For instance, whether similar constraints exist at the species' southern high latitude range boundary could be an area of future study. Our results represent a solid start and could motivate further research with a larger spatial scope.

In summary, our study highlights the importance of considering multiple life stages and multiple aspects of temperature stress when making physiologically based projections of distribution. For instance, had we only considered juvenile/adult LT thresholds and applied these to historical and projected SSTs, we would have concluded that most of the Gulf of Maine is within the blue crab's fundamental niche (Fig. S7), perhaps overestimated range expansion potential, or concluded that other factors (e.g. dispersal) are constraining their distribution. We also demonstrated how constraints can impact not just the location of range boundaries, but also the distribution of abundance within a species' range. Since geographic mosaics in environmental conditions may lead to non-uniform trends and predictions, considering changes in both the spatial (geographical) and temporal (phenological) distribution of temperature under climate change is critical for predicting the responses of ecological populations. Easier to implement than a mech-

anistic species distribution model, our study presents a relatively simple framework where physiological information on different life history stages can be combined with relevant environmental data (i.e. those most applicable to the life history stage in question) to build hypotheses to test species responses to environmental change. Our findings underscore the need for continued studies which combine physiological, environmental, and biogeographic information over a range of scales (Torossian et al. 2016).

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