Ecological and environmental drivers of blue crab population dynamics across scales

by Tanya L. Rogers

B.S. in Biology, University of Puget Sound

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Dissertation directed by

David L. Kimbro
Assistant Professor of Marine and Environmental Sciences
Dedication

On these shores there are echoes of past and future: of the flow of time, obliterating yet containing all that has gone before; of the sea’s eternal rhythms – the tides, the beat of surf, the pressing rivers of the currents – shaping, changing, dominating; of the stream of life, flowing as inexorably as any ocean current, from past to unknown future. For as the shore configuration changes in the flow of time, the pattern of life changes, never static, never quite the same from year to year. Whenever the sea builds a new coast, waves of living creatures surge against it, seeking a foothold, establishing their colonies. And so we come to perceive life as a force as tangible as any of the physical realities of the sea, a force strong and powerful, as incapable of being crushed or diverted from its ends as the rising tide.

Contemplating the teeming life of the shore, we have an uneasy sense of the communication of some universal truth that lies just beyond our grasp… The meaning haunts and ever eludes us, and in its very pursuit we approach the ultimate mystery of Life itself.

Rachel Carson

The Edge of the Sea

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Abstract of Dissertation

Predicting how species will respond to short-term environmental fluctuations and long-term climatic changes is essential for the successful and sustainable management of species in a nonstationary and increasingly variable environment. Accurate forecasting requires an understanding of the intrinsic and extrinsic factors driving variation in species distribution and abundance within and across populations. This research examines how variation in local environmental drivers, species interactions, and population dynamics may scale up to affect regional (biogeographic) distribution patterns and population dynamics in a commercially important species across a range of temporal scales. Specifically, I examined the biotic and abiotic drivers of Atlantic blue crab (Callinectes sapidus) distribution, abundance, and population dynamics across the entire U.S. Atlantic coast, and how these may be modified under future climatic conditions.

I first explored how spatial variation in temperature affects interactions between blue crabs and a co-occurring species, the European green crab (Carcinus maenas). I quantified the temperature-dependency of competitive and predatory interactions between blue crabs and green crabs in laboratory experiments using 3 temperatures reflective of conditions across the Atlantic coast. Using functional response parameters from these experiments, I then constructed a dynamical size-structured intraguild predation model to examine how these interactions might affect coexistence along the temperature gradient of the U.S Atlantic coast. I found that green crabs were likely to competitively exclude blue crabs at lower temperatures, whereas blue crabs were likely to competitively and consumptively exclude green crabs at higher temperatures.

My second chapter investigated long-term trends in blue crab abundance across the U.S Atlantic coast, and how an array of physiological drivers acting on multiple life history stages may affect the species’ current and future distribution using mechanistic models. Using landings (harvest) as a proxy for abundance, I found that while landings in mid-Atlantic and southern populations have declined, landings in northern populations have remained constant or increased. This is suggestive of and consistent with climate-induced biogeographic changes in crab abundance. I also found that environmental conditions during larval stages appeared to be most important in dictating the crab’s northern range limit (Cape Cod), which may be further reinforced by sublethal (but not lethal) cold stress on juveniles and adults, in addition to competition with resident green crabs. Temperature projections suggest potential for increases in
blue crab abundance at and north of Cape Cod. However, just south of Cape Cod, changes in the duration, magnitude, and phenology of summer temperatures may have complex effects on crab reproduction. These results highlight how past and future changes in environmental suitability can vary non-uniformly across the range of a species, requiring consideration of multiple life stages and aspects of environmental stress.

For my final chapter, I investigated spatial variability in blue crab population dynamics and responses to environmental drivers using long-term, fishery-independent time series data from 17 crab populations spanning the U.S. Atlantic coast. Using novel, hierarchical statistical methods based on nonlinear dynamical systems theory, I found that even though these populations were regionally uncorrelated and asynchronous, they shared broadly similar, spatially structured, nonlinear responses to past abundances and environmental drivers. As a result, integrating information across populations was able to improve short-term, regional predictability. Moreover, the time series and models had positive Lyapunov exponents, suggesting that noise and locally chaotic dynamics may destabilize synchrony and obscure hidden dynamical similarities among populations.

Taken together, these results illustrate how quantification of relevant biotic and abiotic drivers at local scales, as well as characterization of how these drivers vary spatially, can be valuable for predicting both long-term trends in distribution and abundance and short-term population dynamics across the biogeographic range of a species. Understanding the key processes at work at multiple spatial and temporal scales is essential for the management of ecologically and economically important species such as blue crabs. This is particular important at a time when anthropogenic climate change is leading to large-scale, non-uniform changes in environmental conditions and environmental variability that likely impact the dynamics of commercially important species.
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Introduction

Climate change is having a range of far-reaching impacts on the world’s ecosystems (Thomas et al. 2004, Parmesan 2006, Doney et al. 2012) through effects on both the mean, variance, and phenology of many biologically-important environmental drivers (Easterling et al. 2000, Burrows et al. 2011, Vasseur et al. 2014). Temperature changes in particular, which may vary spatially, can lead to poleward range expansions of species (Parmesan & Yohe 2003, Perry et al. 2005, Poloczanska et al. 2013), shifts in entire ecological communities (Nye et al. 2009, Lucey & Nye 2010), altered species interactions (Blois et al. 2013), and changes in local abundance, growth, and survival within species current range limits (Ackerly et al. 2015, Carroll et al. 2016). Predicting such changes in species distribution and abundance in response to both short-term environmental variability and long-term climatic change requires an understanding of the intrinsic and extrinsic drivers limiting population expansion and regulating population dynamics (Gaston 2009, Sexton et al. 2009). It is also essential to recognize that different processes may be relevant at different spatial and temporal scales (Levin 1992), that these processes may vary spatially (Crozier & Zabel 2006), and that they are likely to be nonlinear (Burkett et al. 2005). Local and regional processes may also interact with one another across a range of scales, such that local processes affect and inform regional, biogeographic patterns (Levin 1992). The objective of this dissertation research was to investigate biogeographic variability in the patterns and drivers of local population dynamics and how these may scale up to affect regional distribution patterns and population dynamics across a range of temporal scales in a commercially important species.

Environmental drivers such as temperature may show complex spatial patterns (Helmuth et al. 2006) and can interact with physiological traits to affect species abundance both within and across populations (Somero 2005, Pörtner & Farrell 2008). When making predictions across long temporal scales, models typically consider how long-term, non-stationary climate trends may affect mean or equilibrium abundances across species ranges. This is often done through the use of species distribution models, which may use correlative approaches to map the realized niche as a function of environmental predictors (Guisan & Zimmerman 2000, Pearson & Dawson 2003, Elith & Leathwick 2009), or mechanistic models to map the fundamental niche using independently-derived physiological responses and constraints (Kearney & Porter 2009). In contrast, when making predictions across short temporal scales, models typically consider how
short-term environmental variability affects the year-to-year fluctuations of populations or meta-populations. This is often done through explicit models of population dynamics, which can vary greatly in form and complexity, and which in some cases, can be embedded and scaled up within long-term species distribution models (Keith et al. 2008). Since the management of ecosystems and economically important species requires both short-term management and long-term planning, both long- and short-term models that incorporate the effects of environmental drivers are valuable approaches.

It is also important to remember that environmental drivers are not the only factors that can influence the distribution, abundance, and population dynamics at biogeographic scales – a range of additional biotic and abiotic processes may also come into play (Sagarin et al. 2006). Species interactions, including predation, parasitism, competition, and facilitation can alter the realized niche and local abundance of a species, with effects that can span large spatial scales (Davis et al. 1998, Araújo & Luoto 2007, Gilman et al. 2010, Gotelli et al. 2010, Staniczenko et al. 2017). The sign, strength, and stability of those species interactions can also themselves be altered by temperature and vary spatially across a species’ range (Tylianakis et al. 2008, Gilman et al. 2010, Van der Putten et al. 2010, Chamberlain et al. 2014). Additionally, dispersal processes and habitat limitation can may constrain species distribution and abundance within the fundamental niche dictated by physiology (Gaylord & Gaines 2000).

This dissertation research uses novel methods for both long- and short-term prediction to understand how biotic and abiotic drivers influence blue crab (*Callinectes sapidus*) distribution, abundance, and population dynamics across the Atlantic range of the species. I explore and integrate a number of factors which are not typically considered in long-term species distribution models, including temperature-dependent species interactions, multiple life history stages, and multiple aspects of temperature stress. To examine short-term population dynamics, I employ novel empirical methods for quantifying spatial variability and nonlinearity in intrinsic dynamics and responses to recent temperature conditions. Blue crabs are an ideal focal species for this study because they have a broad geographic range (Williams 1973), they show potential for range expansion and distributional shifts in response to regionally warming seas (Johnson 2015), they have a complex life cycle consisting of both larval and adult stages (Millikin & Williams 1984, Epifanio 1995), they are important benthic predators that interact strongly with co-occurring species (Silliman & Bertness 2002, Altieri et al. 2012), and they are an important commercial
and recreational fishery species. In the United States, blue crabs are found in estuaries along the Atlantic and Gulf of Mexico coasts, with the northernmost permanent populations occurring in southern Massachusetts. Despite the fact that the crabs exist as a meta-population linked through larval dispersal, nearly all existing blue crab studies have focused on populations within individual estuaries. Few studies have made cross-estuary comparisons among blue crab populations, or taken a coast-wide perspective on blue crab population and community dynamics. In addition, although the species has been extensively studied in the mid-Atlantic and Gulf of Mexico (particularly in Chesapeake Bay and North Carolina), surprisingly little research has been done on crab populations north of Delaware Bay. Populations in these northern regions are likely to experience the greatest changes in abundance as seas warm, yet are greatly understudied. Thus, a biogeographic examination of population and community dynamics at short and long time scales would provide new and valuable ecological understanding both for species in general and for this ecologically and economically important focal species.

My three chapters explore (1) how spatial variation in temperature affects local interactions between blue crabs and a co-occurring, introduced crab species and how these interactions might affect long-term coexistence across the temperature gradient of the U.S Atlantic coast; (2) how an array of physiological drivers acting on multiple life history stages may affect the species’ current and future distribution using mechanistic models; and how long-term trends in blue crab abundance and projected environmental suitability vary across the U.S. Atlantic coast, and (3) how short-term blue crab population dynamics and responses to environmental drivers vary spatially across the U.S Atlantic coast, and what factors may contribute to asynchrony in the blue crab meta-population. I discuss the potential implications of my results for predicting and managing blue crab populations in the near and more distant future.
Chapter 1: Temperature-dependency of intraguild predation between native and invasive crabs

Tanya L. Rogers, Tarik C. Gouhier, David L. Kimbro
Northeastern University Marine Science Center, 430 Nahant Road, Nahant, MA 01908

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ABSTRACT

Environmental factors such as temperature can affect the geographical distribution of species directly by exceeding physiological tolerances, or indirectly by altering physiological rates that dictate the sign and strength of species interactions. Although the direct effects of environmental conditions are relatively well studied, the effects of environmentally-mediated species interactions have garnered less attention. In this study, we examined the temperature-dependency of size-structured intraguild predation (IGP) between native blue crabs (*Callinectes sapidus*, the IG predator) and invasive green crabs (*Carcinus maenas*, the IG prey) to evaluate how the effect of temperature on competitive and predatory rates may influence the latitudinal distribution of these species. In outdoor mesocosm experiments, we quantified interactions between blue crabs, green crabs, and shared prey (mussels) at 3 temperatures reflective of those across their range, using 2 size classes of blue crab. At low temperatures, green crabs had a competitive advantage and IGP by blue crabs on green crabs was low. At high temperatures, size-matched blue and green crabs were competitively similar, large blue crabs had a competitive advantage, and IGP on green crabs was high. We then used parameter values generated from these experiments (temperature- and size-dependent attack rates and handling times) in a size-structured IGP model in which we varied IGP attack rate, maturation rate of the blue crab from the non-predatory to predatory size class, and resource carrying capacity at each of the 3 temperatures. In the model, green crabs were likely to competitively exclude blue crabs at low temperature, whereas blue crabs were likely to competitively and consumptively exclude green crabs at higher temperatures, particularly when resource productivities and rates of IGP were high. While many factors may play a role in delimiting species ranges, our results suggest that temperature-dependent interactions can influence local coexistence and are worth considering when...
developing mechanistic species distribution models and evaluating responses to environmental change.

INTRODUCTION

Species interactions can play an important role in shaping ecological communities and limiting species distribution and abundance, even at large spatial scales (Davis et al. 1998, Araújo & Luoto 2007, Gilman et al. 2010, Gotelli et al. 2010, Staniczenko et al. 2017). However, many species distribution modeling (SDM) frameworks ignore the effects of (syn)ecological processes such as species interactions, relying either on correlations between broad-scale environmental conditions and species abundances or on autecological mechanistic models (Guisan & Zimmerman 2000, Pearson & Dawson 2003, Elith & Leathwick 2009). In addition, SDM methods that do incorporate species interactions often assume that interaction strengths are constant in space and time, and that the effects of biotic and abiotic drivers are independent. However, environmental factors such as temperature may indirectly affect species distributions by altering the sign, strength, and stability of species interactions (Tylianakis et al. 2008, Gilman et al. 2010, Van der Putten et al. 2010, Chamberlain et al. 2014). Integrating these context-dependent species interactions into SDMs may be important for accurately predicting the realized niche of species in a changing environment (Lany et al. 2017).

Interaction strengths will change along a temperature gradient if the traits of interacting species (e.g. nutrient uptake rates, attack rates) respond asymmetrically to temperature (Dell et al. 2014), as has been shown empirically for a number of predator-prey (e.g. Sanford 1999, Ohlund et al. 2015) and competitive (e.g. Taniguchi & Nakano 2000, Jiang & Morin 2004) interactions. For instance, warming can increase predation pressure on rocky shores (Harley 2011), and reverse competitive dominance among algae in lakes (Tilman et al. 1981). In some cases, temperature-mediated species interactions, not temperature itself, restrict the distribution of a species (Wethey 2002). If temperature-dependent species interactions can be described mechanistically, these relationships could be used to improve SDMs (Kearney & Porter 2009).

Intraguild predation (IGP) is an ideal framework to study the temperature-dependence of species interactions because it is ubiquitous in ecological food webs (Polis et al. 1989, Arim & Marquet 2004), and it integrates the independent and joint effects of temperature and both trophic and non-trophic species interactions, which are highly context-dependent (Chamberlain
et al. 2014). IGP is a combined predation-competition module in which two species consume a common resource \( (R) \), and one of the species (the IG predator, \( P \)) also consumes the other (the IG prey, \( N \)). Theory predicts that stable coexistence of the IG predator and IG prey is only possible if the IG prey is the superior competitor for the shared resource, and the IG predator benefits substantially by consuming the IG prey (Holt & Polis 1997). Although theoretical models have been developed for the temperature-dependence of consumer-resource (Vasseur & McCann 2005, Gilbert et al. 2014) and competitive interactions (Tilman et al. 1981, Urban et al. 2012), no theoretical or empirical studies to date have examined the effect of temperature in IGP modules, or the joint effects of temperature and ontogeny (age- or size-dependency). Since intraspecific variation in body size can drive interaction strengths (Werner & Gilliam 1984) and IGP rates (Woodward & Hildrew 2002), incorporating size-dependent temperature effects is critical for predicting the persistence and stability of predators and prey in IGP modules.

In this study, we examined the temperature-dependency of IGP interactions between 2 crab species using both experiments and theoretical models. In estuaries along the Atlantic coast of North America, blue crabs (Callinectes sapidus) and green crabs (Carcinus maenas) are abundant predators, which can have strong direct and indirect effects on their associated communities (e.g. Silliman & Bertness 2002). Blue crabs are an important commercial and recreational fishery species, whereas the green crabs are an invasive species from Europe introduced in the early 1800s (Carlton & Cohen 2003). The crabs co-occur between Chesapeake Bay and Cape Cod, with green crabs not found south of Chesapeake Bay, and blue crabs not found north of Cape Cod (Williams 1973, de Rivera et al. 2005). The existing literature suggests that interactions between blue and green crabs are a classic case of size-structured IGP. The crabs overlap in their diet and habitat use (Williams 1984), and juvenile blue crabs were found to be competitively inferior to size-matched green crabs in laboratory studies (MacDonald et al. 2007). However, blue crabs grow to a much larger adult size than green crabs, and large blue crabs can consume green crabs (de Rivera et al. 2005). In addition, a study examining the distribution and abundance of these crabs along the Atlantic coast, as well as relative predation rates on tethered green crabs, suggested that predation by blue crabs may control the abundance and limit the southern range of green crabs (de Rivera et al. 2005).

Given the strong temperature gradient that exists along the Atlantic coast, rapid rates of ocean warming in the Northwest Atlantic (Pershing et al. 2015), and recent, isolated observations
of blue crabs north of Cape Cod (Johnson 2015), we examined the effect of temperature on interactions between blue and green crabs, and the potential for temperature-mediated interactions to affect species distribution. We conducted outdoor mesocosm experiments to empirically quantify IGP interactions between blue and green crabs (both the competitive and predatory components of IGP) at 3 temperatures reflective of those across their range. Using 2 different size classes of blue crabs, we also examined the size-dependency of these interactions. In addition, we tested whether IGP rates depended on shared resource density because IGP rates may be lower when shared (alternative) prey density is high. We then used parameter values generated from our experiments (temperature-dependent attack rates and handling times) in a size-structured IGP model to evaluate whether IGP dynamics might affect local species coexistence under different temperature regimes.

METHODS

Study organisms and experimental setup

We conducted trials examining interactions between blue crabs, green crabs, and shared prey at 3 temperatures (16, 22, and 28°C) in mesocosms at the Northeastern University Marine Science Center in Nahant, Massachusetts during the summer (June – September) of 2016. We used 1 size class of green crab (45-55 mm carapace width), and 2 size classes of blue crab: “small blue crabs,” which were size-matched to the green crabs by wet mass (20-43 g, 60-85 mm carapace width), and “large blue crabs,” which were large enough to consume a green crab (>110 mm carapace width). Blue crabs were collected from Shinnecock Bay and Great South Bay on Long Island, New York. Green crabs were collected from locations on Cape Cod, Massachusetts. Both species are present at both collection locations, but due to differing abundances, sufficient quantities of both species could not be collected from one location.

We only used crabs with both claws and most walking legs intact, and crabs were only used once. All crabs used were male, with the exception of small blue crabs, for which we used both males and immature females due to limited crab numbers. Crabs were fed mussels (*Mytilus edulis*) every 2-4 days in outdoor, flow-through holding tanks kept at ambient water temperature and salinity (~14-18°C, 32 ppt). Prior to use in an experimental trial, crabs were fed mussels and then acclimated to the experimental temperature for 48 hours, during which time they were not fed. In both the holding and acclimation tanks, crabs were separated by species and size.
Experimental trials took place in 18 outdoor, circular, flow-through mesocosm tanks made from thick, opaque black plastic (68 cm diameter), each with 2 vertical stand pipes (6 cm diameter) for drainage, located on opposite sides of the tank. Each tank was lined with 3 cm of sieved fine sand and contained 1 aquarium heater (Aquatop Glass Submersible Aquarium Heater, 300 W). Tanks were filled to a depth of 35 cm with seawater (32 ppt), which entered at the top rear of the tank. The top of the tank was covered with a black trash bag that transmitted some light, but prevented visual disturbance of crab behavior by the experimenter. The rear 10% of the tank was left uncovered to allow entry of the seawater inflow pipe.

The 3 water temperatures used reflect the different thermal conditions experienced across the ranges of these species during the summer months (June-September; Fig. 1.1), which is when the crabs are most active and when the experiments were conducted. By adjusting the aquarium heater settings and the seawater inflow rate (which ranged from 0.3-1.5 liters per minute), we maintained the acclimation and experimental tanks within 1-1.5°C of the target temperature.

**Per capita competitive ability of crabs**

We measured the relative per capita competitive ability of blue and green crabs for resources by generating functional response curves for solitary crabs foraging on small mussels (*Mytilus edulis*, 10-15 mm shell length) at each of the 3 temperatures. The parameters derived from the curves (attack rates and handing times) reflect the relative ability of each species to acquire resources in the absence of interference competition. To generate the functional response curves, we used 9 mussel densities for the green and small blue crabs (2, 4, 6, 8, 10, 20, 30, 50, and 70 mussels tank$^{-1}$), and 8 mussel densities for the large blue crabs (4, 8, 20, 50, 70, 100, 150, and 200 mussels tank$^{-1}$). To begin a trial, we evenly scattered the mussels across the bottom of the tank, and then added the crab through the uncovered slot at the back of the tank. Trials began in the late morning. We allowed the crab to feed for 2 hours, and then quantified the number of mussels consumed (we excluded trials in which the crab did not eat any mussels). We performed 2-4 replicates for each combination of mussel density and temperature. Due to limited quantities of crabs, we conducted fewer replicates for the lower mussel densities because in pilot studies, we observed little variability in consumption among replicates at lower densities due to prey depletion. Between trials, we removed all shell fragments, drained the tanks completely, homogenized the sand, and replaced the top 1 cm of sand with sand that had been sitting dry for at least 1 week.
Following Juliano (2001), we evaluated the functional response type by fitting first and second order logistic regressions to the proportion of mussels consumed for each temperature and crab type (all were found to be Type II). We then fit nonlinear functional response curves (Rogers type II decreasing prey function, which accounts for prey depletion) to the number of mussels consumed for each temperature and crab type. The model fits produced estimates of the parameters $a$ (attack rate) and $h$ (handling time). For green crabs and small blue crabs, we compared the parameters between species within temperature treatments, and between temperature treatments within species, using the ‘delta’ method (Juliano 2001) and Holm’s correction (i.e., sequential Bonferroni) for multiple comparisons. We performed these analyses using the ‘frair’ package (Pritchard 2016) in R (v. 3.3.1).

**Competitive and predatory interactions between paired crabs**

We ran additional trials with paired crabs to examine the effect of temperature and mussel density on competition for shared prey in the presence of a heterospecific, as well as predation by blue crabs on green crabs. While these experiments did not produce IG attack rate estimates that could be used in the model (we lacked the resources to generate full functional response curves for predation on green crabs), we performed these trials to evaluate the relative rates of IGP at each temperature, the sensitivity of IGP rates to alternate prey availability, the potential for interference competition between crab species, and to directly estimate IG handling times at each temperature.

For these trials, we placed 1 green crab in a tank together with either a small or large blue crab at each of the 3 temperatures, with either a low or high density of mussels (20 or 70 mussels tank$^{-1}$). The experimental procedure was the same as above, except that a camera (Go-Pro Hero 3+) was mounted beneath the trash bag, 17 cm above the water surface in the center of the tank, facing downwards. At the start of the trial, both crabs were added to the tank at the same time, from opposite sides of the tank. We performed 5-6 replicates for each size of blue crab, temperature, and mussel density.

From the video, we quantified the number of mussels consumed by each species. For trials pairing green and small blue crabs, we calculated the difference in the proportion of mussels consumed by the paired crabs in each tank (mussels eaten by blue crab/total mussels – mussels eaten by green crab/total mussels). We used a two-way ANOVA to evaluate the effect of temperature and mussel density on this difference in mussel consumption. For trials pairing
green and large blue crabs, we also recorded whether the blue crab consumed the green crab. If
the blue crab did not kill the green crab, but attacked and successfully removed and consumed
claws and/or legs, this was considered a sublethal predation event. The proportion of trials with
lethal or sublethal predation was compared across temperatures and mussel densities. The
handling time to subdue and consume a green crab was also estimated from the videos.

**IGP model predictions**

To investigate how temperature may affect local species coexistence and population
stability via its effects on attack rates and handling times, we utilized an IGP model. We used
the model formulation in Mylius et al. (2001) for IGP with a size-structured predator population
and Type II functional responses, but allowed for size-specific attack rates and handling times of the
IG predator and used a logistic growth term for the resource.

\[
\frac{dp_2}{dt} = mP_1 - \mu_p P_2 
\]

(1)

\[
\frac{dp_1}{dt} = \frac{b_p a_{P_2} R + \beta a_n P_2}{1 + h_{R P_2} a_{P_2} R + h_{N P_2} a_N} - (m + \mu_p)P_1
\]

(2)

\[
\frac{dN}{dt} = \frac{b_N a_n R}{1 + h_{R N} a_N R} N - \frac{\alpha P_2}{1 + h_{R P_2} a_{P_2} R + h_{N P_2} a_N} N - \mu_N N
\]

(3)

\[
\frac{dR}{dt} = \left( r - \frac{R}{R} \right) R - \frac{a_{N N} R}{1 + h_{R N} a_N R} R - \frac{a_{P_1 P_1} R}{1 + h_{R P_1} a_{P_1} R} R - \frac{a_{P_2 P_2}}{1 + h_{R P_2} a_{P_2} R + h_{N P_2} a_N} R
\]

(4)

In this model, \( R \) is the shared basal resource (mussels), \( N \) is the IG prey (green crab), \( P_1 \) is the
small size class of IG predator (small blue crab), and \( P_2 \) is the large size class of IG predator
(large blue crab). Consistent with our knowledge and observations of blue and green crabs, only
\( P_2 \) can prey on \( N \) (Eq. 3), and only \( P_2 \) can reproduce (Eq. 2). The parameters \( a_N, a_{P_1}, \) and \( a_{P_2} \)
are the attack rates of \( N, P_1, \) and \( P_2 \) on \( R \), with associated handling times \( h_{R N}, h_{R P_1}, \) and \( h_{R P_2} \).
The parameters \( b_N \) and \( b_p \) represent the conversion efficiency of \( R \) into new individuals of \( N \) and
\( P_1 \) (reproduction), and \( \mu_N \) and \( \mu_p \) are density-independent natural mortality rates (assumed to be
the same for \( P_1 \) and \( P_2 \)). The parameters \( \alpha \) and \( \beta \) are analogous to \( a \) and \( b \), but represent the
attack rate of \( P_2 \) on \( N \) (IGP) and associated conversion efficiency, with associated handling time
\( h_{N P_2} \). \( P_1 \) matures to \( P_2 \) at rate \( m \), which we assumed is independent of consumption, as factors
other than prey availability may potentially limit maturation rate (e.g. environment and
physiology). Lower maturation rates indicate inefficient growth (greater allocation of energy to
somatic maintenance) and higher rates indicate efficient growth (greater allocation to increasing
body mass). $K$ is the carrying capacity or productivity of basal resource $R$, and $r$ is its intrinsic rate of growth. The variables and parameters used in the model are summarized in Table 1.1.

To incorporate temperature-dependency, we ran the model under 3 different temperature regimes corresponding to those used in our lab experiments, which represent conditions in the northeast, central, and southeast Atlantic coast (Fig. 1.1). We examined the equilibrium outcome of the model at each temperature using fixed, temperature-specific values for all $a$ and $h$ parameters, which came directly from our lab experiments, and varying 3 other parameters of interest across a range of values. Specifically, we varied $a$ (intraguild attack rate) and $K$ (resource carrying capacity) at 2 different levels of $m$ (maturation rate), and varied $m$ and $K$ for 2 different levels of $a$. The 2 maturation rates used in the first analysis corresponded to 50% and 80% of the predator lifetime spent as $P_2$, which is given by $1 - \mu_p/(\mu_p + m)$ (Mylius et al. 2001). Using this range of different values at each temperature allowed us to examine how maturation rate, IG attack rate, resource availability, and the temperature-dependent consumption rates interact to affect the model outcome. The other parameters in the model (conversion efficiencies, mortality rates, and resource growth rate) were held constant across temperature. Although these other parameters are likely also temperature-dependent, we held them constant to isolate the effect of temperature-dependent species interactions and the varied parameters. Since the values of these constant parameters were unknown, we used arbitrary values, but assumed $\beta > b_p = b_N$ and $\mu_N = \mu_p$. Extensive sensitivity analyses suggested that changing these parameters affected the quantitative thresholds at which different model behaviors occurred, but not the general qualitative trends, or the relative differences among temperatures.

Since the equilibrium abundances could not be calculated analytically (Mylius et al. 2001), we ran 2 replicate simulations for each unique parameter combination at each temperature level. The replicate simulations had different initial values for the state variables: $N=10$ and $P_1=P_2=0.1$; or $N=0.1$ and $P_1=P_2=10$. All simulations began with $R=K$. We ran each simulation for 50,000 time steps, and then estimated the equilibrium abundance of each species by computing the mean for the last 500 time steps. For each simulation, we determined which species had persisted (a species was considered extinct if its mean abundance was $<10^{-6}$), and classified the outcome as either (i) "extinction" (resource persists but IP prey and IG predator do not), (ii) "IG prey" (resource and IG prey persist but IG predator does not), (iii) "IG predator" (resource and IG predator persist but IG prey does not), or (iv) "coexistence" (resource, IP prey
and IG predator persist). To examine the (local) stability of each outcome, we substituted the equilibrium abundances into the Jacobian matrix and computed the eigenvalues numerically (Eq. S1.1). We also calculated the temporal variance of each species’ abundance for the last 500 time steps in order to detect limit cycles. An outcome was classified as a stable node if all eigenvalues were negative. If the temporal variance of any species’ abundance was $>10^{-6}$ or if at least one of the eigenvalues was positive, we classified the outcome as unstable. Additionally, if the replicate simulations produced different outcomes, this provided evidence for alternative states dependent on initial conditions, and we classified these parameter combinations according to the 2 possible outcomes. We verified the classification of the simulation results by examining the model time series output directly for a subset of parameter combinations. Overall, we performed 240,000 simulations on a High-Performance Computing cluster using the R language and the package ‘deSolve’ to numerically solve the differential equations via the fourth order Runge-Kutta method.

RESULTS

Per capita competitive ability of crabs

Crabs in all treatments exhibited Type II functional responses (Table S1.1; see raw data with fit curves in Fig. S1.1, S1.2). For green crabs, both attack rates and handing times were lower at 22°C than at 16°C (attack rate, $z = 3.30$, adj. $p = 0.008$; handling time, $z = 7.9$, adj. $p < 0.001$), and did not differ between 22 and 28°C (attack rate, $z = -0.03$, adj. $p = 1.0$; handling time, $z = -1.4$, adj. $p = 0.41$; Fig. 1.2a,b). For small blue crabs, attack rates did not differ among the 3 temperatures (all adj. $p > 0.7$). In contrast, handling times for small blue crabs decreased with increasing temperature (16°C vs. 22°C, $z = 5.75$, adj. $p < 0.001$; 22°C vs. 28°C, $z = 2.13$, $p = 0.033$, adj. $p = 0.16$).

At 16°C, green crabs had a higher attack rate than small blue crabs ($z = 3.36$, adj. $p = 0.007$; Fig. 1.2a), but attack rates were not different between species at 22 and 28°C (22°C, $z = -0.57$, adj. $p = 1.0$; 28°C, $z = -1.32$, adj. $p = 0.94$; Fig. 1.2b). Handling times were not different between species at 16 and 22°C (16°C, $z = -1.12$, adj. $p = 0.41$; 22°C, $z = -1.49$, adj. $p = 0.41$). At 28°C, small blue crabs had a lower handling time than green crabs, although after correction for multiple comparisons this difference was not significant at the $\alpha = 0.05$ level ($z = 2.04$, $p = 0.04$, adj. $p = 0.16$).
Large blue crabs had shorter handling times than small blue and green crabs at all temperatures, and handling times for large blue crabs were lowest at 22 and 28°C (Fig. 1.2b). Attack rates of large blue crabs were the lowest at 16°C (lower than small blue and green crabs), but attack rates were similar to those of small blue and green crabs at 22 and 28°C (Fig. 1.2a).

**Competitive and predatory interactions between paired crabs**

For paired green and small blue crabs, temperature affected the difference in mussel consumption between species (temperature, $F_{2.25} = 3.95$, $p = 0.032$; Fig. 1.3). Small blue crabs consumed more mussels than green crabs in the 28°C treatments than in the 16 to 22°C treatments, where mussel consumption was roughly even. Mussel density did not affect the relative consumption of mussels (density, $F_{1.25} = 0.34$, $p = 0.56$), and there was no interaction between mussel density and temperature (temperature x density, $F_{2.25} = 0.29$, $p = 0.74$). No small blue crabs consumed green crabs. Trial results with paired green and small blue crabs are compared to equivalent trials with solitary crabs in Figs. S1.3, S1.4.

For large blue crabs, only one instance of predation was observed at 16°C (Fig. 1.4). At 22 and 28°C, over half of trials resulted in lethal or sublethal predation (Fig. 1.4). Rates did not differ between 22 and 28°C, except that sublethal predation was only observed at 22°C in the 70 mussel treatment. Handling times of blue crabs consuming green crabs decreased with increasing temperature. We estimated handling times to be approximately 2 hr at 16°C, 1.2 hr at 22°C, and 0.6 hr at 28°C.

**IGP model predictions**

At low maturation rates ($m = 0.1$), the effect of $K$ depended on temperature and the IGP rate, $a$ (Fig. 1.5a). At low temperature (16°C), the IG prey could persist stably at intermediate $K$ levels, but increasing $K$ to high levels lead to unstable IG prey dynamics (limit cycles). No level of $a$ or $K$ we tested was sufficient to allow the IG predator to persist. At higher temperatures (22 and 28°C), intermediate levels of $K$ and sufficiently high levels of $a$ lead to coexistence of IG prey and IG predator, but increasing $K$ to high levels lead to the exclusion of the IG prey. The predator was able to persist at lower $K$ and $a$ values at 28°C than at 22°C, leading to a larger zone of coexistence at 28°C. Where $a$ was too low to enable coexistence, but $K$ was high enough to support the IG predator, alternative stable states were possible depending on the initial densities of the IG prey and IG predator.
Increasing the maturation rate \((m = 0.4)\) further promoted the persistence of the IG predator at the expense of the IG prey (Fig. 1.5b). The IG prey and IG predator could both persist at 16°C if \(\alpha\) was sufficiently high, but as \(K\) increased, the IG prey became unstable and was replaced by the IG predator at high levels of \(K\). At higher temperatures (22 and 28°C), the IG prey largely went extinct. Complete exclusion of the IG prey occurred at 28°C, regardless of the level of \(\alpha\).

The results were similar when holding \(\alpha\) constant and varying the maturation rate, \(m\) (Fig. 1.5c,d). As \(K\) increased, IG prey population dynamics became unstable. Unstable dynamics in the IG prey population began at a lower \(K\) value at 16°C than at the higher temperatures. At 16°C, IG predator dynamics also became unstable if \(\alpha\) and \(m\) were high and \(K\) was intermediate. Exclusion of the IG prey occurred at lower values of \(K\) and \(m\) at 16°C than at the higher temperatures. When \(m\) was very high (a high percentage of the IG predator population existed as \(P_2\)), IG prey was excluded at 22 and 28°C irrespective of \(K\) and \(\alpha\). Lowering \(m\) enabled a zone of coexistence. In all scenarios, neither the IG prey nor the IG predator could persist at low levels of \(K\) due to insufficient resources.

**DISCUSSION**

Our experimental results suggest a temperature-mediated reversal in competitive dominance of our focal species and an increase in IGP rate with increasing temperature. At low temperatures, green crabs had a competitive advantage and IGP on green crabs was low, whereas at high temperatures, size-matched blue and green crabs were competitively similar, large blue crabs had a competitive advantage, and IGP on green crabs was high. The maximum attack rates and ingestion rates \((1/h)\) occurred at higher temperatures for blue crabs than green crabs, suggesting differences in the temperature of peak performance (Englund et al. 2011, Dell et al. 2014). A drop off in IGP rates occurred at 16°C, which we observed in our videos was due to slow attack behaviors of the blue crab relative to the escape behaviors of the green crab. Asymmetric responses in the movement rates of the IG prey and IG predator such as this likely lead to stronger (potentially threshold) effects of temperature on IGP rates than on resource predation rates because IGP is typically an active-capture interaction, whereas the resource is typically nonmobile or less mobile (Dell et al. 2014, Ohlund et al. 2015).
In our model, lower temperatures favored dominance by green crabs, but at higher temperatures, blue crabs were likely to exclude green crabs, particularly when IGP rates and resource productivities were high. In order for blue crabs to persist in our model, much lower values of $\alpha$ (intraguild attack rate) and $m$ (maturation rate) were required at 22°C and 28°C than at 16°C. Consistent with IGP theory, our results showed that a zone of coexistence was often possible as IGP rates increased, as dictated by the combination of $\alpha$ and $m$. However, very high rates of IGP lead to exclusion of green crabs. While interactions are clearly not the only factors influencing the coexistence of these species, our results suggest that temperature-dependent interactions have at least the potential to influence local coexistence independently of other factors and could affect the geographical distribution of these species. More specifically, poleward expansion of blue crabs may be inhibited by competition with green crabs, where IGP is insufficient to compensate for the blue crabs’ competitive disadvantage. Our results also support the findings of de Rivera et al. (2005) that predation by blue crabs may prevent equatorward expansion of green crabs, where green crabs lose their competitive advantage.

In addition to temperature, our model results also provide support for resource productivity ($K$) as a potential driver of species distribution. Consistent with other studies examining IGP outcomes along an enrichment gradient (Diehl & Feißel 2000, Mylius et al. 2001), we found that high productivity favored blue crabs at all temperatures, with a zone of coexistence at intermediate levels. The productivity values at which these transitions occurred depended on temperature. In our study system, productivity is likely also a function of temperature, given that salt marsh productivity increases with decreasing latitude (Kirwan et al. 2009), and ribbed mussel density is higher in marshes to the south than to the north of Cape Cod (Pennings & Bertness 2000). This could provide an additional advantage to blue crabs at lower latitudes.

Only large blue crabs consumed green crabs in our experiments, confirming the additional importance of body size as a driver of IGP in food webs (Woodward & Hildrew 2002). In our model, high temperatures and high maturation rates ($m$) led to exclusion of green crabs even when $\alpha$ was 0, because large blue crabs had an advantage in handling time. Lowering $m$ enabled a zone of coexistence and allowed for green crabs to persist for a greater range of productivity values. This is consistent with other theoretical work suggesting that an initial non-predatory life stage of the IG predator increases the range of resource productivities where
coexistence is possible (Mylius et al. 2001). Overall, this suggests that ontogeny can exert a strong influence on coexistence in IGP modules.

In terms of population stability, we found that in some scenarios, unstable green crab dynamics at high productivity values could be stabilized by blue crab establishment, although these domains of stable coexistence were rather narrow, and rapidly transitioned to exclusion of green crabs. However, these results are consistent with studies by McCann and Hastings (1997) finding that in a 3 species food chain model exhibiting non-equilibrium dynamics, the addition of omnivory (IGP) could stabilize population dynamics and enhance persistence. In our study system, the effect of blue crabs on green crab persistence would be expected to depend on the degree to which blue crabs reduce green crab temporal variability (and thus reduce their stochastic extinction risk), versus reduce green crab mean abundance (and thus increase their extinction risk). The possibility of alternative states in our model is also worth noting, as it suggests that under certain temperature and productivity conditions, the initial abundance of a species at a particular site may dictate whether or not the other can establish. In these circumstances, invasion success would depend on the balance between the recruitment rate of the invading species and the abundance of resident species.

In addition to range limits, temperature-dependent interactions may also influence the relative abundance of blue and green crabs in the region where they coexist. The crabs co-occur between Chesapeake Bay and Cape Cod, their abundances increasing and decreasing, respectively, with decreasing latitude (de Rivera et al. 2005). This zone of coexistence has mean summer temperatures between 22 and 28°C (Fig. 1.1). At these temperatures, our model predicts a relatively narrow domain of coexistence; however, this domain is likely to be wider in reality on account of dynamics omitted from the model for clarity. Factors such as the presence of refugia for green crabs, use of alternate prey resources by the blue and green crabs, segregation of habitat (e.g. different salinity preferences), and cannibalism of small blue crabs by large blue crabs (Hines & Ruiz 1995) may also regulate crab populations and promote coexistence (Holt & Polis 1997, Holt & Huxel 2007, Rudolf 2007). For instance, if alternative resources exist for the IG prey, coexistence need not require that the IG prey be a superior competitor for the shared resource (Holt & Huxel 2007). Our results also suggest some level of interference competition, which would reduce the likelihood of coexistence: at 28°C, attack rates and handling times were not statistically different between green and small blue crabs foraging alone, but small blue crabs
consumed more mussels than green crabs when paired. Extensions of the model might incorporate these additional dynamics.

We assumed in our model that conversion efficiencies and mortality rates did not differ with temperature or between species, but is unlikely to be the case in reality. Although the temperatures we used were well within the thermal window for these species and did not lead to any mortality, mortality rate is generally thought to increase with temperature, and the relative responses of consumption efficiency and mortality to temperature change are important in determining the effect of temperature change on consumer-resource interactions (Gilbert et al. 2014). In terms of conversion efficiency, the effect of temperature depends on the relative responses of ingestion and metabolic rate. Some studies have found metabolic rates to increase faster than ingestion rates with increasing temperature, leading to lower ingestion efficiency (Rall et al. 2010, Vucic-Pestic et al. 2011). However, other studies have assumed conversion efficiencies to be temperature-independent, citing insufficient evidence for a general relationship (Gilbert et al. 2014). We also assumed the maturation rate was independent of resource consumption and used a range of values at each temperature to examine its effect on model outcome; however, it is likely that maturation rate does vary geographically. Blue crabs reach maturity more quickly (although at a smaller size) in southern populations (Tagatz 1968a) than in more northern populations (Van Engel 1958), which could be due to greater resource productivity at lower latitudes, or to greater growth efficiency at higher temperatures. In either case, this would act to further promote blue crab dominance at lower latitudes. Extensions of this work could explore these relationships, or attempt to estimate the unknown parameters by fitting the model to empirical distribution and abundance data.

Although our strategic model allowed us to explore the effects of temperature, productivity, and other parameters on coexistence in size-structured communities at local scales, accurately predicting the distribution and range expansion of these species requires more complex and biologically realistic SDM frameworks that incorporate the effects of regional propagule dispersal and spatiotemporal environmental heterogeneity. A number of oceanographic variables such as wind forcing can strongly influence the dispersal of marine species (Epifanio & Garvine 2001) including blue and green crabs, which have a relatively long pelagic larval durations and which experience asymmetric dispersal on account of prevailing southward coastal currents in the northeastern United States (Pringle et al. 2011). Dispersal
processes and larval supply can strongly influence community composition and the relevance of local-scale species interactions (Roughgarden et al. 1988). For instance, spatio-temporal variability in dispersal, due either to environmental processes or interspecific differences in larval biology, can promote coexistence of competitors where exclusion would otherwise occur by creating ephemeral spatiotemporal niches (Berkley et al. 2010, Aiken & Navarrete 2014). Asymmetric dispersal may also shift species range limits downstream of where they would be expected to occur based on local-scale interactions (Pringle et al. 2017). Rather, range boundaries may cluster in areas of high larval retention, such as southern Cape Cod, which is an oceanographically retentive area and the northern range boundary of many species including blue crabs (Pringle et al. 2017). Overall, this suggests that understanding how regional dispersal interacts with local processes such as species interactions and environmental conditions is critical in order to develop tactical models that accurately predict the distribution of species across scales. Models would also need to define the explicit functional relationship between key environmental variables such as temperature and each parameter.

In summary, this study provides an empirical example of how IGP rates are affected by temperature and the implications this could have, independently of other factors, on local coexistence across a geographic temperature gradient. These non-stationary relationships between interaction strengths and temperature may lead to errors in correlative SDMs that focus exclusively on autecological processes or that incorporate species interactions only as static associations. Embedding our strategic model into tactical SDMs would help highlight how local temperature-dependent and size-structured competition and predation rates interact with regional dispersal and environmental heterogeneity to structure ecological communities in a changing world. This applies whether one is considering native species, or as in this case, interacting native and non-native species.
Table 1.1. Variables and parameters used in the IGP model.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Value</th>
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<tbody>
<tr>
<td>$R$</td>
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<td>$N$</td>
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<td>Small IG predator</td>
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<tr>
<td>$P_2$</td>
<td>Large IG predator</td>
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<td>$R$ carrying capacity</td>
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<td>$a_{P_2}$</td>
<td>Attack rate on $R$ by $P_2$</td>
<td>from experiments</td>
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<td>$\alpha$</td>
<td>Attack rate on $N$ by $P_2$</td>
<td>varied in simulations</td>
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Fig. 1.1. (a) Presence of blue and green crabs in Atlantic coast estuaries and (b) associated annual summer water temperatures (June-September) for the years 2002-2015. Key applies to both panels. Dashed horizontal lines are the 3 temperatures used in the mesocosm experiments. Data are from NOAA National Estuarine Research Reserve System (NERRS) water quality monitoring stations (from left to right on horizontal axis, respective stations are Inlet, Sage Lot, Great Bay, Nag Creek, Buoy 126, Scotton Landing, Goodwin Islands, Research Creek, St. Pierre, Lower Duplin). Years with more than 15 days of missing data during these months were excluded. Data accessed from the NOAA NERRS Centralized Data Management Office website: http://www.nerrsdata.org; accessed 16 December 2016.
Fig. 1.2. (a) Attack rates and (b) handling times for green crabs (G), small blue crabs (SB), and large blue crabs (LB) at 3 temperatures. Error bars are 95% confidence intervals. Within species, temperatures treatments sharing letters do not differ (adj. p > 0.05, capital letters for G, lowercase for SB). *At a given temperature, G and SB treatments differ (adj. p < 0.05).
Fig. 1.3. Difference in mussel consumption between paired green and small blue crabs at 3 temperatures and 2 mussel densities (vertical axis is the proportion of mussels consumed by the blue crab – proportion of mussels consumed by the green crab). Positive values indicate that the blue crab consumed more mussels than the green crab. Error bars are ± 1 SE.
Fig. 1.4. Proportion of trials in which large blue crabs consumed green crabs at 3 temperatures and 2 mussel densities. Sublethal predation events were trials in which the blue crab attacked the green crab and removed and consumed claws and/or legs, but did not kill the green crab.
Fig. 1.5. Equilibrium results of the IGP model, varying $\alpha$ (intraguild attack rate) and $K$ (resource carrying capacity) at 2 different levels of $m$ (maturation rate) (a, b), and varying $m$ and $K$ at 2 different levels of $\alpha$ (c, d). Colors indicate the species present at equilibrium (coexistence = both consumers present, extinction = neither consumer present), whether the equilibrium dynamics were stable (no added text) or unstable, and whether alternative states exist (separated by “or”).
Chapter 2:
Multifactorial effects of climate change on the distribution of species with complex life cycles

Tanya L. Rogers, Tarik C. Gouhier, David L. Kimbro
Northeastern University Marine Science Center, 430 Nahant Road, Nahant, MA 01908

ABSTRACT
Mechanistic species distribution models, which map the fundamental niche of species based on physiological constraints, have been used to understand and predict shifts in species distribution in a changing climate. However, these models often fail to consider how different facets of the environment affect the distinct life history stages of species characterized by complex life cycles. Addressing this knowledge gap is critical in order to understand which environmental conditions and life history stages govern the distribution of species in space and time. In this study, we explored how the abundance of an ecologically and economically important species, the blue crab *Callinectes sapidus*, may be changing across its range on the Atlantic coast of the United States. In addition, we examined how an array of physiological drivers acting on multiple life history stages may affect the species’ current and future distribution using simple mechanistic models. Using landings (harvest) data as a proxy for abundance, we found that landings in mid-Atlantic and southern states have declined; in contrast, landings in northeastern states have remained constant or increased. We also found that environmental conditions affecting larval stages appeared to be most important in dictating the crab’s northern range limit (Cape Cod), and the growth and reproduction of any juvenile crabs that do settle north of Cape Cod may be further inhibited by sublethal (but not lethal) cold stress. Temperature projections based on the business-as-usual emission scenario suggest potential for range expansion beyond Cape Cod over the course of the 21st century, as well as increases in abundance at the current range boundary. However, just south of Cape Cod, changes in the duration, magnitude, and phenology of summer temperatures may have complex effects on crab reproduction. Our physiological and landings results highlight how past and future changes in environmental suitability can vary regionally and non-uniformly across the range of a species. This study demonstrates how the performance of mechanistic species distribution models can be improved through the examination of multiple aspects of temperature stress and multiple life history stages both within and beyond a species’ current range.
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). Physiology can often dictate range limits (Somero 2005), and mechanistic species distribution models that map the fundamental niche of species based on physiological responses and constraints (Kearney & Porter 2009) offer an alternative to correlative approaches based on occurrence data. The match of biophysical models to observed species distributions can be used to identify where physiological tolerances may constrain species ranges, and in cases where the fundamental niche exceeds the realized niche, where biotic interactions and/or dispersal limitation may be important (Buckley 2008). Additionally, an increasing number of studies are beginning to show that 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). Predicting changes in response to environmental variability and climate change thus requires an understanding of the drivers limiting current distribution patterns over a range of scales (Sexton et al. 2009). Since mechanistic models are not restricted to species range edges, and can incorporate non-analog environmental conditions, they can be useful a tool for understanding and predicting biogeography changes in key species not just at range boundaries, but across a species’ entire range in response to climate change.

It is not common, however, for such models to consider all life history stages of an organism, which may have different physiological requirements and constraints (Kearney et al. 2008, Russell et al. 2011). This is particularly problematic for marine organisms with complex life cycles, as any one of several stages may act as a potential bottleneck. Since climate change can also shift the seasonal timing of temperatures (Burrows et al. 2011), it is important to consider the potential for phenological mismatches between the timing of life history events and environmental conditions, which can also dictate species range limits (Crickenberger & Wethey 2017). Finally, multiple aspects of a single environmental driver such as temperature can play alternating roles in setting distribution patterns on local and geographic scales (Woodin et al. 2013, Seabra et al. 2015). These aspects include not just the mean, but minima, maxima, and both the intensity and duration of exposure to both lethal and sublethal extremes (Rezende et al. 2014). The relevant life stages and environmental drivers may vary across the range of the
species. Thus, improved understanding and prediction of biogeographic shifts can be gained through a mechanistic examination of how different aspects of the environment constrain multiple life history stages both within and beyond species ranges.

In the United States, blue crabs (*Callinectes sapidus*) are an ecologically and economically important species with a broad geographic range spanning the Atlantic and Gulf of Mexico coasts. The northernmost permanent populations 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 range edge, and there is potential for a range shift in response to regionally warming seas (Pershing et al. 2015). Blue crab abundance and environmental suitability may also potentially change within the species’ current range; however, these impacts have not been investigated. In addition, blue crabs have a 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). These life stages are subject to different environmental conditions (e.g. onshore vs. offshore water temperatures), have different environmental constraints and tolerances, and may be differentially affected by environmental change. Thus, blue crabs are an ideal system to investigate how a different aspects of temperature stress acting on the distinct physiological tolerances of multiple life history stages may affect this species’ current and future spatial distribution using a mechanistic modeling approach. To achieve this goal, we (1) examined historical trends in blue crab abundance across the U.S. Atlantic coastline using data on blue crab landings (harvest); (2) compared the lower thermal tolerances of larval and juvenile/adult crabs to ecologically relevant aspects of water temperature across the coastline; and (3) evaluated how projected changes in ecologically relevant aspects of water temperature may affect crabs in different regions of the coastline.

**METHODS**

**Study system**

Blue crabs are a major commercial and recreational fishery species, as well as important benthic predators with strong effects on their associated estuarine communities (Silliman & Bertness 2002, Altieri et al. 2012). Although the blue crab has been extensively studied in the
mid-Atlantic and Gulf of Mexico, surprisingly little research has been done on populations north of Delaware Bay, and few studies have made biogeographic comparisons of populations.

The blue crab life cycle is well-described and has been studied primarily in the mid-Atlantic region (Millikin & Williams 1984, Epifanio 1995). After mating in low salinity waters, female blue crabs migrate to high salinity waters at the mouths of estuaries, where peak spawning occurs in July and August. In offshore surface waters, the planktonic larvae develop through 7 zoeal stages over the course of approximately 1 month (Costlow & Brookhout 1959), with zoeal abundance peaking in August and September (Epifanio et al. 1984). 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. Although some blue crab larvae return to their parent estuary, they can be transported among estuaries depending on oceanographic conditions (Epifanio et al. 1989, Johnson & Hess 1990), and genetic studies suggest that high gene flow occurs among neighboring estuaries over ecological time scales (McMillen-Jackson et al. 1994, McMillen-Jackson & Bert 2004). 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. North of Cape Hatteras (35.3°N), adult and juvenile crabs hibernate during the winter months, buried in sediment and in deep channels. South of Cape Hatteras, the crabs are active year-round.

**Trends in blue crab landings**

To examine historical trends in blue crab abundance across the Atlantic coast, we examined state-level commercial blue crab landings (harvest) from 1950 to 2015, and quantified the linear trend in landings over the past 35 years for each state. To account for autocorrelation of residuals, generalized least squares (GLS) models with AR(1) correlation structures were used, and data were standardized within states to mean 0 and standard deviation 1 to allow for comparison of slopes (change in landings per year) across states. We acknowledge limitations of equating landings with abundance (Pauly et al. 2013); however, most of the time series from fishery-independent blue crab surveys were not long enough to examine long-term trends, and the surveys had limited spatial coverage.

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1 Data obtained from NOAA Fisheries, [http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html](http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html)
Mechanistic modeling of physiological constraints

To examine physiological constraints on the blue crabs, as well as the life history stages acting as potential population bottlenecks, we first obtained blue crab lower thermal tolerances for all developmental stages (egg, zoea, megalops, juvenile, and adult) from the literature. Since distributional limits can be set by short term exposure to temperatures below the lower lethal limit (LT$_{\text{min}}$), or by chronic exposure to temperatures above LT$_{\text{min}}$ but below the temperature at which physiological performance is zero (CT$_{\text{min}}$) (Woodin et al. 2013), we considered both of these thresholds where information was available. Temperature tolerances varied among studies, so ranges are presented for each life history stage (Table 2.1). A summary of the methods and results of each study, which we used to identify these ranges, are presented in Table S2.1.

Juvenile/adult crabs

For juvenile and adult blue crabs, CT$_{\text{min}}$ corresponds to 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$_{\text{min}}$ 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 Darnell et al. (2009). LT$_{\text{min}}$ for adult/juvenile crabs corresponds to the temperature below which mortality is observed during hibernation. Estimates for LT$_{\text{min}}$ 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. The amount of mortality below this threshold depended on a variety of factors including acclimation temperature, salinity, crab size, and duration of the cold stress.

We compared lower tolerances to estuarine bottom water temperatures. We specifically examined the number of days per year above CT$_{\text{min}}$ and below LT$_{\text{min}}$. As a data source, we used daily mean bottom water temperatures from 10 National Estuarine Research Reserve (NERR) sites spanning the U.S. Atlantic coast (Fig. 2.2a).² Start dates ranged from 1994-2002, and the time series ended in 2015. Gaps in the time series of less than 30 days were linearly interpolated. If, after this interpolation, a year still contained missing values between May and September, or between January and March, the year was excluded from the analysis of days above CT$_{\text{min}}$ and

below LT\textsubscript{min}, respectively. Many years from northern sites were excluded from the LT\textsubscript{min} analysis due to missing data during winter months. Since temperature tolerance estimates varied among studies, we used mean estimates for the main analysis, and then conducted a sensitivity analysis using the minimum and maximum estimates for CT\textsubscript{min} and LT\textsubscript{min}.

**Larval crabs**

For blue crab larvae, information was available only on CT\textsubscript{min}, the temperature below which development does not progress. For early life history stages, eggs and megalopae tolerated temperatures as low as 16°C and 15°C respectively, 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\textsubscript{min}.

We compared lower tolerances to offshore sea surface temperature (SST). We specifically examined (1) the number of days per year above CT\textsubscript{min}, (2) the median day of the year above CT\textsubscript{min} and the median day 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 logistic model for larval survival (with survival rate equal to 0.01 at CT\textsubscript{min}).

As a data source, we used daily SST measurements from the Optimum Interpolation Sea Surface Temperature dataset (OISST v2, Reynolds et al. 2007) from 1982 to 2015.\(^3\) We obtained temperatures for points spanning the Atlantic coast, at each 0.25 degrees of latitude (the available grid size), located 0.5 degrees from shore (Fig. 2.3a). We conducted a sensitivity analysis using 3 versions of the logistic model, which varied in the “slope” at which survival probability increased above CT\textsubscript{min} (50% survival probability at 0.5, 1.5, and 2.5°C above CT\textsubscript{min}).

**Temperature projections**

We repeated the analysis for larval (zoeal) stages using daily SST projections from the IPCC Coupled Model Intercomparison Project (CMIP5, Taylor et al. 2012) from 2000 to 2098, using the business-as-usual Representative Concentration Pathway scenario (RCP8.5). We obtained multimodel mean temperatures (from 19 models, Table S2.2) for points spanning the Atlantic coast, at each 1 degree of latitude (the available grid size), located 1 degree from shore (Fig. 2.3a). 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

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\(^3\) Data obtained from the NOAA National Climatic Data Center, https://www.ncdc.noaa.gov/oisst
the CMIP5 and OISST data during the period of overlap (2000-2015) following the methods in Wethey et al. (2016).

RESULTS

Trends in blue crab landings

Across the Atlantic coastline, blue crab commercial harvest varied by several orders of magnitude (Fig. 2.1b). Landings were highest in the mid-Atlantic, with landings from northern states (Connecticut, New York, New Jersey, and Delaware) making up only 6% of the total U.S. harvest from 2010-2015. Blue crabs are present and recreationally harvested in Rhode Island and Massachusetts, but the crabs are not commercially harvested in these states. Within the last 35 years, landings have increased in New Jersey and showed no linear trend in Connecticut, New York, and Delaware. South of Delaware, there was a trend of decreasing landings in many states (Fig. 2.1a,c).

Mechanistic modeling of physiological constraints

Adult/juvenile crabs

In estuaries in winter, locations north and south of the current range boundary both contained an appreciable number of days below 3°C (adult/juvenile LT$_{\text{min}}$) (Fig. 2.2b). South of Cape Hatteras (~35°N), few to no days were below 3°C. Sites also varied in the number days above 12°C (adult/juvenile CT$_{\text{min}}$) (Fig. 2.2c). Locations north of Cape Cod, between Cape Cod and Cape Hatteras, and south of Cape Hatteras, had 100-175, 150-250, and 250-365 days above 12°C, respectively. Using the minimum estimates for LT$_{\text{min}}$ (0°C) and CT$_{\text{min}}$ (9°C) did not have a strong impact on the amount of overlap across sites (Fig S2.1). When using the maximum estimates for LT$_{\text{min}}$ (5°C) and CT$_{\text{min}}$ (15°C), the northernmost location was more separated from the other locations, having more days below 5°C and fewer days above 15°C (Fig S2.1).

Larval crabs

South of Cape Cod, historical summer SSTs were nearly always above 20°C (zoeae CT$_{\text{min}}$) for at least 30 days, but north of Cape Cod, the number of days dropped sharply to 0 (Fig. 2.3b). Only since 2007 have SSTs north of Cape Cod regularly exceeded 20°C. The median date above 20°C tended to be in mid-August (around calendar day 225), and there were no clear phenological shifts over the historical period (Fig. 2.3d). 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. S2.2a). Using historical mean August temperatures, the logistic model for larval survival (with 50% survival probability at 1.5°C above CT_{min}) indicated a drop off in larval survival north of ~41°N (just south of the current range boundary, Fig. 2.4b,d).

**Temperature projections**

Model projections indicate a continued rise in the number of days above 20°C north of Cape Cod, which is particularly pronounced at the end of the century (Fig. 2.2c). At locations between 35 and 45°N, there was also a rise in the number of days above 20°C. During the period of overlap with the historical data, the projections tended to overestimate the number of days 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. S2.3).

The projections also suggest that the median date above 20°C may shift later in the year for locations south of Cape Cod between 36 and 40°N (Fig. 2.2e). The highest temperatures of the year were also projected to shift later in the year for latitudes between 38 and 40°N (Fig. S2.2b). Phenological trends in maximum temperatures were not as clear at lower latitudes, perhaps due to lower seasonality.

Projected mean August temperatures (bias corrected) suggest that conditions may become less suitable for larval development between 38-41°N, in line with projected decreases in August SSTs at these latitudes (Fig. 2.4c,e). 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. Since the CMIP5 models tended to underestimate August SST during the period of overlap with the historical data, using uncorrected projections resulted in the prediction that most of the coastline would be unsuitable for larval survival, which is likely inaccurate (Fig. S2.4). When a steeper increase in survival probability above CT_{min} was used, range expansion occurred more quickly, and conditions remained largely suitable for larvae at all latitudes south of the current range boundary, using both the corrected and uncorrected projections (Fig. S2.4). Results using mean September temperatures were similar to those using mean August temperatures.

**DISCUSSION**

In this study, we found that thermal constraints on early life history stages were a likely bottleneck influencing the distribution of our focal species, and that changes in historical abundance and in projected environmental suitability were non-uniform across the species’
Atlantic range. Cold conditions during summer larval stages appeared to be most important in dictating the northern range limit of blue crabs, and sublethal (but not lethal) cold stress may further inhibit the ability of any juvenile crabs that do settle north of the current range boundary from successfully growing and reproducing. Temperature projections suggested increasingly suitable conditions for larval stages at and north of the current range boundary (Cape Cod), which are in line with recent trends in blue crab landings and sightings north of Cape Cod. However, in the region just south of Cape Cod, long-term changes in the duration, magnitude, and phenology of summer temperatures may have complex effects on crab reproduction. Farther south, cold stress is likely not constraining. Our results highlight how non-uniform environmental changes can occur both within and beyond the current range of the species, which may affect the current and future distribution and abundance of this ecologically and economically important species. This insight would not have been possible without examination of multiple aspects of temperature stress and multiple life history stages using a range-wide, mechanistic modeling approach.

Cold temperatures during the summer are known to dictate the range limits of a number of invertebrate species through their effects on larval stages (Sanford et al. 2006, de Rivera et al. 2007), which are often less stress-tolerant than adults (Andronikov 1975). However, the range limits of some tropical species, such as the barnacle Megabalanus coccopoma, are set not by larval development (they are capable of successful development north of their current range boundary), but by overwinter survival of adults (Crickenberger 2016, Crickenberger et al. 2017). In the case of blue crabs, we found that temperature conditions suitable for larvae dropped off sharply at Cape Cod, suggesting that larval development is not possible north of this range limit. For juvenile/adult crabs, we found that while acute cold stress (number of days below LT_{min}) did not differ appreciably between the north and south side of Cape Cod, the number of days above CT_{min} was lower north of Cape Cod, which may hinder growth to maturity. Thus, our study demonstrates how it is important to examine both chronic and acute stress, as well as multiple life stages, when trying to quantify environmental suitability.

In addition to constraints at the range edge, our comparison of thermal thresholds to historical temperature data can reveal and explain some patterns within the range of the species. In the mid-Atlantic, the number of days below juvenile/adult LT_{min} was quite variable, and in some years, relatively high. This result is consistent with studies finding that winter severity can
regulate the overwinter survival of hibernating adult/juvenile blue crabs in the mid-Atlantic region (Rome et al. 2005, Bauer & Miller 2010a). South of Cape Hatteras, temperature conditions were greater than $CT_{\text{min}}$ for nearly the entire year, and rarely to never below $LT_{\text{min}}$, which is consistent with the lack of hibernation in blue crabs below this latitude, and suggests these southeastern populations do not experience cold-induced mortality. However, the largest blue crab harvests occurred in mid-Atlantic, not in the Southeast. Assuming harvest is proportional to abundance, this suggests the regions of lowest environmental stress do not always have the largest populations, and that other factors (e.g. estuary/habitat size, predation, disease) may regulate populations in these areas. Since the blue crab range extends farther south into the Gulf of Mexico and Caribbean, it is unlikely that heat stress is a constraint in the Southeast, however, we did not examine this explicitly.

Temperature projections suggested changes in the suitability of environmental conditions for blue crabs that also appeared to vary regionally. At and north of the current range edge, both maximum and minimum temperatures are projected to increase, resulting in an increase in both August temperature and days above larval $CT_{\text{min}}$. Thus, as a result of increasingly suitable conditions for crab larvae, populations at the current range edge may increase in abundance as conditions become more similar to those farther south, and there is potential for crabs to expand their range into the Gulf of Maine and Atlantic Canada. In addition, although they do not necessarily reflect conditions close to shore, increases in minimum SSTs across the region may further reduce cold stress on juvenile and adult crabs. It appears that areas in the northern Gulf of Maine may always be too cold for blue crabs and may create a range discontinuity, although this was only seen using the bias corrected temperature projections and assumes stationarity in temperature differentials. Currently, relatively persistent populations of blue crabs in Great Bay, New Hampshire (W. Watson, pers comm) and Kejimkujik, 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). If range expansion occurs, we also speculate blue crabs are 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 two 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. 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.

At latitudes just south of the current northern range boundary (Cape Cod), we found that mean August temperatures were projected to decrease, but number of days above the larval physiological threshold were projected to increase. This finding produced conflicting predictions in terms of suitability for larval survival. Examination of the time series indicated that these results were due to a decrease in temporal variability at these locations (decreases in annual maxima, and increases in annual minima). Whether larval survival will increase or decrease ultimately depends on the sensitivity of larvae to conditions just above $CT_{\min}$, which is unclear. Future research that a better characterizes the relationship between temperature and development time could be used to estimate a degree-days requirement integrating both the magnitude and duration of suitable thermal conditions.

Within this same region just south of Cape Cod, 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 $CT_{\min}$ appears to result from additional days later in the calendar year. If these shifts in peak temperatures are not accompanied by shifts in spawning, this could potentially lead to mismatches that may negatively affect reproduction. Alternatively, if spawning behavior is plastic, a longer spawning season may benefit crabs and enhance reproduction. These results 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 the species.

Along with our physiological results, changes in blue crab landings over the past few decades also revealed patterns within the range of the species which appeared to vary regionally. Whereas landings in mid-Atlantic and Southeast have declined, landings in northern populations have remained constant or increased, which is suggestive of and consistent with climate-induced biogeographic changes in crab abundance. Although harvest is an imperfect proxy for abundance (Pauly et al. 2013), our results suggest that harvest data can potentially be a valuable tool for detecting biogeographic shifts within a species’ range, as well as impending range shifts, particularly for data poor species or stocks. Many fished species are shifting faster than they can be managed (Pinsky & Fogarty 2012), and so examination of large-scale trends and awareness of possible non-stationarity, even through imperfect proxies, can provide useful information. In the
case of blue crabs, our overall findings also underscore the need for more studies of blue crab biology and population dynamics north of Delaware Bay, where the fishery has begun (and is likely to continue) to increase in size, and where blue crab stock assessments currently do not exist. This study suggests multiple, complex interactions between temperature and life stage may lead to changes within the current range, and so there is a need for further research on the exact drivers influencing trends in abundance (landings) within the species’ range.

Although our results are suggestive that physiological thresholds in part maintain the northern range boundary of blue crabs, it is also important to consider 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). 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 likely not an issue, as there are numerous estuaries north of Cape Cod similar to those inhabited by blue crabs farther south. However, large marsh systems do become less common in Maine.

Species interactions are another factor that can 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, previewed by current assemblages south of Cape Cod. It is important to remember that climate change will affect the distribution and abundance of not just one species, but of entire communities species across the landscape (Lucey & Nye 2010).

Geographic variation in thermal tolerance and the potential for local adaptation are also possible complications not considered here (Sanford & Kelly 2011). An important caveat in this study is that the temperature tolerance limits we obtained from the literature were for blue crabs from Chesapeake Bay and North Carolina, which is where the vast majority of blue crab studies have been conducted. It would be very informative for future studies to examine the temperature tolerance of crabs from more northern locations, which to date has not been done. Although rates of gene flow in the species are estimated to be relatively high (McMillen-Jackson et al. 1994, McMillen-Jackson & Bert 2004), it is certainly possible that populations near the northern range limit may be more cold-tolerant due to local selection. In addition, blue crab breeding phenology in the Northeast, which has not been described in the literature, may differ from that in the mid-Atlantic.

In summary, we demonstrate how various aspects of temperature stress can act on multiple life history stages to impact not just the location of range boundaries, but also distribution and abundance within a species’ range. We found that geographic mosaics in environmental conditions may lead to non-uniform trends and predictions, and so 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. While all of these issues have been raised by previous studies, to our knowledge this is among the first to combine these techniques in a single study to explore changes in the distribution of ecologically and commercially important species over local and geographic scales (Mangano et al. 2018). Our study presents a 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 predict 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).
Table 2.1. Lower thermal tolerances of blue crabs at different life stages. For details on the methods and results for each reference, see Table S2.1.

<table>
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<th>Life Stage</th>
<th>Threshold</th>
<th>Temp. (°C)</th>
<th>References</th>
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<td>juvenile/adult</td>
<td>$LT_{\text{min}}$</td>
<td>0-5</td>
<td>Tagatz 1969, Rome et al. 2005, Bauer &amp; Miller 2010b</td>
</tr>
<tr>
<td>megalops</td>
<td>$CT_{\text{min}}$</td>
<td>15-20</td>
<td>Costlow &amp; Brookhout 1959, Costlow 1967</td>
</tr>
<tr>
<td>zoea</td>
<td>$CT_{\text{min}}$</td>
<td>20-25</td>
<td>Sandoz &amp; Rogers 1944, Costlow &amp; Brookhout 1959</td>
</tr>
<tr>
<td>egg</td>
<td>$CT_{\text{min}}$</td>
<td>16-19</td>
<td>Sandoz &amp; Rogers 1944, Amsler &amp; George 1984</td>
</tr>
</tbody>
</table>
Fig. 2.1. Trends in blue crab landings. (a) Annual commercial blue crab landings in U.S. Atlantic states. A linear regression is shown for the years 1980 – 2015. (b) Mean blue crab landings in U.S. Atlantic states for all years. (c) Linear trend in blue crab landings (data within states scaled to mean 0 and standard deviation 1) for the years 1980 – 2015, from a generalized least squares model with AR(1) correlation structure. Error bars are +/- 1 SE. * slopes different from 0 (p<0.05).
Fig. 2.2. Temperature conditions in relation to blue crab adult/juvenile lower temperature tolerances. (a) Map of points from which water temperature data were obtained. (b) Days below 3°C ($LT_{\text{min}}$). (c) Days above 12°C ($CT_{\text{min}}$). Horizontal black line is the historical blue crab northern range limit. Data are from NOAA National Estuarine Research Reserve System (NERRS) water quality monitoring stations (from top to bottom in legend, respective stations are Inlet, Great Bay, Sage Lot, Nag Creek, Buoy 126, Scotton Landing, Goodwin Islands, Research Creek, St. Pierre, Lower Duplin). For sensitivity analysis, see Fig. S2.1.
**Fig. 2.3.** Historical and projected temperature conditions in relation to blue crab larval (zoeal) lower temperature tolerances. (a) Map of points from which water temperature data were obtained. OISST = Optimum Interpolation Sea Surface Temperature, CMIP5 = IPCC Coupled Model Intercomparison Project. (b,c) Days above 20°C ($CT_{\text{min}}$). Contour for 0 days is shown in white, and contour for 30 days is shown in pink. (d,e) Median day of the year (days after January 1) above 20°C. White areas are locations/years with no days above 20°C. Horizontal black line is the historical blue crab northern range limit.
Fig. 2.4. Historical and projected temperature conditions in relation to blue crab larval (zoeal) lower temperature tolerances. (a) Map of points from which water temperature data were obtained. OISST = Optimum Interpolation Sea Surface Temperature, CMIP5 = IPCC Coupled Model Intercomparison Project. (b,c) Mean August water temperature. (d,e) Suitability for larval survival probability given historical and mean August water temperatures. Horizontal black line is the historical blue crab northern range limit. For sensitivity analysis, see Fig. S2.4.
Chapter 3:
Hidden similarities in the asynchronous dynamics of Atlantic blue crab populations

Tanya L. Rogers\textsuperscript{a}, Stephan B. Munch\textsuperscript{b}
\textsuperscript{a}Northeastern University Marine Science Center, 430 Nahant Road, Nahant, MA 01908
\textsuperscript{b}Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, CA 95060

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Abstract
Information on spatial synchrony has a number of implications for metapopulation stability, persistence, and extinction risk. While many studies have sought to document and understand the drivers of synchrony, rarely have studies attempted to distinguish among the potential drivers of asynchrony, particularly in cases where synchrony is predicted but not observed. In many marine species, populations are coupled by dispersal and subject to correlated environmental drivers, yet are not strongly synchronous. A variety of factors including noise, spatially variable dynamics, and nonlinear dynamics might lead to asynchrony, but disentangling these factors in field data has been challenging. We present a hierarchical time-delay embedding framework based on Gaussian process regression that can empirically quantify nonlinear population dynamics, and which provides a novel and interpretable way to distinguish among alternative explanations for asynchrony. In particular, this approach produces a “dynamic correlation” metric quantifying similarity in the response of populations to predictor variables, as opposed to, and irrespective of, correlation (synchrony) in observed abundances across time. In the first empirical application of this method, we examined the dynamics of blue crabs (Callinectes sapidus) from 17 populations across the U.S. Atlantic coast using fishery-independent time series data. Although estimates of synchrony among populations were negligible, dynamic correlations among populations were strong, broadly similar, and exhibited spatial patterning. Moreover, the time series for all populations had positive Lyapunov exponents, suggesting chaotic dynamics. These results suggest that noise and nonlinearity may destabilize synchrony and obscure hidden dynamical similarities among nearby populations that appear superficially independent.
Significance
Identifying the relevant spatial scales of population variability and understanding the complexity and context-dependency of ecological dynamics are important goals in ecology. Asynchrony among populations might lead one to believe that local, intrinsic dynamics differ widely across sites, and that populations are incomparable. However, we found that for asynchronous populations of Atlantic blue crabs, this apparent complexity belies a consistent, spatially-structured dynamical response to past abundances and environmental drivers, and that integrating information across populations improves predictability. Our results also provide the first evidence that chaos, as opposed to spatial variability in dynamics or asynchrony in the environment, is a potential driver of asynchrony in natural populations. The hierarchical, nonlinear methods we present and employ are broadly applicable and could be used to uncover hidden dynamical similarities in other seemingly unrelated populations.

Introduction
Information about spatial synchrony, defined as coincident fluctuations in abundance across time and space, is useful for identifying relevant spatial scales of population variability (Levin 1992), and has implications for the spatiotemporal stability and persistence of populations (Heino et al. 1997, Earn et al. 2000, Schindler et al. 2010). Synchrony in spatially structured metapopulations has been studied extensively since the 1990s (Bjørnstad et al. 1999, Liebhold et al. 2004), and has been documented in a number of systems including mammals, birds, insects, and infectious diseases. The theoretical drivers of spatial synchrony (or, more generally, spatial autocorrelation) are now well understood, with correlated drivers and coupling via migration being the most prominent explanations. The earliest hypotheses showed that synchrony could arise among populations experiencing spatially correlated environmental fluctuations (the Moran effect; Moran 1953, Ranta et al. 1997) or via interactions with another species that is spatially synchronized (Ims & Steen 1990, Blasius et al. 1999, Cazelles & Boudjema 2001). Synchrony can also emerge via dispersal between geographically segregated populations (Molofsky 1994, Ranta et al. 1998). Laboratory experiments provide empirical support for this theory (e.g. Fontaine & Gonzalez 2005, Fox et al. 2011).

In marine systems, many populations are coupled through dispersive larval stages (Cowen & Sponaugle 2009) and are thought to respond strongly to spatially correlated, large-
scale, exogenous drivers such as temperature (e.g. Harley et al. 2006, Lucey & Nye 2010). In light of existing theory, spatial synchrony should be ubiquitous in marine species. In reality however, synchrony is not often observed (e.g. Lagos et al. 2007, Rogers & Schindler 2008). As a focal example, blue crabs (*Callinectes sapidus*) on the Atlantic coast of the United States have nearly panmictic larval dispersal (McMillen-Jackson et al. 1994, McMillen-Jackson & Bert 2004, Rodrigues et al. 2017), and their dynamics are thought to be strongly influenced by spatially synchronized environmental drivers such as temperature and precipitation (e.g. Rome et al. 2005). However, as we document below, blue crab populations across the Atlantic coastline display little evidence of synchrony.

While there have been many investigations into the drivers of synchrony in field populations, rarely have studies attempted to disentangle the potential drivers of *asynchrony*, or to explain frequent discrepancies between theoretical expectations (which predict synchrony) and observations. In studies of spatiotemporal dynamics, asynchrony is often the null hypothesis, yet a number of different mechanisms can lead to asynchrony, which have different implications for population fluctuations and predictability. Based on existing theory, we propose 4 non-mutually exclusive explanations for asynchrony in field populations: (I) It is possible that the data are contaminated by enough observation noise that the time series do not reflect true abundances, and they are simply unpredictable (Rouyer et al. 2008). Relatively small amounts of stochasticity can reduce spatial autocorrelation and eliminate perfect synchrony (Pecora & Carroll 2015). (II) The relevant environmental drivers may be uncorrelated (the reverse Moran effect), which could also include spatial variation in the presence of an interacting species. (III) Spatial variability (intrinsic differences) in local population dynamics may prevent synchronization (Swanson & Johnson 1999, Peltonen et al. 2002, Ringsby et al. 2002). Geographically variable population dynamics are known to exist for a number of species (e.g. Bjørnstad et al. 1995, Williams & Liebhold 2000), and may arise from factors such as local adaptation or genetic drift. (IV) Population trajectories may diverge as a result of nonlinearity (chaos) (Allen et al. 1993, Ranta et al. 1998) or process noise. Chaotic systems may display asynchronous behavior even if their underlying dynamics are identical, and are more difficult to synchronize than stable and cyclic systems (Vasseur & Fox 2009, Becks & Arndt 2013). Process noise, which is always a consideration in ecological modeling, may also produce a similar signature.
Differentiating among these possible explanations has been a major challenge, in large part because of methodological limitations for evaluating spatial variability in noisy, potentially nonlinear, local dynamics. In this study, we present methods that can empirically quantify spatial variation in nonlinear population dynamics, and help to distinguish among alternative explanations for asynchrony. Using a combination of these and existing methods, we then evaluate the 4 proposed hypotheses for asynchrony in the case of Atlantic blue crabs.

**Statistical framework**

Our main methodological novelty lies in developing a nonparametric approach to quantify the similarity between the dynamics of different populations. Nonparametric time series methods based on Takens’ (1981) theorem of time-delay embedding, variously known as state space reconstruction (SSR) and empirical dynamic modeling (EDM), are able to quantify nonlinear dynamics, do not require an underlying model specification, and produce relatively accurate short-term forecasts (Perretti et al. 2013, Ye et al. 2015). EDM has been extended to combine data from multiple, identical populations (Hsieh et al. 2008) and to leverage spatially explicit time series to improve forecasts (Glaser et al. 2011). Here, we used a hierarchical Bayesian extension of the time-delay embedding framework based on Gaussian process (GP) regression (Munch et al. 2017) to partition regional dynamics, local dynamics, and process noise (see Materials and Methods). This model allows estimation of a “dynamic correlation” metric ($\rho$) that quantifies similarity in the response of populations to predictor variables (i.e. their correlation across predictor space), irrespective of their correlation in time (Poynor & Munch 2017). This is in contrast to the correlation metrics used to evaluate synchrony (e.g. Pearson’s), which quantify similarity in observed abundances across time.

To illustrate the relevance of this, consider time series ($x_1$ and $x_2$) generated by two uncoupled but identical maps, i.e. $x_i(t + 1) = x_i(t)\exp[r - x_i(t) + \sigma \varepsilon(t)]$. For sufficiently large values of $r$ or $\sigma$ the resulting time series will be completely uncorrelated, despite having identical dynamics. In this simple example, despite the lack of correlation, we could test whether the dynamics are the same by fitting the above model to the time series and comparing parameter estimates. However, in the real-world case where the dynamics are more complicated and the model unknown, we need a more general approach. To this end, we construct nonparametric estimates of the delay-coordinate maps for each time series, say $f$ and $g$, and estimate the
correlation between maps, i.e. $\rho \approx \frac{(f,g)}{\sqrt{(f,f)(g,g)}}$. Regardless of the correlation between time series, when the estimated maps are identical, this “dynamic” correlation metric will be close to 1 (see SI Appendix, SI Text 3.1, Fig. S3.1).

We applied these methods to long-term, fishery-independent time series data from 17 blue crab populations across the U.S Atlantic coast (Fig. 3.1A; SI Appendix, Table S3.1). As predictors of blue crab abundance, we used 4 lags each of past crab abundances; 3 known, local environmental drivers (August sea surface temperature [AugT], January air temperature [JanT], and Palmer Drought Severity Index [PDSI]); and commercial blue crab harvest (landings). These predictors were selected based on prior studies and the natural history of the species (SI Appendix, SI Text 3.2, Table S3.2).

To address hypothesis I, we tested within-population predictability using population-specific GP models for nonlinear forecasting. If asynchrony arises because of observation error, the prediction error should be comparable to the variance. To address hypothesis II, we evaluated the spatial synchrony of the environmental drivers and crab populations using Pearson correlation and Mantel correlograms. If asynchrony results from spatial variation in environmental drivers, the spatial autocorrelation should drop off at a rate comparable to that of the crab abundance series (Koenig 1999). To address hypothesis III, we used the dynamic correlation metric to quantify similarity in dynamics across populations. We also compared the performance of models with different dynamic correlation structures, and visualized the modeled responses of each population to each predictor. To address hypothesis IV, we estimated Lyapunov exponents for each population using both the fitted GP models and a direct regression-based approach. Finally, as further tests of the different mechanisms for asynchrony, we compared the observed spatial synchrony to the spatial synchrony among the out-of-sample predicted values from the full model (to test for the effect of noise), a model in which all populations were modeled with identical dynamics (to test for the effect of local differences in dynamics), and a model in which the regional mean values of the environmental drivers were used for all sites (to test for the effect of local differences in the environment).
Results

As a test for observation noise contamination, we fit a hierarchical model in which the
dynamics of the populations were independent ($\rho = 0$). Crab abundances in each population were
predictable from this model, with an average within-sample $R^2$ of 0.55.

We next examined the spatial synchrony of the 3 environmental drivers in relation to
synchrony in blue crab abundance. Blue crab spatial synchrony dropped to zero within a few
hundred kilometers, and Mantel correlations among populations <200 km apart averaged around
0.2 (Fig. 3.1B). In contrast, the environmental drivers remained highly correlated at lag distances
of 1,400 kilometers or more (Fig. 3.1B). Pairwise Pearson correlations among the environmental
drivers displayed strong spatial patterning (within drivers, but not across drivers; SI Appendix,
Fig. S3.2), whereas correlations among crab populations did not (Fig. 3.2A). As an additional
test for synchrony among blue crab populations (since Pearson correlations are not always able
to capture synchronous fluctuations) we also conducted a pairwise wavelet coherence analysis,
which quantifies how the local correlation between population fluctuations varies across
different frequencies and over time (Cazelles et al. 2008). The crab populations displayed
irregular and sporadic periods of synchrony, with no clear trends or patterns.

To evaluate differences in population dynamics across sites, we used the hierarchical
model to estimate the dynamic correlation ($\rho$) between each pair of populations. Dynamic
correlations among sites (Fig. 3.2C) were much stronger than Pearson correlations among sites
(Fig. 3.2A), and exhibited strong spatial patterning (higher values near the diagonal). Dynamic
correlations were also high from a reduced model without environmental drivers, but they did
not show this patterning (Fig. 3.2B).

As a further test for dynamic similarity, we calculated the marginal likelihoods of 4
variations on the hierarchical model corresponding to different choices of the dynamic
correlation parameter $\rho$: one in which all populations were modeled as identical ($\rho = 1$), one in
which all populations had independent dynamics ($\rho = 0$), the general hierarchical model ($\rho$ is a
single, free parameter), and the pairwise correlation model ($\rho$ values taken from the pairwise
dynamic correlation matrix, Fig. 3.2C). The general hierarchical model (free $\rho$) performed
substantially better than the model where the populations had independent dynamics ($\rho = 0$),
moderately better than the pairwise correlation model, and only slightly better than the model in
which all dynamics were identical ($\rho = 1$) (Table 3.1). In the general hierarchical case, the model estimate for $\rho$ was 0.99.

Our next step was to use the general and pairwise models to estimate and visualize the influence of each predictor on crab abundance and how these effects differed among populations. We evaluated the posterior mean for each predictor over the range of observed values, holding all other predictors fixed at their mean. The general hierarchical model indicated nearly identical responses to predictors across populations (SI Appendix, Fig. S3.3). In the pairwise model, the responses resembled those in the general model, were similar across locations, and exhibited fairly smooth gradients (Fig. 3.3; SI Appendix, Fig. S3.4). The predictor with the largest effect was crab population size the previous year (lag 1). This relationship was nearly linear, with high abundances the previous year promoting higher abundances in the current year. The effect of JanT at lag 1 was unimodal in the general hierarchical model, and unimodal or increasing in the pairwise model. The effect of AugT at lag 1 was increasing in both models, with higher temperatures promoting higher crab abundance. In contrast, for JanT at lag 2 and AugT at lags 2 and 3, higher temperatures promoted lower crab abundance. This reversal of effect direction is particularly interesting and is discussed further below. Predictors with very weak effects (not shown in Fig. 3.3) were PDSI, landings, and lag 4 of all predictors (see SI Appendix, Fig. S3.4 for plots of responses for all predictors).

To test for chaotic or noisy dynamics, we estimated the dominant Lyapunov exponents for each population using regression-based methods and using the Jacobian of the pairwise model. The Lyapunov exponent quantifies sensitivity to initial conditions, with positive values indicating trajectory divergence. All of the regression-based Lyapunov exponents were positive, and around 0.1 (Fig. 3.4). All of the model-based Lyapunov exponents were also positive and close to the regression-based estimates, with the exception of a few populations which had Lyapunov exponents between 0 and 0.02 (Fig. 3.4).

Correlations among predicted values from the pairwise model (Fig. 3.2D) were generally low, and resembled the correlations among the observed values (Fig. 3.2A), but were slightly higher and had slightly more spatial patterning (correlation among sites within 200 km averaged around 0.4 as opposed to 0.2, SI Appendix, Fig. S3.5C). Predictions from the model in which all populations were modeled as identical ($\rho = 1$) had slightly higher correlations and slightly more spatial patterning than predictions from the pairwise model (correlation among sites within 200.
km averaged around 0.5, SI Appendix, Fig. S3.5A,C). When using regional mean values of the environmental drivers that were identical across all sites, correlations among the predicted values were higher (correlation among sites within 200 km averaged around 0.6), and these correlation did not decline as quickly with distance (SI Appendix, Fig. S3.5B,C). Plots of the observed and out-of-sample predicted time series can be found in SI Appendix, Fig. S3.6.

Discussion

Many marine species defy the theoretical prediction that they should be synchronized by larval dispersal and correlated spatial drivers. We found evidence that synchrony in the Atlantic blue crab metapopulation is destabilized not by large differences in local dynamics, but by nonlinearity in these dynamics, as well as differences in the local environment. The dynamic correlation metric revealed hidden similarities in these seemingly unrelated populations, and suggests that the responses of disparate populations to key predictors may not be as different as they may first appear.

We found little evidence that asynchrony in blue crabs was driven purely by observation noise (hypothesis I), as crab abundance was predictable within populations. Differences in the local environment (hypothesis II) did appear to play some role, since forecasting with spatially uniform drivers increased predicted synchrony among populations. Since the environmental drivers were highly synchronous across the region (much more so than crab abundance), divergence among crab populations potentially results from differences in local environmental means.

Idiosyncratic local dynamics can also lead to temporally uncorrelated abundances (asynchrony), but we found weak support for asynchrony being driven by intrinsic differences in population dynamics across sites (hypothesis III). Dynamic correlations across populations were strong and showed spatial patterning, largely as a result of their responses to environmental drivers. In addition, hierarchical models that integrated information across populations performed far better than models assuming independent dynamics. Responses to predictors were broadly similar across populations, with some local variability and gradients suggested in the pairwise model. However, these differences alone were not sufficient to explain the absence of synchrony; The model assuming identical dynamics performed nearly as well as hierarchical models allowing for differences in dynamics across sites. Fixing all populations to have identical
dynamics did somewhat increase the correlation among forecasted values, which suggests that populations-specific differences in dynamics can explain some, but not all, of the observed asynchrony. Overall, these results suggest even though the crab populations were asynchronous, their intrinsic dynamics and responses environmental drivers were broadly similar.

We found the strongest support for asynchrony being driven by chaos or noise (hypothesis IV). The dominant Lyapunov exponents were positive, both from the regression-based estimates (which are sensitive to noise) and from the model-based estimates (which are noise-free). The Lyapunov exponent values (around 0.1) suggest that populations with slight differences in initial values should diverge in 5-10 years. For nearby population, correlations among the (noise-free) predicted values from the model were higher (but not dramatically higher) than the observed correlations, which suggests that noise can explain some, but not all, of the observed asynchrony. In addition, the correlation structure for crab abundance was not directly proportional to the correlation structure of the environment, as would expected if the dynamics were approximately linear (Roughgarden 1975). Rather, differences in local environmental means may contribute to asynchrony as a result of shared nonlinear responses to the full range of environmental conditions, even though the environment is highly synchronous across the region. This insight would not have been apparent had we used regional environmental drivers or indices (e.g. Atlantic Multidecadal Oscillation) as predictors, or used a linear model. Collectively, the results suggest that asynchrony among crab populations arises from locally nonlinear, chaotic dynamics interacting with differences in local environmental conditions. The intermittent coherence observed, primarily among nearest neighbors, is also consistent with the crab metapopulation being a weakly coupled set of non-identical nonlinear oscillators.

Previous attempts to identify chaotic dynamics in natural populations have generally concluded that chaotic dynamics are rare (Turchin & Ellner 2000, Benincà et al. 2015). In this context, it may be surprising that the dynamics of blue crabs seem to be in the chaotic regime. However, chaos can be readily demonstrated in laboratory mesocosms with dynamics that are much simpler than those of natural ecosystems (Costantino et al. 1997, Benincá et al. 2008). Moreover, as noted by Perretti et al. (2013), Lyapunov exponents from parametric models fit to short, noisy time series tend to be biased toward stability. In light of this, we suggest that it may
be worth revisiting the question of chaotic dynamics in nature now that more data and better analytical tools are available.

There are practical implications of these results as well, particularly with regards to management strategies and ecological forecast horizons (Petchey et al. 2015). Nonlinear dynamics are a common feature of fishery species (Glaser et al. 2014), which are notoriously difficult to forecast (Myers 1998, Ward et al. 2014, Glaser et al. 2014). Thus the use of nonlinear dynamical approaches is likely be of great utility for understanding and predicting the response of populations to changing environmental conditions across their range. Although not our main focus, we note that the existence of spatially similar chaotic dynamics among blue crab populations suggests basing management decisions on short-term coastwide forecasts rather than state-specific estimates of steady-state sustainable yields as is the current practice.

The trends and spatial gradients found in the responses to predictors were largely consistent with prior knowledge of the species. Intrinsic dynamics (lagged abundances) and temperature were important drivers of crab abundance. While the temperature effects are not directly interpretable in terms of physiology, it is worth noting that the effects at lag 1 displayed unimodal or increasing relationships similar to thermal performance curves. The reversed effects of temperature at preceding lags may seem counterintuitive in this light. However, they can be understood as the result of an indirect effect mediated by temperature. For instance, if the abundance of a crab predator is also positively influenced by temperature, this would appear in the delay coordinates for crabs as a negative response to temperature with a lag. It is also worth noting that the visualization in Fig. 3.3 does not capture interactions among predictors, which are implicitly accounted for in the model, although it is possible to produce surface plots for pairs of predictors. Compactly visualizing these and higher order interactions is more difficult however.

Ecological dynamics are often assumed to be highly complex and context-dependent. The asynchronous nature of blue crabs might lead one to believe that their dynamics differ widely across sites, and that the populations are best modeled independently. However, we found that this apparent complexity belies a consistent dynamical response to environmental conditions, and that predictability can be improved by integrating information across populations. The tools we used are generically applicable to any collection of population time series data, and we anticipate them being valuable in testing for dynamical similarity in other metapopulations.
**Materials and methods**

**Gaussian Process Time-Delay Embedding**

Takens’ theorem justifies modeling the dynamics of a single abundance time series \(y\) from site \(i\) as a function of its lags, \(y_{i,t} = f_t(y_{i,t-1}, \ldots, y_{i,t-L})\) for some unknown map \(f_t\) and ‘embedding dimension’ \(L\) which is at least twice the dimension of the attractor (Takens 1981). The delay coordinate vector, which we write as \(x_{i,t} = \{y_{i,t-1}, \ldots, y_{i,t-L}\}\), may also include relevant external covariates. In practice, the mapping includes approximation and process error and thus we are attempting to infer \(y_{i,t} = f_t(x_{i,t}) + \epsilon_{i,t}\) where \(\epsilon_{i,t} \sim N(0, V_e)\) and \(V_e\) is the observation and process variance.

The functional form of the relationship between the predictors and the response variable (which may be nonlinear) is fit nonparametrically, implicitly accounts for any interactions among the predictors, and includes an estimate of uncertainty. In this application, we estimate the shape of the nonlinear functions \(f_t\) using Bayesian Gaussian process (GP) regression (Munch et al. 2017). This approach produces results comparable to the widely used simplex (nearest-neighbor interpolation; Sugihara & May 1990) and S-map (locally weighted multiple regression; Sugihara 1994) methods for time-delay embedding with single data sets, but is more readily extended to a hierarchical model structure for comparing multiple time series. The method is summarized here; for a full description and justification of the model structure see Munch et al. (2017).

The GP generalizes the multivariate normal distribution from vectors to functions, and thus can be considered a probability distribution over functions (Rasmussen & Williams 2006). The shape of a GP function distribution is defined by a mean function \(\mu\) and a covariance function \(\Sigma\). Absent prior information on the shape of \(f\), we can set \(\mu = 0\) and hence the covariance function (informed by the data) controls the shape of \(f\). The covariance function used here is chosen to facilitate inference of the embedding dimension \(L\) and relevant lags. Specifically, the covariance between \(f\) for two given input vectors \(x_t\) and \(x_s\) is given by

\[
\Sigma(x_t, x_s) = \tau^2 \prod_{k=1}^{L_{\text{max}}} \exp(-\phi k |y_{t-k} - y_{s-k}|^2 / r^2).
\]

In other words, the covariances in the matrix \(\Sigma\) are a function of the multivariate Euclidean distance between the predictor variables for each pair of observations, the lengthscale parameter \(\phi\) which dictates how quickly the correlation decays with distance for each predictor, and the
parameter $\tau^2$ which is the prior variance in $f$ at a given point (i.e. the diagonal of $\Sigma$). The factor $r = \max(y) - \min(y)$ scales the Euclidean distance to the unit interval, and $l_{\text{max}}$ is the maximum estimable embedding dimension which scales roughly as $\sqrt{T}$ (Cheng & Tong 1992), where $T$ is the length of the time series.

If the lengthscale parameter $\phi = 0$, $f$ is flat (the predictor has no effect on the response variable). With small values of $\phi$, correlation decays slowly with distance, resulting in a more smooth function. With large values of $\phi$, correlation decays more quickly with distance, resulting in a more “wiggly” function. We used a prior on $\phi$ that places the most weight on $\phi = 0$, so that predictors without a sufficiently strong influence are effectively “dropped” from the model. In the machine learning literature, this is referred to as automatic relevance determination (ARD, Neal 1996). This enables us to identify the lags (and covariates) that are important.

To integrate information from multiple sites without assuming the local dynamics are identical, we use a hierarchical model structure. Specifically, we decompose the site-specific map into shared and independent components, $f_i = \mu + z_i$ where $\mu \sim \text{GP}(0, \Sigma)$ and $z_i \sim \text{GP}(0, \Sigma)$. In other words, the mean function $\mu$ is modeled as a GP itself with mean 0 and covariance $\Sigma$, and this mean function is shared across sites. The covariance function $\Sigma$ is defined analogously to $\Sigma$ but with point-wise variance $\sigma^2$. Thus the total point-wise prior variance in $f_i$ is partitioned into within- and across-site components, given by $\sigma^2 = \tau^2 + \sigma^2$. If we write $\sigma^2 = \rho \sigma^2$ and $\tau^2 = (1 - \rho) \sigma^2$ with $\rho$ between 0 and 1, the correlation between two site-specific maps, $f_i(x)$ and $f_j(x)$ reduces to $\rho$. Thus $\rho$ (the “dynamic correlation”) indicates the similarity of the reconstructed maps between sites. The $f$’s are identical when $\rho = 1$ and independent when $\rho = 0$. We set a uniform prior on $\rho$ over the interval $[0,1]$.

The hierarchical GP model for this case is given by
\begin{align*}
p[y_{it} | f_{it}, x_{it}, \theta] &\sim N(f_i(x_t), V_{\epsilon}) \\
p[f_i | \theta] &\sim \text{GP}(\mu, \Sigma) \\
p[\mu | \theta] &\sim \text{GP}(0, C) \\
p[\theta] &\text{(2)} \end{align*}
where $\theta$ collects $V_{\epsilon}$, $\sigma$, $\rho$, and the length-scale parameters, i.e. $\theta = \{V_{\epsilon}, \sigma, \rho, \phi_1, ..., \phi_{l_{\text{max}}}\}$. 

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We use the R-prop algorithm developed for neural networks (Riedmeiller & Braun 1993) to find the maximum a posteriori (MAP) estimates for $V_e$ and the hyper-parameters in $\theta$. Since $y$ is normally distributed, the posterior for $f$ (also a GP) can be computed directly given the data and the MAP parameter estimates: $p[f|x,y,\{\tau^2, \phi, V_e\}_{\text{MAP}}] \sim GP(m_c, \Sigma_c)$ where $m_c$ and $\Sigma_c$ are the posterior mean and covariance functions obtained using standard formulae for conditioning in multivariate normals.

Out-of-sample predictions from the models were made sequentially, conditioning only on the data prior to the time being predicted. Although other approaches (e.g. leave-N-out crossvalidation) are certainly possible, the sequential prediction error gives us a good sense of how we would expect the model to perform in an actual application.

For details on the estimation of Lyapunov exponents from the GP models (and the model-free regression-based estimates) see SI Appendix, SI Text 3.4.

**Blue Crabs**

Blue crabs are commercially important, predatory crustaceans that live in coastal estuaries. In the United States, blue crabs are found along the Atlantic and Gulf of Mexico coasts, with the northernmost permanent populations occurring in southern Massachusetts (Williams 1973). The crabs have a typical lifespan of 2-3 years, and a maximum lifespan of 4-6 years (Churchill 1919, Van Engel 1958). Crabs in the southeast Atlantic may reach reproductive maturity within one year of hatching (Tagatz 1968a), whereas crabs farther north require a longer period to reach maturity (Van Engel 1958). The relatively short generation time of blue crabs, the availability of long-term monitoring data over a large spatial scale, and evidence for nonlinear dynamics in the time series data (SI Appendix, SI Text 3.3, Table S3.3) make blue crabs an ideal species for this study. Also, despite being extensively researched, surprisingly few studies have made biogeographic comparisons among blue crab populations, or examined populations north of Delaware Bay. More information about the blue crab life cycle is provided in SI Appendix, SI Text 3.2.

We compiled long-term (19-57 yr) time series data on blue crab abundance (arithmetic mean total annual catch per unit effort [cpue]) for 17 populations sampled in regular fishery-independent surveys in estuaries across the U.S. Atlantic coast (Fig. 3.1A; SI Appendix, Table S3.1). Although there is substantial variability in the survey methods employed across
populations, which sample different subsets of the local crab population, the methods used within each survey have remained consistent over time, and we assume the abundance indices generated are an accurate index of annual variation within each population. Thus, to enable comparison of dynamics across populations and remove scale differences across sites resulting from differences in gear efficiency, the crab cpue time series were standardized by dividing by the within-site mean cpue and then taking logs. Since we were primarily interested in comparing the dynamics of crab populations across estuaries and not in the absolute abundance of crabs, we feel our use of standardized log-abundance indices is appropriate, and allows us to make use of the only available long-term, fishery-independent data sources on this species across this geographic region. Unlike the one previous study examining synchrony in blue crab populations (Colton et al. 2014), which used correlation and dynamic factor analysis (DFA), we did not use stock assessment model output as input to our analysis. Not only has the approach been criticized (Brooks et al. 2015), but stock assessment models do not exist for the populations north of Delaware Bay included in our study. For a detailed description and justification of the predictor variables used, see SI Appendix, SI Text 3.2.

All analyses were performed in Matlab, with the exception of the Mantel correlograms and pairwise wavelet coherence analyses, which were conducted using the ‘ncf’ (Bjornstad 2016) and ‘biwavelet’ (Gouhier et al. 2017) packages, respectively, in R v.3.3.1 (R Core Team 2016).
Table 3.1. Marginal likelihoods for models predicting crab abundance. NLL = negative log likelihood.

<table>
<thead>
<tr>
<th>Dynamic correlation (ρ)</th>
<th>NLL</th>
<th>delta NLL</th>
</tr>
</thead>
<tbody>
<tr>
<td>free</td>
<td>142.92</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>181.93</td>
<td>39.02</td>
</tr>
<tr>
<td>1</td>
<td>143.51</td>
<td>0.60</td>
</tr>
<tr>
<td>pairwise</td>
<td>152.08</td>
<td>9.17</td>
</tr>
</tbody>
</table>
Fig. 3.1. (A) Location of blue crab populations along the U.S. Atlantic coast that were used in this study. Sources and metadata are provided in Table S3.1. (B) Mantel correlogram for crab abundance, January temperature (JanT), August temperature (AugT), and Palmer Drought Severity Index (PDSI) using 100 km bins. Bands are +/- 1 standard deviation.
Fig. 3.2. Correlation matrices for blue crab populations. Matrices show (A) Pearson correlations of observed crab abundance, (B) dynamic correlations ($\rho$) estimated without environmental drivers, (C) dynamic correlations estimated with environmental drivers (full model), and (D) Pearson correlations of predicted crab abundance (sequential out-of-sample) from the pairwise correlation model. Because strong association with a Pearson correlation can be either 1 or -1, we used absolute values for this analysis.
Fig. 3.3. Expected crab abundance (scaled to mean 0) evaluated over each predictor variable for each population, holding all other predictors fixed at their mean value, using the hierarchical model with pairwise $\rho$ values, for lags 1-3. Results for all predictor variables are shown in Fig. S3.3.
Fig. 3.4. Regression- and model-based estimates of the dominant Lyapunov exponent for 17 blue crab populations. Error bars on regression estimates are 95% confidence intervals.
Conclusions

This research explored how environmental drivers and species interactions influence the distribution, abundance, and population dynamics of Atlantic blue crabs (*Callinectes sapidus*) across the U.S. Atlantic coastline. Taken together, the results suggest that physiology likely limits the northernmost extent of blue crabs, most likely through effects on sensitive larval stages, but potentially also because of a shorter growing season for juveniles and adults. During the growing season north of the range boundary, green crabs can also likely outcompete blue crabs for resources. Within the species’ range, blue crabs are able to consume and outcompete green crabs, and blue crabs potentially regulate the abundance and southern range limit of green crabs. Blue crab populations across the coastline were found to exhibit correlated responses to environmental drivers over much larger spatial scales than populations themselves were correlated. Intrinsic population dynamics and temperature were important drivers of short-term population dynamics, and there is indirect evidence that species interactions may play a role. In the long term, changes in the suitability of environmental conditions for blue crabs may vary along the coastline as a result of non-uniform changes in a range of temperature variables, potentially leading to discontinuous range expansion and changes in environmental suitability within the current range of the species.

This research was able to use fishery-independent survey data, which are a more accurate reflection of population size than fishery-dependent landings data, to obtain information on blue crab population dynamics across the coastline. At the same time, this research was able to use fishery-dependent landings data (which were much longer-term than the survey data), to gain insight into potential long-term trends not detectable in the shorter time series. Of course, landings may increase or decrease for a number of reasons other than changes in abundance, and these limitations need to be considered, but in cases where other data sources are lacking (in space or time), they can be of value. This research highlights how both fishery-independent and fishery-dependent data sources have advantages and disadvantages and how both can be useful for addressing different research questions.

More generally, the results illustrate how long-term trends in distribution and abundance across the range of a species can be understood and predicted through spatially-explicit characterization of the relevant physiological and biotic constraints, and changes in the relevant environmental drivers. At the same time, short-term (year-to-year) fluctuations in abundance
across the range of a species can be understood and predicted through characterization of nonlinear population dynamics. In the case of blue crabs, integrating information across populations, which shared similar dynamics, was able to improve short-term, regional predictability, although the presence of chaos would prevent prediction beyond a certain forecast horizon (Petchey et al. 2015). In addition, noise and nonlinearity may destabilize synchrony and obscure hidden dynamical similarities among nearby populations that appear superficially independent. Understanding the key processes at work at multiple spatial and temporal scales is essential for the forecasting and management of ecologically and economically important species such as blue crabs. This is particular important at a time when anthropogenic climate change is leading to large-scale, non-uniform changes in environmental conditions and environmental variability.
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Theoretical perspectives. Ecology 88:2706–2712
764
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and future climates. Ecolography 31:423–434
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Species Interactions in Species Distribution Models. Integr Comp Biol 57:159–167
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suffocating parasite may have reduced the numbers of this species along the Eastern
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Chapter 1 – Appendix

Table S1.1. Tests for Type II vs. Type III functional response type. Logistic regressions are fit to the proportion of prey items consumed, as outlined in Juliano (2001).

<table>
<thead>
<tr>
<th>Species</th>
<th>Temp</th>
<th>Func. Resp. Type</th>
<th>Coefficient</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>z value</th>
<th>P value</th>
<th>AIC</th>
</tr>
</thead>
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<td>G</td>
<td>16</td>
<td>Type 2</td>
<td>density</td>
<td>-0.0779</td>
<td>0.0057</td>
<td>-13.591</td>
<td>0.000</td>
<td>135.22</td>
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<td></td>
<td></td>
<td>Type 3</td>
<td>density</td>
<td>-0.1314</td>
<td>0.0356</td>
<td>-3.686</td>
<td>0.000</td>
<td>134.59</td>
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<td>density^2</td>
<td>0.0005</td>
<td>0.0004</td>
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<td>density</td>
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<td>-7.975</td>
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<td>density</td>
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<td>-8.657</td>
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<td>Type 2</td>
<td>density</td>
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<td>density</td>
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<td>0.0003</td>
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<td>LB</td>
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<td>Type 2</td>
<td>density</td>
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<td>-7.990</td>
<td>0.000</td>
<td>553.46</td>
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<td>density^2</td>
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<td>0.0000</td>
<td>1.356</td>
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<tr>
<td>LB</td>
<td>22</td>
<td>Type 2</td>
<td>density</td>
<td>-0.0138</td>
<td>0.0011</td>
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<td>Type 3</td>
<td>density</td>
<td>-0.0049</td>
<td>0.0058</td>
<td>-0.841</td>
<td>0.400</td>
<td>511.39</td>
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<td>density^2</td>
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<tr>
<td>LB</td>
<td>28</td>
<td>Type 2</td>
<td>density</td>
<td>-0.0133</td>
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<td>-13.127</td>
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<td>0.695</td>
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Fig. S1.1. Raw functional response data with fit curves for green crabs (G) and small blue crabs (SB) at 3 temperatures.
Fig. S1.2. Raw functional response data with fit curves for large blue crabs (LB) at 3 temperatures.
**Fig. S1.3.** Proportion of mussels consumed in paired species trials (green and small blue crabs). Gray lines connect paired crabs (crabs in the same tank together). Columns are 3 temperatures in °C, rows are 2 mussel densities.
**Fig. S1.4.** Proportion of mussels consumed in single species trials (green and small blue crabs). Columns are 3 temperatures in °C, rows are 2 mussel densities.
Equation S1.1. Jacobian matrix for IGP model

\[
\begin{bmatrix}
\frac{-\mu_P}{N_0 + N_R + m} & m \\
\frac{-\alpha_N}{N_0 + N_R + m} & 0 \\
\frac{R_{aP1}}{N_0 + N_R + m} & \frac{-\mu_P}{N_0 + N_R + m} \\
\frac{R_{aP2}}{N_0 + N_R + m} & \frac{R_{aP1}}{N_0 + N_R + m}
\end{bmatrix}
\]

\[
R \left( \frac{N_0 R_{aP1}}{(N_0 + N_R + m)^2} - \frac{r}{K} + \frac{P_1 a_{aP1} h_{R_{aP1}}}{(R_{aP1} h_{R_{aP1}} + m)^2} + \frac{(P_2 a_{aP2} h_{R_{aP2}})^2}{(N_0 + N_R + m)^2} \right) - r \left( \frac{R}{K} - 1 \right) - \frac{N_0}{N_0 + N_R + m} - \frac{P_1 a_{aP1}}{R_{aP1} h_{R_{aP1}} + m} - \frac{P_2 a_{aP2}}{N_0 + N_R + m}
\]
### Chapter 2 – Appendix

**Table S2.1.** Summary of studies on blue crab lower thermal tolerances at different life stages.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Threshold</th>
<th>Temp. (°C)</th>
<th>Reference</th>
<th>Methods</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>juvenile/adult</td>
<td>$L_{T_{\text{min}}}$</td>
<td>0-5</td>
<td>Tagatz 1969</td>
<td>Quantified 48 hour median thermal tolerance ($T_{L_{m}}$ or $L_{D_{50}}$) for adult and juvenile crabs acclimated to different temperatures and salinities.</td>
<td>In full seawater, crabs acclimated to 6 and 14°C had $T_{L_{m}}$ values below the lowest temperature tested (0°C), while crabs acclimated to 22 and 30°C had $T_{L_{m}}$ values around 2.5 and 4.7°C, respectively. In 20% seawater, crabs were 0.2-2°C less cold tolerant than in full seawater. Juveniles were less cold tolerant than adults, but differences were very slight (within 0.5°C).</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Rome et al. 2005</td>
<td>For Chesapeake Bay, examined relationship between February bottom water temperature and crab mortality (%) in winter dredge surveys.</td>
<td>Mortality of crabs increased from ≤ 3% to 6-14.5% when February bottom water temperatures dropped below 2°C.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Bauer &amp; Miller 2010b</td>
<td>Exposed crabs to 3°C (typical winter conditions) for 60 days, 5°C (mild winter conditions) for 60 days, or to 1°C (cold snap) for 30 days followed by 3°C for 30 days, using different life stages and 3 salinities. Performed survival analyses.</td>
<td>Crabs exposed to the cold snap died more quickly than crabs held at 3°C for the entire period. Survival rates did not differ between the 3 and 5°C treatments. Mature females were less cold tolerant than small and medium juveniles. Survival rates were lower at lower salinities.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Smith 1997</td>
<td>Compiled growth data from previously published studies (Tagatz)</td>
<td>Extrapolation of regression gave a $T_{L_{\text{min}}}$ estimate of 8.9°C.</td>
</tr>
</tbody>
</table>

References:
- Tagatz 1969
- Rome et al. 2005
- Bauer & Miller 2010b
- Churchill 1919
- Leffler 1972
- Smith 1997
1968b, Fitz & Wiegert 1991). Extrapolated regression (inverse intermolt period as a function of temperature) to x-intercept to obtain $T_{min}$ estimate (temperature at which growth ceases).

<table>
<thead>
<tr>
<th>Species</th>
<th>$CT_{min}$</th>
<th>Reference</th>
<th>Description</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>megalops</td>
<td>15-20</td>
<td>Costlow &amp; Brookhout 1959</td>
<td>Reared larvae under 3 temperature treatments (20, 25, 30°C) and 4 salinity treatments.</td>
<td>Only zoea raised at 25°C reached the megalops stage, and these megalopae completed development at this temperature. Survival was reduced at lower salinities.</td>
</tr>
<tr>
<td>zoea</td>
<td>20-25</td>
<td>Sandoz &amp; Rogers 1944</td>
<td>Reared zoea under range of temperature and salinity treatments.</td>
<td>First stage zoea did not molt at temperatures below 20°C.</td>
</tr>
<tr>
<td>egg</td>
<td>16-19</td>
<td>Sandoz &amp; Rogers 1944</td>
<td>Reared eggs under range of temperature and salinity treatments.</td>
<td>Eggs hatched successfully between 19 and 29°C, with little variation in hatching percentage within this range. All eggs failed to hatch at 14 and 17°C.</td>
</tr>
<tr>
<td>egg</td>
<td>26°C</td>
<td>Amsler &amp; George 1984</td>
<td>Reared early season eggs at 16°C at late season eggs at 26°C.</td>
<td>Egg hatching occurred at 16°C but with delayed development.</td>
</tr>
</tbody>
</table>

Brylawski & Miller 2006: Quantified growth of juvenile crabs held at under 5 temperature treatments (16, 20, 24, 28°C). Extrapolated regression (inverse intermolt period as a function of temperature) to x-intercept to obtain $T_{min}$ estimate (temperature at which growth ceases). Crabs grew at all experimental temperatures (growth rates decreased with temperature). Extrapolation of regression gave a $T_{min}$ estimate of 10.8°C.
Table S2.2. CMIP5 Climate Models used to obtain daily multimodel mean sea surface temperatures.

<table>
<thead>
<tr>
<th>Model Name</th>
<th>Modeling Center (or Group)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACCESS1-3</td>
<td>Commonwealth Scientific and Industrial Research Organization (CSIRO) and Bureau of Meteorology (BOM), Australia</td>
</tr>
<tr>
<td>CMCC-CM</td>
<td>Centro Euro-Mediterraneo per I Cambiamenti Climatici</td>
</tr>
<tr>
<td>CMCC-CMS</td>
<td>Centro Euro-Mediterraneo per I Cambiamenti Climatici</td>
</tr>
<tr>
<td>CNRM-CM5</td>
<td>Centre National de Recherches Météorologiques / Centre Européen de Recherche et Formation Avancée en Calcul Scientifique</td>
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<td>Met Office Hadley Centre</td>
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<tr>
<td>HadGEM2-ES</td>
<td>Met Office Hadley Centre (additional HadGEM2-ES realizations contributed by Instituto Nacional de Pesquisas Espaciais)</td>
</tr>
<tr>
<td>INM-CM4</td>
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</tr>
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</tr>
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<td>IPSL-CM5A-MR</td>
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<td>IPSL-CM5B-LR</td>
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<td>MIROC5</td>
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<td>Norwegian Climate Centre</td>
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<td>NorESM1-ME</td>
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Fig. S2.1. Sensitivity analysis for temperature conditions in relation to blue crab adult/juvenile lower temperature tolerances. Different values of LT$_{\text{min}}$ (left) and CT$_{\text{min}}$ (right) are used.
Fig. S2.2. Median day of the year (days after January 1) at which temperatures are above the 80th percentile, from (a) daily OISST (historical) and (b) CMIP5 (projected) temperature datasets.

Fig. S2.3. Bias quantification for number of days above 20°C (larval CT_{min}), calculated as the deviation of CMIP5 (projected) results from OISST (historical) results during the period of overlap (2000-2015).
**Fig. S2.4.** Sensitivity analysis for temperature conditions in relation to blue crab larval (zoeal) lower temperature tolerances. Three models of larval survival probability (top panels, 50% survival probability at 0.5, 1.5, and 2.5°C above CT\textsubscript{min}) are applied to historical, projected, and bias-corrected projected mean August temperature conditions (left panels).
SI Text

3.1. Temporal v. Dynamic correlation

To illustrate the need for an general approach to measuring the similarity between dynamics that is not based on temporal correlations we simulated two sets of time series from the model $x_i(t + 1) = x_i(t)\exp[r - x_i(t) + \sigma \epsilon(t)]$. In the first set, we used 10 values of $r$ ranging between 3.75 and 4 with $\sigma$ fixed at 0.01. In the second set, $r$ was fixed at 3.75 and we used 10 values of $\sigma$ ranging between 0.01 and 0.2.

For each value of $r$ and $\sigma$ we simulated 20 time series of length 100 timesteps initialized from random starting values. For each pair of series, say $x_i$ and $x_j$, we calculated the Pearson correlation across contemporaneous values and used the hierarchical GP to estimate the dynamic correlation metric. The Pearson correlations for time series generated by these identical models were heavily centered on 0, with a median (25th and 75th percentiles) of 0.008 (-0.06, 0.07) for the variable $r$, fixed $\sigma$ set and 0.01 (-0.07, 0.10) for the variable $\sigma$, fixed $r$ set (Fig. S3.1B). In contrast, the dynamic correlations indicate the dynamics are quite similar with estimated rho of 0.98 (0.94, 1) for the variable $r$, fixed $\sigma$ set and 0.96 (0.88, 0.99) for the fixed $r$ variable $\sigma$ set (Fig. S3.1C).

3.2. Description and justification of environmental drivers

Blue crabs (*Callinectes sapidus*) have a well-described, complex life cycle (Millikin & Williams 1984, Epifanio 1995). After mating in low salinity waters, female blue crabs migrate to high salinity waters at mouths of estuaries, where peak spawning occurs in July and August. In offshore surface waters, the planktonic larvae develop through 7 zoeal stages over the course of approximately 1 month (Costlow & Brookhout 1959), with zoeae abundance peaking in August and September (Epifanio et al. 1984). 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. Although many blue crab larvae return to their parent estuary, they can be transported among estuaries depending on oceanographic conditions (Epifanio et al. 1989, Johnson & Hess 1990). Genetic studies suggest that high gene flow occurs among neighboring estuaries over ecological time scales (McMillen-Jackson et al. 1994, McMillen-Jackson & Bert 2004, Rodrigues et al. 2017). Settled juveniles migrate up-estuary to lower salinity waters, where they grow to maturity. Crab growth rates increase with increasing temperature (Leffler 1972). North of Cape Hatteras, adult and juvenile crabs hibernate during the winter months, buried in sediment and in deep channels. South of Cape Hatteras, the crabs are active year-round.

As predictors, we also compiled site-specific time series data on 3 local environmental drivers (Table S3.2) and blue crab harvest. All data were obtained from a common source, and were measured consistently over space and time.

The first environmental driver we selected was sea surface temperature (SST) just outside the surveyed estuary(ies) during the month of August (AugT), which is the time and location of the peak larval development. In this study region, August is typically the month of maximum water
temperature. Research suggests that summer water temperatures likely limit the northern range of the blue crab via effects on early larval stages, which are the least cold-tolerant of the blue crab life history stages (Rogers et al. in prep). A similar mechanism was found to limit the northern range of fiddler crabs in this region (Sanford et al. 2006). For AugT, we utilized two satellite data sources, one higher resolution (OISST) and one lower resolution (ERSST). Since some of the crab time series exceeded the length of the higher resolution SST dataset, we averaged the long-term low resolution and short-term high resolution datasets for overlapping years as a compromise between accuracy and continuity, and to avoid introducing artifacts.

The second environmental driver we selected was air temperature in January (JanT) as a proxy for nearshore water temperature, which is predicted to affect the overwinter survival of adult and juvenile crabs (Tagatz 1969, Rome et al. 2005, Bauer & Miller 2010b). In this study region, January is typically the month of minimum water temperature. Winter air temperature has been found to be a reasonable proxy for winter water temperature in shallow nearshore environments (Hare & Able 2007), where long-term data are often unavailable and satellite data are inaccurate.

The third environmental driver we selected was the Palmer Drought Severity Index (PDSI) as a proxy for freshwater discharge (salinity), which is suspected to influence crab survival in the southeast (Lee & Frischer 2004), although correlational results have been mixed (Gandy et al. 2011).

Since most crab surveys took place during the summer (or summer sampling months accounted for the majority of crabs observed), we used AugT of the previous year, JanT of the same year, and PDSI averaged over September of the previous year to August of the same year as “lag 1”. Environmental drivers were scaled across sites to mean 0 and variance 1.

Since blue crabs are harvested by humans and fishing pressure may also affect crab abundance, we compiled additional, state-level data on annual blue crab commercial harvest (landings in metric tons) from NOAA Fisheries. As a predictor, we used a landings index calculated as the log of the ratio of raw landings to raw cpue, scaled within sites to mean 0, variance 1. Since Massachusetts and Rhode Island have no commercial blue crab fisheries, the landings indices for populations 1 and 2 were set to 0.

For the models, we used 4 lags of population size, each of the 3 environmental drivers, and landings index, because we found all variables to be relevant (based on the inferred length scale, $\phi$) for at least 1 population when models were fit to each population separately (Fig. S3.7). As part of the model comparison, we also fit general hierarchical models in which different predictors were omitted (Table S3.4). We performed these tests not for any formal model selection, but rather to provide a relative measure of model performance and as an indicator of predictor relevance. Using only population size or only environmental drivers as predictors strongly decreased model performance. The omission of lag 4 of all predictors, or of landings as a predictor, only slightly decreased model performance.

The models in this study might be improved by including additional abiotic and biotic drivers that may be relevant, such as wind stress, which is known to affect larval transport and retention of blue crabs (Epifanio 1995).
### 3.3. Nonlinearity of blue crab time series

Following the univariate methods summarized in Ye et al. (2015), we tested for nonlinear dynamics in each of the 17 fishery-independent blue crab time series used in this study (Table S3.1). Using simplex projection and embedding dimensions (E) ranging from 1 to 5, we identified the embedding dimension (E\text{max}) which maximized forecast skill using leave-one-out cross validation. Using the s-map procedure, and E=2, 3, or E\text{max} we varied the tuning parameter θ from 0 to 8, and identified the values of θ which maximized forecast skill using leave-one-out cross validation. Values of θ>0, which give stronger weighting to nearby points, provide evidence for nonlinear dynamics. We performed these tests using the package ‘rEDM’ (Ye et al. 2016) in R v.3.3.1. Results are presented in Table S3.3.

### 3.4. Estimation of Lyapunov exponents

Lyapunov exponents are one of several commonly used indicators for chaotic dynamics. However, estimates of Lyapunov exponents based directly on empirical time series can be sensitive to noise and time series length (e.g. Gencay & Dechert 1992, Kantz 1994). On the other hand, model-based estimates are sensitive to model structure (Perretti et al. 2013). In light of this, Lyapunov exponents were estimated in two complementary ways. The first is the method of Rosenstein et al. (1993) based on the divergence rate of nearest neighbors and the second is based on the Jacobian of the GP model, analogous to the nonparametric regression method of McCaffrey et al. (1992). Details on both methods are provided below.

Recall that the dominant Lyapunov exponent, \( \lambda \), is the maximal rate at which trajectories emanating from neighboring points diverge or converge averaged over the attractor, i.e.

\[
\|\Delta x(t)\| \sim e^{\lambda t} \|\Delta x(0)\|
\]

Where \( \| \| \) is the Euclidean distance between points. Note that this definition only holds in the limit \( \Delta x(0) \to 0 \). Since the attractor is bounded, the period of exponential growth from a finite (rather than infinitesimal) \( \Delta x(0) \) is also finite.

This definition provides the basis for the direct, regression based estimates of (Rosenstein et al. 1993, Kantz 1994). For each point on the attractor, we find its nearest neighbor, compute the initial distance between them and the subsequent distances as we follow both points into the future. If we think about the distance between \( i^{th} \) pair of nearest neighbors, say \( d_i \), we can take logs to find that

\[
\ln [d_i(t)] = \ln [d_i(0)] + \lambda t + err
\]

which has the form of a linear regression of log-distance on time with slope \( \lambda \). Distances between points were measured in terms of the complete set of delay coordinates used to model the dynamics. Since this distance will ultimately saturate, it is important to set the maximum t relatively low to avoid underestimating \( \lambda \). We used \( t=\{0,\ldots,5\} \) for which the d versus t trajectories remained nearly linear. Note that this method is totally model-free, but is somewhat sensitive to the presence of noise (Dämmig & Mitschke 1993). This is why we also computed Lyapunov exponents using the estimated delay-coordinate map.
In the limit of infinitesimal perturbations, the dominant Lyapunov exponent is also given by

\[ \lambda = \lim_{T \to \infty} \frac{1}{T} \ln \prod_{t=0}^{T-1} \mathbf{J}(\mathbf{x}_t) \]

where \( \mathbf{J} \) is the Jacobian, i.e. the matrix of partial derivatives for the system dynamics, evaluated at each successive point on the trajectory. Direct computation of \( \lambda \) from this equation is numerically unstable, and a QR algorithm was used. McCaffrey et al. (1992) introduced the idea of estimating the Lyapunov exponent from mapping inferred using a neural network which we apply here to the mapping inferred with a GP. In the delay coordinate map, the dynamics are given by \( \mathbf{x}_t = f(\mathbf{x}_{t-1}, \ldots, \mathbf{x}_{t-E}) \) so the Jacobian is given by

\[
\mathbf{J}(\mathbf{x}_t) = \begin{bmatrix}
\frac{\partial f}{\partial x_{t-1}} & \frac{\partial f}{\partial x_{t-2}} & \cdots & \frac{\partial f}{\partial x_{t-E}} \\
1 & 0 & 0 & 0 \\
0 & \ddots & 0 & \vdots \\
0 & 0 & 1 & 0
\end{bmatrix}
\]

Since \( f \) is modeled as a GP and derivatives of a GP are themselves GPs, we can compute the Jacobian without numerical differentiation. Specifically,

\[ E \left( \frac{\partial f(\mathbf{x})}{\partial x_j} \middle| \text{data} \right) = \frac{\partial \mathcal{C}(\mathbf{x}, \mathbf{x}_d)}{\partial x_j} [\mathcal{C}(\mathbf{x}_d, \mathbf{x}_d) + \nu I]^{-1} y_d \]

Moreover, since we used a squared exponential covariance of the form

\[ \mathcal{C}(\mathbf{x}, \mathbf{y}) = \exp \left\{ -\sum_{i=1}^{E} \varphi_i (x_i - y_i)^2 \right\} \]

\[ E \left( \frac{\partial f(\mathbf{x})}{\partial x_j} \middle| \text{data} \right) = -2\varphi_j [(x_j - \mathbf{x}_d) \circ \mathcal{C}(\mathbf{x}, \mathbf{x}_d)] [\mathcal{C}(\mathbf{x}_d, \mathbf{x}_d) + \nu I]^{-1} y_d \]

Where \( \circ \) is the Hadamard or elementwise product.

For each point on the attractor, we used this to compute \( E(\mathbf{J}(\mathbf{x}_t)|\text{data}) \) which was plugged into the recursive QR algorithm of Eckmann et al. (1986) to extract the dominant Lyapunov exponent.
<table>
<thead>
<tr>
<th>Pop. Num.</th>
<th>Survey Code</th>
<th>Survey Name</th>
<th>Survey Type</th>
<th>Start Year (Duration)</th>
<th>Location</th>
<th>Source</th>
<th>Stations</th>
<th>Sampling Months</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>MA</td>
<td>MA Young-of-Year Flounder Seine Survey</td>
<td>seine</td>
<td>1976 (40)</td>
<td>6 estuaries along Southern Cape Cod</td>
<td>Massachusetts Division of Marine Fisheries</td>
<td>fixed</td>
<td>J F M A M J J A S O N D</td>
</tr>
<tr>
<td>2</td>
<td>RI</td>
<td>Univ. of Rhode Island Fish Trawl Survey</td>
<td>trawl</td>
<td>1959 (57)</td>
<td>2 locations in Narragansett Bay</td>
<td>Univ. of Rhode Island Grad. School of Oceanography</td>
<td>fixed</td>
<td>x x x x x x x x x x x x</td>
</tr>
<tr>
<td>3</td>
<td>NYpec</td>
<td>Peconic Bay Trawl Survey</td>
<td>trawl</td>
<td>1987 (29)</td>
<td>Peconic Bay (E. Long Island)</td>
<td>New York State Dept. of Environmental Conservation</td>
<td>gridded</td>
<td>x x x x x x x x x x</td>
</tr>
<tr>
<td>4</td>
<td>LIS</td>
<td>Long Island Sound Trawl Survey</td>
<td>trawl</td>
<td>1992 (24)</td>
<td>All of Long Island Sound</td>
<td>Connecticut Dept. of Energy and Environmental Protection</td>
<td>stratified</td>
<td>x x x x x</td>
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<tr>
<td>5</td>
<td>NYwli</td>
<td>Western Long Island Seine Survey - North</td>
<td>seine</td>
<td>1988 (28)</td>
<td>Little Neck and Manhasset Bay</td>
<td>New York State Dept. of Environmental Conservation</td>
<td>fixed</td>
<td>x x x x x x x x x x x x</td>
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<tr>
<td>6</td>
<td>NYjam</td>
<td>Western Long Island Seine Survey - South</td>
<td>seine</td>
<td>1988 (28)</td>
<td>Jamaica Bay</td>
<td>New York State Dept. of Environmental Conservation</td>
<td>fixed</td>
<td>x x x x x x x x x x x x</td>
</tr>
<tr>
<td>7</td>
<td>NYhud</td>
<td>Hudson River Young-of-Year Striped Bass Seine Survey</td>
<td>seine</td>
<td>1988 (28)</td>
<td>Brackish area of Hudson River</td>
<td>New York State Dept. of Environmental Conservation</td>
<td>fixed</td>
<td>x x x x x x x x x x x x</td>
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<td>8</td>
<td>NJ</td>
<td>Rutgers Trawl Survey</td>
<td>trawl</td>
<td>1996 (19)</td>
<td>Great Bay, New Jersey</td>
<td>Rutgers University</td>
<td>fixed</td>
<td>x x x x x x x x x x x x</td>
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<td>9</td>
<td>DE</td>
<td>Delaware Blue Crab and Juvenile Finfish Trawl Survey</td>
<td>trawl</td>
<td>1978 (38)</td>
<td>Delaware Bay, Delaware</td>
<td>Delaware Division of Fish and Wildlife</td>
<td>fixed</td>
<td>grid x x x x x x x x</td>
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<td>10</td>
<td>MDco</td>
<td>Maryland Coastal Bays Trawl Survey</td>
<td>trawl</td>
<td>1989 (27)</td>
<td>Maryland Coastal Bays</td>
<td>Maryland Dept. of Natural Resources</td>
<td>fixed</td>
<td>x x x x x x x x x x x x</td>
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<tr>
<td>11</td>
<td>MDcb</td>
<td>Chesapeake Bay Blue Crab Summer Trawl Survey</td>
<td>trawl</td>
<td>1977 (39)</td>
<td>6 rivers in Chesapeake Bay</td>
<td>Maryland Dept. of Natural Resources</td>
<td>fixed</td>
<td>x x x x x x x x x x x x</td>
</tr>
<tr>
<td>12</td>
<td>VA</td>
<td>VIMS Juvenile Fish and Blue Crab Trawl Survey</td>
<td>trawl</td>
<td>1956 (60)</td>
<td>3 rivers in Chesapeake Bay</td>
<td>Virginia Institute of Marine Science</td>
<td>random</td>
<td>x x x x x x x x x x x x</td>
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<tr>
<td>13</td>
<td>NCas</td>
<td>Juvenile Anadromous Trawl Survey (P100)</td>
<td>trawl</td>
<td>1984 (32)</td>
<td>Pamlico Sound</td>
<td>North Carolina Division of Marine Fisheries</td>
<td>fixed</td>
<td>x x x x x x x x x x x x</td>
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<td>NCps</td>
<td>Pamlico Sound Survey (P195)</td>
<td>trawl</td>
<td>1987 (29)</td>
<td>Pamlico Sound</td>
<td>North Carolina Division of Marine Fisheries</td>
<td>stratified</td>
<td>x x x x x x x x x x x x</td>
</tr>
<tr>
<td>15</td>
<td>SC</td>
<td>South Carolina Blue Crab Pot Survey</td>
<td>pot</td>
<td>1988 (28)</td>
<td>6 rivers in coastal South Carolina</td>
<td>South Carolina Dept. of Natural Resources</td>
<td>fixed</td>
<td>x x x x x x x x x x x x</td>
</tr>
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<td>16</td>
<td>GA</td>
<td>Ecological Monitoring Trawl Survey</td>
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<td>6 estuarine sound systems in Georgia</td>
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<td>stratified</td>
<td>x x x x x x x x x x x x</td>
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<tr>
<td>17</td>
<td>FL</td>
<td>Fisheries Independent Monitoring Survey, 183-m seine</td>
<td>seine</td>
<td>1997 (19)</td>
<td>North Indian River Lagoon</td>
<td>Florida Fish and Wildlife Conservation Commission</td>
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<td>x x x x x x x x x x x x</td>
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### Table S3.2. Sources of environmental data used as predictors.

<table>
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<tr>
<th>Predictor Name</th>
<th>Dataset Name</th>
<th>Start Year</th>
<th>Measurement Source</th>
<th>Resolution</th>
<th>Data Type</th>
<th>Time Period Used</th>
<th>Source</th>
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Table S3.3. Embedding dimensions (E) and tuning parameters (θ) which maximize univariate forecast skill in 17 blue crab time series. Survey codes match those in Table S1.

<table>
<thead>
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<th>Pop. Num</th>
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<th>$E_{\text{max}}$</th>
<th>$\theta_{\text{max}}$ with $E = 2$</th>
<th>$\theta_{\text{max}}$ with $E = 3$</th>
<th>$\theta_{\text{max}}$ with $E = E_{\text{max}}$</th>
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</thead>
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Table S3.4. Marginal likelihoods for a range of models predicting crab abundance (N). NLL = negative log likelihood.

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<th>Factors in model</th>
<th>lags</th>
<th>$\rho$</th>
<th>NLL</th>
<th>delta</th>
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<td>N</td>
<td>JanT</td>
<td>AugT</td>
<td>PDSI</td>
<td>Landings</td>
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<td>x</td>
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<td>x</td>
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Fig. S3.1. Simulation results comparing Pearson and dynamic correlations for time series generated with identical parameters. (A) Illustration of 10 series generated with the same dynamics. (B) Histograms of Pearson (blue) and dynamic (red) correlations for the case where $r$ varies between 3.75 and 4 and the noise standard deviation is constant at 0.01. (C) Results for the case where $r$ is fixed at 3.75 and the noise standard deviation ranges from 0.01 to 0.2.
Fig. S3.2. Pearson correlations among environmental drivers associated with each population. Within panels, sites are ordered north to south.
Fig. S3.3. Expected crab abundance (scaled to mean 0) evaluated over each predictor variable for each population, holding all other predictors fixed at their mean value, using the hierarchical model with a single $\rho$ value, for all lags.
Fig. S3.4. Expected crab abundance (scaled to mean 0) evaluated over each predictor variable for each population, holding all other predictors fixed at their mean value, using the hierarchical model with pairwise $\rho$ values, for all lags.
Fig. S3.5. Pairwise Pearson correlation matrices for predicted crab abundance (sequential out-of-sample) from (A) the hierarchical model using a dynamic correlation ($\rho$) fixed to 1 (uniform dynamics), and (B) the pairwise correlation model using regional mean values of the environmental drivers that were identical across all sites (uniform environment). Because strong association with a Pearson correlation can be either 1 or -1, we used absolute values for this analysis. (C) Mantel correlograms for observed crab abundance (Fig. 3.2A), predicted abundance from the pairwise correlation model (Fig. 3.2D), and predicted abundance from the models with uniform dynamics (A) and uniform environment (B).
**Fig. S3.6.** Observed population sizes (blue circles), out-of-sample predicted population sizes from the pairwise hierarchical model (red lines), and predicted population sizes from a linear model (black lines) for each population. Panels are labeled with the population number.

**Fig. S3.7.** Estimated length scale parameters ($\phi$) for all predictor variables at 4 lags, fitting each population separately. Populations are ordered north to south.