

# Temperature dependency of intraguild predation between native and invasive crabs

TANYA L. ROGERS,<sup>1</sup> TARIK C. GOUHIER, AND DAVID L. KIMBRO

*Northeastern University Marine Science Center, 430 Nahant Road, Nahant, Massachusetts 01908 USA*

**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 three temperatures reflective of those across their range, using two 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 three 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.

**Key words:** *Callinectes sapidus*; *Carcinus maenas*; competitive reversal; crabs; intraguild predation; species interactions; temperature dependence.

## 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 and 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 and Zimmerman 2000, Pearson and Dawson 2003, Elith and 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 (Sanford 1999, Ohlund et al. 2015) and competitive (Taniguchi and Nakano 2000, Jiang and 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 (Wetthey 2002). If temperature-dependent species interactions can be described mechanistically, these relationships could be used to improve SDMs (Kearney and 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 and 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

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<sup>1</sup>E-mail: rogers.ta@husky.neu.edu

competitor for the shared resource, and the IG predator benefits substantially by consuming the IG prey (Holt and Polis 1997). Although theoretical models have been developed for the temperature-dependence of consumer–resource (Vasseur and 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 and Gilliam 1984) and IGP rates (Woodward and 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 two 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 (Silliman and 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 and 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 three temperatures reflective of those across their range. Using two 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 three temperatures (16°C, 22°C, and 28°C) in mesocosms at the Northeastern University Marine Science Center in Nahant, Massachusetts, USA during the summer (June–September) of 2016. We used one size class of green crab (45–55 mm carapace width), and two 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 d 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 h, 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 two 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 one 300 W submersible glass aquarium heater (Aquatop Aquatic Supplies, Brea, CA, USA). 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 three water temperatures used reflect the different thermal conditions experienced across the ranges of these species during the summer months (June–September; Fig. 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 L/min), 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 three temperatures. The parameters derived from the curves (attack rates and handling times) reflect the relative ability of each

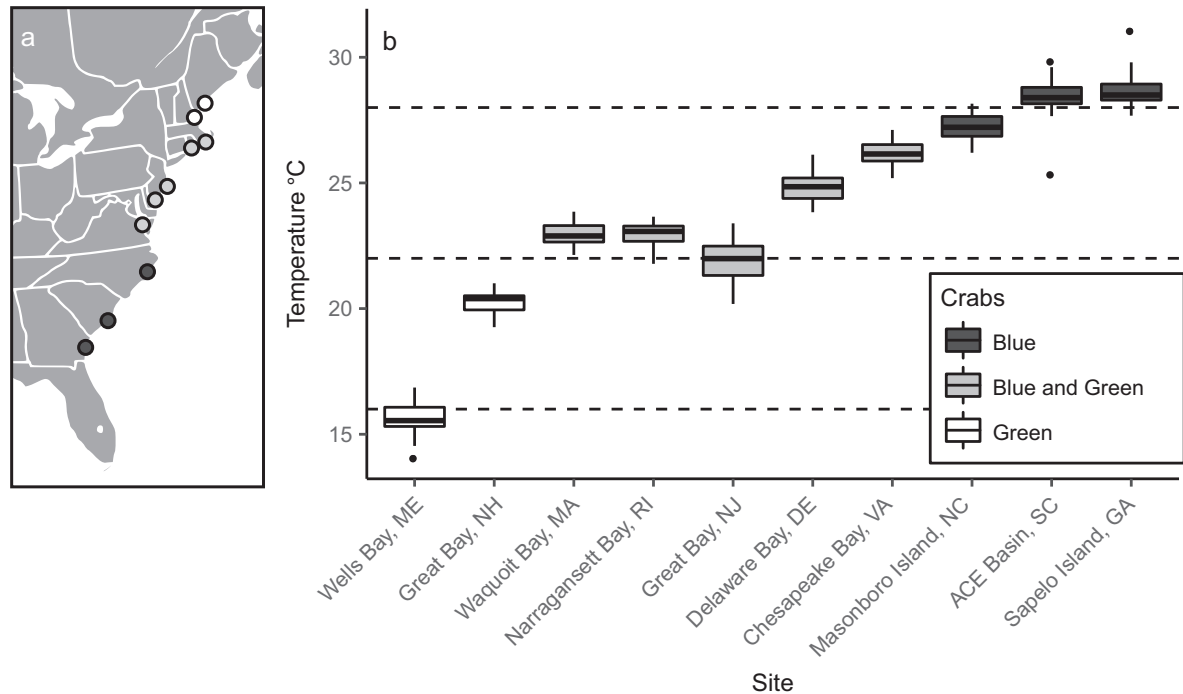


FIG. 1. (a) Presence of blue and green crabs in Atlantic coast estuaries and (b) associated annual summer water temperatures (June–September) for the years 2002–2015. Key applies to both panels. Dashed horizontal lines are the three temperatures used in the mesocosm experiments. Data are from NOAA National 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). State abbreviations are ME, Maine; NH, New Hampshire; MA, Massachusetts; RI, Rhode Island; NJ, New Jersey; DE, Delaware; VA, Virginia; NC, North Carolina; SC, South Carolina; GA, Georgia. Years with more than 15 d of missing data during these months were excluded. Data accessed from the NOAA NERRS Centralized Data Management Office website: <http://www.nerrsdata.org>.

species to acquire resources in the absence of interference competition. To generate the functional response curves, we used nine mussel densities for the green and small blue crabs (2, 4, 6, 8, 10, 20, 30, 50, and 70 mussels/tank), and eight mussel densities for the large blue crabs (4, 8, 20, 50, 70, 100, 150, and 200 mussels/tank). 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 h, and then quantified the number of mussels consumed (we excluded trials in which the crab did not eat any mussels). We performed two to four 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; R Core Team 2016).

#### *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 one green crab in a tank together with either a small or large blue crab at each of the three temperatures, with either a low or high density of mussels (20 or 70 mussels/tank). The experimental procedure was the same as above, except that a camera (Go-Pro Hero 3+, Go-Pro

Inc., San Mateo, CA, USA) 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 five or six 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

$$\frac{dP_2}{dt} = mP_1 - \mu_P P_2 \tag{1}$$

$$\frac{dP_1}{dt} = \frac{b_P a_{P_2} R + \beta \alpha N}{1 + h_{RP_2} a_{P_2} R + h_{NP_2} \alpha N} P_2 - (m + \mu_P) P_1 \tag{2}$$

$$\frac{dN}{dt} = \frac{b_N a_N R}{1 + h_{RN} a_N R} N - \frac{\alpha P_2}{1 + h_{RP_2} a_{P_2} R + h_{NP_2} \alpha N} N - \mu_N N \tag{3}$$

$$\frac{dR}{dt} = \left( r \left( 1 - \frac{R}{K} \right) \right) R - \frac{a_N N}{1 + h_{RN} a_N R} R - \frac{a_{P_1} P_1}{1 + h_{RP_1} a_{P_1} R} R - \frac{a_{P_2} P_2}{1 + h_{RP_2} a_{P_2} R + h_{NP_2} \alpha N} R. \tag{4}$$

In this model, *R* is the shared basal resource (mussels), *N* is the IG prey (green crab), *P*<sub>1</sub> is the small size class of IG predator (small blue crab), and *P*<sub>2</sub> is the large size class of IG predator (large blue crab). Consistent with our knowledge and observations of blue and green crabs, only *P*<sub>2</sub> can prey on *N* (Eq. 3), and only *P*<sub>2</sub> can reproduce (Eq. 2). The parameters *a*<sub>*N*</sub>, *a*<sub>*P*<sub>1</sub></sub>, and *a*<sub>*P*<sub>2</sub></sub> are the attack rates of *N*, *P*<sub>1</sub>, and *P*<sub>2</sub> on *R* with associated handling times *h*<sub>*RN*</sub>, *h*<sub>*RP*<sub>1</sub></sub>, and *h*<sub>*RP*<sub>2</sub></sub>. The parameters *b*<sub>*N*</sub> and *b*<sub>*P*</sub> represent the conversion efficiency of *R* into new individuals of *N* and *P*<sub>1</sub> (reproduction), and *μ*<sub>*N*</sub> and *μ*<sub>*P*</sub> are density-independent natural mortality rates (assumed to be the same for *P*<sub>1</sub> and *P*<sub>2</sub>). The parameters *α* and *β* are

analogous to *a* and *b*, but represent the attack rate of *P*<sub>2</sub> on *N* (IGP) and associated conversion efficiency, with associated handling time *h*<sub>*NP*<sub>2</sub></sub>. *P*<sub>1</sub> matures to *P*<sub>2</sub> 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.

To incorporate temperature dependency, we ran the model under three different temperature regimes corresponding to those used in our lab experiments, which represent conditions in the northeast, central, and southeast Atlantic coast (Fig. 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 three other parameters of interest across a range of values. Specifically, we varied *α* (intraguild attack rate) and *K* (resource carrying capacity) at two different levels of *m* (maturation rate), and varied *m* and *K* for two different levels of *α*. The two maturation rates used in the first analysis corresponded to 50% and 80% of the predator lifetime spent as *P*<sub>2</sub>, which is given by 1 – *μ*<sub>*P*</sub> / (*μ*<sub>*P*</sub> + *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

TABLE 1. Variables and parameters used in the IGP model.

Symbol	Description	Value
<i>R</i>	basal resource	
<i>N</i>	IG prey	
<i>P</i> <sub>1</sub>	small IG predator	
<i>P</i> <sub>2</sub>	large IG predator	
<i>K</i>	<i>R</i> carrying capacity	varied in simulations
<i>r</i>	<i>R</i> growth rate	1
<i>b</i> <sub><i>N</i></sub>	conversion efficiency of <i>N</i> feeding on <i>R</i>	0.01
<i>b</i> <sub><i>P</i></sub>	conversion efficiency of <i>P</i> <sub>2</sub> feeding on <i>R</i>	0.01
<i>β</i>	conversion efficiency of <i>P</i> <sub>2</sub> feeding on <i>N</i>	0.4
<i>μ</i> <sub><i>N</i></sub>	natural mortality rate of <i>N</i>	0.1
<i>μ</i> <sub><i>P</i></sub>	natural mortality rate of <i>P</i> <sub>1</sub> and <i>P</i> <sub>2</sub>	0.1
<i>m</i>	maturation rate of <i>P</i> <sub>1</sub> to <i>P</i> <sub>2</sub>	varied in simulations
<i>h</i> <sub><i>RN</i></sub>	handling time of <i>R</i> by <i>N</i>	from experiments
<i>h</i> <sub><i>RP</i><sub>1</sub></sub>	handling time of <i>R</i> by <i>P</i> <sub>1</sub>	from experiments
<i>h</i> <sub><i>RP</i><sub>2</sub></sub>	handling time of <i>R</i> by <i>P</i> <sub>2</sub>	from experiments
<i>h</i> <sub><i>NP</i><sub>2</sub></sub>	handling time of <i>N</i> by <i>P</i> <sub>2</sub>	from experiments
<i>a</i> <sub><i>N</i></sub>	attack rate on <i>R</i> by <i>N</i>	from experiments
<i>a</i> <sub><i>P</i><sub>1</sub></sub>	attack rate on <i>R</i> by <i>P</i> <sub>1</sub>	from experiments
<i>a</i> <sub><i>P</i><sub>2</sub></sub>	attack rate on <i>R</i> by <i>P</i> <sub>2</sub>	from experiments
<i>α</i>	attack rate on <i>N</i> by <i>P</i> <sub>2</sub>	varied in simulations

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 two 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 (1) "extinction" (resource persists but IP prey and IG predator do not), (2) "IG prey" (resource and IG prey persist but IG predator does not), (3) "IG predator" (resource and IG predator persist but IG prey does not), or (4) "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 (Appendix S1). 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 two 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 (Appendix S2: Table S1; see raw data with fit curves in Appendix S2: Figs. S1, S2). For green crabs, both attack rates and handling times were lower at 22°C than at 16°C (attack rate,  $z = 3.30$ , adjusted  $P = 0.008$ ; handling time,  $z = 7.9$ , adjusted  $P < 0.001$ ), and did not differ between 22°C and 28°C (attack rate,  $z = -0.03$ , adjusted  $P = 1.0$ ; handling time,  $z = -1.4$ , adjusted  $P = 0.41$ ; Fig. 2a, b). For small blue crabs, attack rates did not differ among the three temperatures (all adjusted  $P > 0.7$ ). In contrast, handling times for small blue crabs decreased with

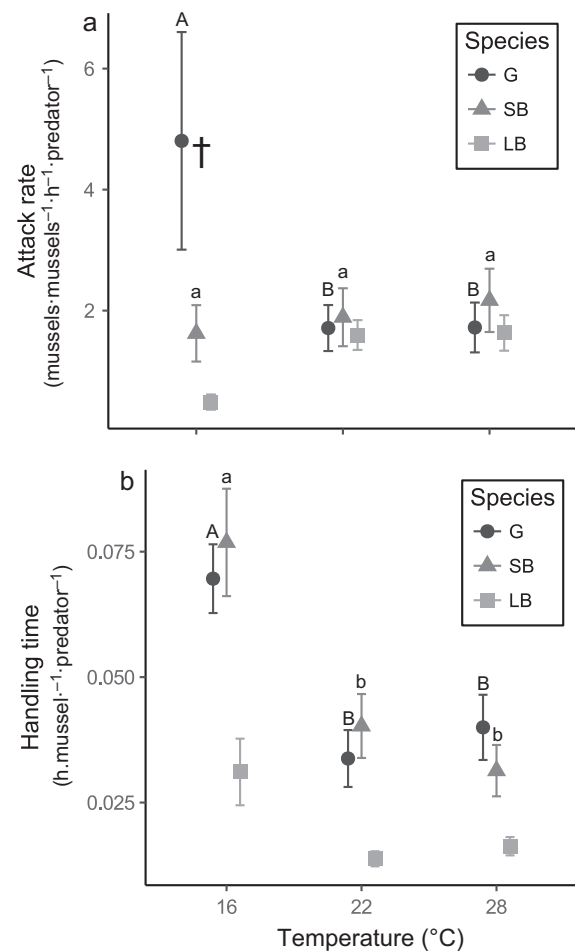


FIG. 2. (a) Attack rates and (b) handling times for green crabs (G), small blue crabs (SB), and large blue crabs (LB) at three temperatures. Error bars are 95% confidence intervals. Within species, temperature treatments sharing letters do not differ (adjusted  $P > 0.05$ , capital letters for G, lowercase for SB). †At a given temperature, G and SB treatments differ (adjusted  $P < 0.05$ ).

increasing temperature (16°C vs. 22°C,  $z = 5.75$ , adjusted  $P < 0.001$ ; 22°C vs. 28°C,  $z = 2.13$ ,  $P = 0.033$ , adjusted  $P = 0.16$ ).

At 16°C, green crabs had a higher attack rate than small blue crabs ( $z = 3.36$ , adjusted  $P = 0.007$ ; Fig. 2a), but attack rates were not different between species at 22°C and 28°C (22°C,  $z = -0.57$ , adjusted  $P = 1.0$ ; 28°C,  $z = -1.32$ , adjusted  $P = 0.94$ ; Fig. 2b). Handling times were not different between species at 16°C and 22°C (16°C,  $z = -1.12$ , adjusted  $P = 0.41$ ; 22°C,  $z = -1.49$ , adjusted  $P = 0.41$ ). 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 ( $z = 2.04$ ,  $P = 0.04$ , adjusted  $P = 0.16$ ).

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°C and 28°C (Fig. 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°C and 28°C (Fig. 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. 3). Small blue crabs consumed more mussels than green crabs in the 28°C treatments than in the 16°–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  $\times$  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 Appendix S2: Figs. S3, S4.

For large blue crabs, only one instance of predation was observed at 16°C (Fig. 4). At 22°C and 28°C, over one-half of trials resulted in lethal or sublethal predation (Fig. 4). Rates did not differ between 22°C 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 h at 16°C, 1.2 h at 22°C, and 0.6 h at 28°C.

### IGP model predictions

At low maturation rates ( $m = 0.1$ ), the effect of  $K$  depended on temperature and the IGP rate,  $\alpha$  (Fig. 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  $\alpha$  or  $K$  we tested was sufficient to allow the IG predator to persist. At higher temperatures (22°C and 28°C), intermediate levels of  $K$  and sufficiently high levels of  $\alpha$  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  $\alpha$  values at 28°C than at 22°C, leading to a larger zone of coexistence at 28°C. Where  $\alpha$  was too low

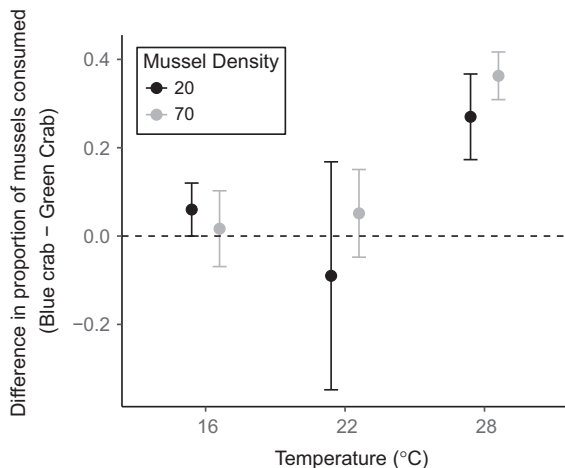


FIG. 3. Difference in mussel consumption between paired green and small blue crabs at three temperatures and two mussel densities (vertical axis is the proportion of mussels consumed by the blue crab minus the proportion of mussels consumed by the green crab). Positive values indicate that the blue crab consumed more mussels than the green crab. Error bars are  $\pm$  1 SE.

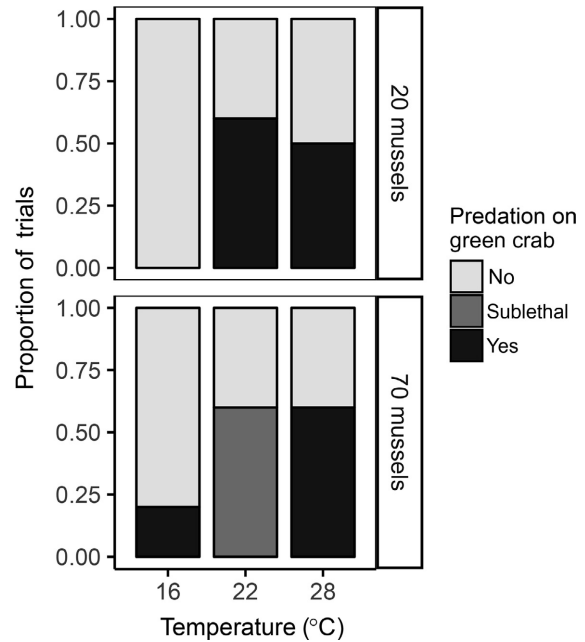


FIG. 4. Proportion of trials in which large blue crabs consumed green crabs at three temperatures and two mussel densities. Sublethal predation events were trials in which the blue crab attacked the green crab and removed and consumed claws and/or legs, but did not kill the green crab.

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. 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°C 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. 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°C 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-

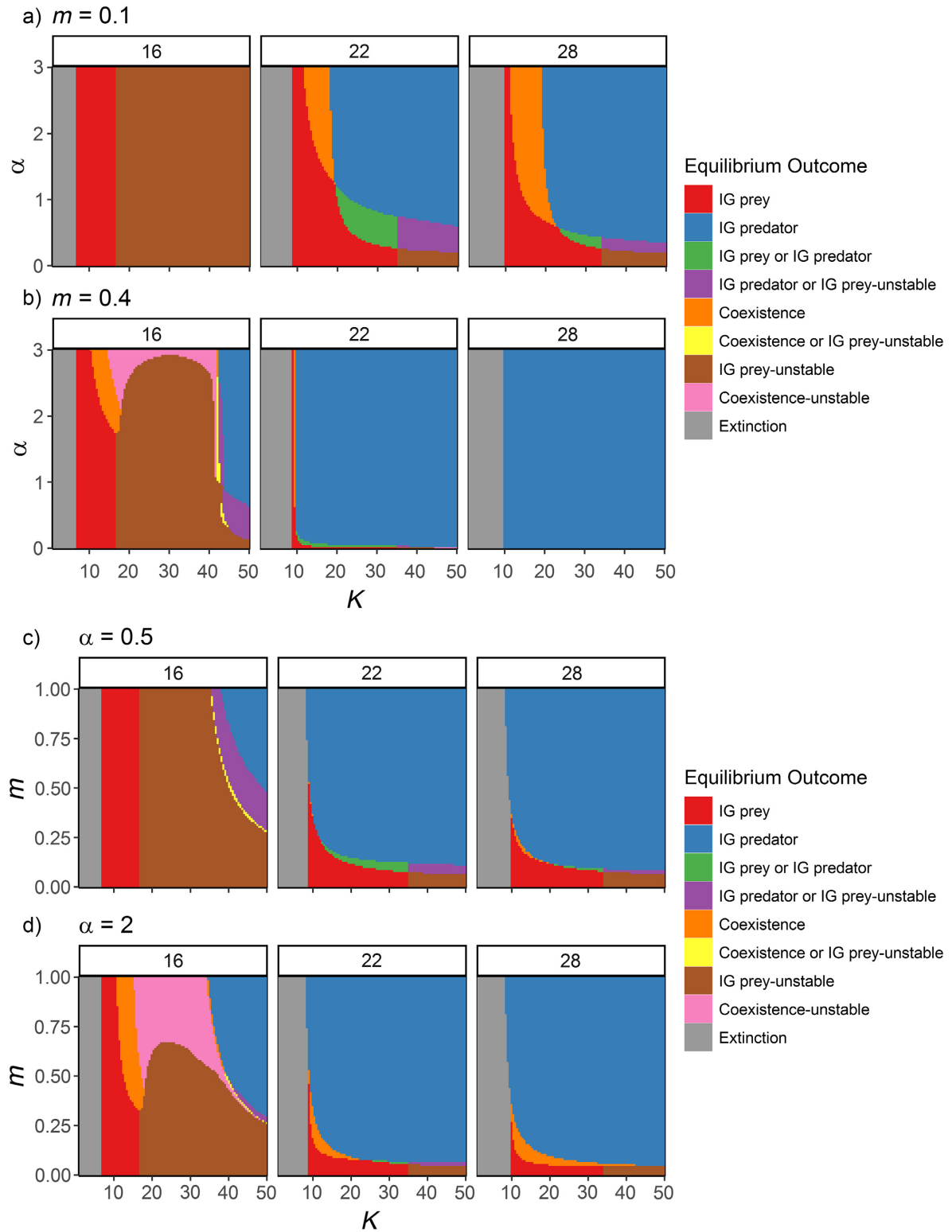


FIG. 5. Equilibrium results of the intraguild predation (IGP) model (a, b) varying  $\alpha$  (intraguild attack rate) and  $K$  (resource carrying capacity) at two different levels of  $m$  (maturation rate) and (c, d) varying  $m$  and  $K$  at two different levels of  $\alpha$ . Colors indicate the 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”). Panels are 3 temperatures in °C.

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 and Feiße 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 and 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 and 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 three 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), vs. 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°C and 28°C (Fig. 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 and Ruiz 1995) may also regulate crab populations and promote coexistence (Holt and Polis 1997, Holt and 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 and 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 1968) 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 and 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, spatiotemporal 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 and 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 nonnative species.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2157/supinfo>

## DATA AVAILABILITY

Data and code associated with this study are available from the Northeastern University Digital Repository Service: <http://hdl.handle.net/2047/D20261838>