

Environment and phenology shape local adaptation in thermal performance

Andrew R. Villeneuve<sup>1</sup>, Lisa M. Komoroske, Brian S. Cheng

Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, MA 01003,  
USA.

Gloucester Marine Station, University of Massachusetts Amherst, Gloucester, MA 01930, USA.

ORCID ID: ARV - 0000-0001-7303-5931, LMK – 0000-0003-0676-7053, BSC – 0000-0003-1679-8398

<sup>1</sup>Corresponding author: andrewrvilleneuve@gmail.com

## Abstract

Populations within species often exhibit variation in traits that reflect local adaptation and further shape existing adaptive potential for species to respond to climate change. However, our mechanistic understanding of how the environment shapes trait variation remains poor. Here, we used common garden experiments to quantify thermal performance in eight populations of the marine snail *Urosalpinx cinerea* across thermal gradients on the Atlantic and the Pacific coasts of North America. We then evaluated the relationship between thermal performance and environmental metrics derived from time-series data. Our results reveal a novel pattern of “mixed” trait performance adaptation, where thermal optima was positively correlated with spawning temperature (cogradient variation), while maximum trait performance was negatively correlated with season length (countergradient variation). This counterintuitive pattern likely arises because of phenological shifts in the spawning season, whereby “cold” populations delay spawning until later in the year when temperatures are warmer compared to “warm” populations that spawn earlier in the year when temperatures are cooler. Our results show that variation in thermal performance can be shaped by multiple facets of the environment and are linked to organismal phenology and natural history. Understanding the impacts of climate change on organisms therefore requires the knowledge of how climate change will alter different aspects of the thermal environment.

## Keywords

Countergradient variation; environmental drivers; latitudinal gradients; local adaptation; seasonality;  
thermal performance curve

## Introduction

Understanding the potential for organisms to evolve in response to rapidly changing environmental conditions is a key challenge to forecasting species vulnerability to climate change [1,2]. One method for uncovering evolutionary responses to climate change is to quantify genetic and phenotypic adaptive change using experimental evolution [3,4]. However, such an approach is typically used with model organisms possessing rapid generation times (e.g. *Drosophila* spp.) and may not be well suited for understanding climate change effects that arise via altered conditions over longer time scales (such as prolonged season length) because they experience only small temporal slices of the environment per generation [1,5–8]. Our expectations of what aspects of the environment that selection and plasticity are reacting to are thus influenced by generational and environmental time scales. Examining organismal traits across populations within non-model ectothermic species whose life histories encompass multiannual variation can reveal insights into spatial adaptation to varying seasonal conditions [9] and can contribute to our understanding of how species may respond to ongoing and future climate change (“space for time substitution”, [10,11]). Adaptive divergence may arise in the presence of intraspecific variation [12], wherein populations distributed along environmental gradients display local adaptation [13,14]. Investigating the potential for such divergence is important because the assumption that populations are homogenous (“niche conservatism”, [15]) can lead to over- or underestimated impacts of climate change [11,16,17]. Understanding patterns and mechanisms generating intraspecific variation in physiological traits is therefore critical for revealing species’ potential to adapt to climate change.

Growth rate should experience balancing selection to reduce trade-offs with growth and other traits and result in high fitness in locally adapted populations [18,19]. For ectothermic species distributed across broad temperature gradients, one might expect populations in warm locations to have higher rates of growth as compared to cool habitats because of the positive relationship between temperature and metabolic processes [20]. However, locally adapted species may exhibit ‘latitudinal compensation,’

wherein high-latitude populations express elevated physiological rates as compared to low-latitude populations at a given temperature [21]. Latitudinal compensation can arise via four different models of spatial adaptation (three described previously and one proposed here). The first is cogradient variation (CoGV) or ‘thermal adaptation’, wherein performance is highest at the mean temperature a given population experiences. In this case, a “cool” population exhibits a lower thermal optima ( $T_{opt}$ ) than a “warm” population, generating greater physiological rates at low temperatures (figure 1a & 1e, [22,23], e.g. [24]). In contrast, warm populations perform best at higher temperatures, but have lower performance than cool populations at cooler temperatures [23]. The second model is countergradient variation (CnGV), a pattern in which cool populations express higher maximum trait performance (MTP) than warm populations, but at the same  $T_{opt}$  (figure 1b and 1f, [22,23,25], e.g. [26]). CnGV is hypothesized to be adaptive for cool populations in high latitudes where growing temperatures occur over much shorter seasonal windows than warm, low latitude populations [6,23,27]. The third and fourth models incorporate elements of both CoGV and CnGV and are described as “mixed” models. Under Mixed Model 1, cool populations express higher MTP as in CnGV but lower  $T_{opt}$  than warm populations as in CoGV (figure 1c and 1g, e.g. [23,28]). Finally, we propose in this paper the existence of Mixed Model 2, wherein MTP increases in cool populations as in CnGV, but in contrast  $T_{opt}$  increases in cool populations (figure 1d & 1h). One example of how this unintuitive result can arise is seen with European frogs at high latitudes that develop and hatch later in the season than low latitude populations. Temperature during early development periods was higher at high latitudes because of more rapid warming in the late high latitude spring compared to early low latitude spring, which resulted in northern frogs that expressed higher growth rates at relatively higher thermal optima [18,29], but see [30]. This is significant because mean temperature during spawning is not correlated with the environmental aspects that are commonly used to differentiate thermal performance along gradients, such as latitude or mean annual temperature (e.g., [31]). Therefore, identifying the environmental parameters most strongly driving selection is necessary for predicting patterns of phenotypic variation, as different mechanistic parameters can drive divergent spatial patterns of trait performance. In a climate change context, differentiating between Mixed Model 1

and 2 is important because they suggest opposing responses to climate warming. Mixed Model 1 suggests that warming of mean temperatures should drive an increase in thermal optima whereas Mixed Model 2 suggests a decrease. Thus, differentiating between these models is an important step in forecasting species potential for adapting to change.

While there is broad support for spatial patterns of CnGV, there is uncertainty in the environmental mechanisms that give rise to these patterns of intraspecific performance [18,25,28]. CnGV is generally interpreted as a response to altered season length across populations, selecting for individuals with greater growth and developmental rates in habitats with short growing seasons [25,28,32]. However, experiments have also revealed CnGV arising in fish populations that experience no difference in seasonality but range across a latitudinal temperature gradient, which suggests a role for mean temperature in driving spatial patterns of divergence [26]. Distinguishing between these environmental drivers of spatial adaptation is critical to our ability to forecast how species and populations will respond to rapid climate change, as an erroneous understanding of these environmental drivers may result in inaccurate predictions of organismal response to climate change [33].

To address this gap in knowledge, we examined environmental drivers of adaptive divergence in the growth rate of an ecologically important marine gastropod. We used common garden experiments to quantify growth rates of lab reared Atlantic oyster drills (*Urosalpinx cinerea*; hereafter *Urosalpinx*) produced from populations across the Atlantic and Pacific coasts of North America. We then constructed models to evaluate the relationship between physical conditions derived from *in situ* environmental data loggers and metrics of thermal performance ( $T_{opt}$  and MTP). Thus, our goals were to 1) quantify patterns of trait performance in latitudinally separated populations of *Urosalpinx*, and 2) identify which environmental correlates best explain spatial patterns of adaptive divergence. We hypothesized that *Urosalpinx* trait performance would manifest as a countergradient variation that was largely driven by differences in season length across populations. Through our experiments and analysis, we sought to

highlight the importance of phenology and environmental conditions on determining patterns of trait divergence across populations.

## Materials and Methods

### (a) Natural History and Environmental Context

*Urosalpinx* is a predatory snail that is native from Florida to Nova Scotia and was introduced to the Pacific coast of North America in the late 1800s via American oyster (*Crassostrea virginica*) culture [34,35]. We quantified patterns of thermal performance from populations sampled across both the native and introduced coasts because they experience radically different thermal regimes. For example, while mean temperature and growing season length both decrease strongly from south to north along the Atlantic coast of North America, the gradient is much weaker and cooler on the Pacific coast [26,36]. Non-native species, such as *Urosalpinx*, provide an opportunity to compare intraspecific trait performance across different environmental gradients [37]. Although demographic history and founder effects have the potential to alter population responses to environmental regime and can confound interpretation of physiological trait data [38,39], the introduction of *Urosalpinx* to the west coast largely ended by the 1900s when transcontinental oyster imports ceased [40,41], allowing for 120 years of potential adaptation to the non-native climate regime. Further, in San Francisco Bay alone, 1.7 million kg of eastern oysters (*Crassostrea virginica*) were transplanted. Due to unregulated collection and transport processes at the time, large amounts of *Urosalpinx* were probably also introduced [41], which would greatly decrease the likelihood of a strong genetic bottleneck with drastic reduction of genetic diversity compared to source populations. Further, because this species undergoes direct development (i.e. there is no planktonic larval stage), dispersal and gene flow are likely limited among populations, suggesting a high potential for local adaptation [13,42].

### (b) Broodstock Field Collection and Common Garden Experiment

We examined physiological performance of lab-reared offspring from broodstock mothers sourced from eight populations of *Urosalpinx* to evaluate the effects of environmental drivers on local

adaptation. Experiments were conducted on juveniles that experienced controlled environmental conditions for their entire embryonic and juvenile life until cessation of experiments described below. To produce juvenile *Urosalpinx*, we collected broodstock adult *Urosalpinx* from eight sites, six from the Atlantic and two from the Pacific from March 15-June 9, 2019 (figure 2, table S1, [42]). See Supplementary Text S1 for further details on broodstock collection.

To construct *Urosalpinx* thermal performance curves, we conducted a common garden experiment. We exposed hatchlings from the 8 populations to 6 chronic experimental temperatures (16, 20, 24, 26, 28, and 30°C) chosen to capture  $T_{opt}$  based on past experiments [43]. These temperatures are also realistic when compared to habitat temperature across populations (min-max: 2–37.5°C). Growth rate was measured using snail shell height, which is correlated with body mass [42]. First, juvenile snails were measured for an initial shell height and then randomly assigned into common garden temperature treatments. Snails were less than 24 hours of age (post-hatch) when they entered the common garden experiment that lasted for 24 days. On the last day, we measured shell height and calculated growth rate as the difference between initial and final size. We counted snails that died over the duration of the experiment to quantify survivorship in the common garden experiment, but these data points were excluded from growth analyses. See Supplementary Material S1 for further details about common garden experimental design and measurement of *Urosalpinx* growth rate.

### (c) Environmental Predictors

In order to quantify environmental drivers of variation in growth rates in *Urosalpinx*, we derived nine metrics from four years of temperature data sourced from environmental loggers co-located within 14 km of the collection site for each population. One exception was the Georgia data logger, which was located 70 km away from the collection location but was highly correlated with local temperature logger that had a shorter record (Supplementary Material S1). We selected four years of temperature data from 2012-2019 based on the completeness of the record and to maximize temporal overlap among sites (table S1, Supplementary Material S1). From this data, we calculated: 1) latitude, 2) summer mean temperature

(June 1 – Sept 30), 3) upper 25<sup>th</sup> temperature percentile of the summer period, 4) upper 10<sup>th</sup> temperature percentile of the summer period, 5) maximum recorded temperature, 6) season length (number of days) where daily mean exceeded 10°C, 7) season length where daily mean exceeded 12.5°C, 8) the mean temperature for the first month of spawning, and finally 9) the mean temperature for the maximum period of spawning (table S2). We included length of season as a predictor because theory predicts organisms exposed to shorter growing seasons (i.e. high latitudes) are selected for faster growth [5,6,27]. We selected two likely lower temperature limits to calculate season length for *Urosalpinx*, 10°C and 12.5°C, based on reported absolute lower limit for feeding [44,45] and a breakpoint in oxygen consumption rates [46], respectively. We included mean temperature during spawning, as one of our hypotheses of  $T_{opt}$  behavior with environment is that high latitude populations experience warmer spawning periods than do low latitude populations [18]. We determined initial and maximum spawning periods as reported by [34] from the Atlantic and observations from the Pacific [47]; where no records of spawning periods could be found for a site, we used the closest neighbor site (table S4). We selected this broad range of variables as we did not necessarily know *a priori* which were relevant, and because the grouping of correlated predictors in AIC tables indicate what aspects of the environment best explain trait adaptation (i.e. season length generally, as opposed to season length above a specific threshold).

#### (d) Statistical Analysis

We used a two-step analysis framework to determine the environmental mechanisms driving growth rates in *Urosalpinx* populations in R [48]. First, we constructed and fit nonlinear regression models to thermal performance curves with initial snail size as a random effect (contributing 2.4% variance, means ranging from  $1.44 \pm 0.180$  to  $1.69 \pm 0.204$  mm among populations) using the *rTPC* and *nls.multstart* packages for each population to quantify thermal performance curve attributes ( $T_{opt}$  and MTP, temperature at which maximum growth occurs and the maximum growth rate, respectively) for each population across the six common garden temperatures using the Rezende equation [49,50]. For each of the eight populations we fit three models based on the three replicate bins across the six common

garden temperatures where populations were randomly assigned (figure S1). To produce 95% confidence intervals about each model prediction, we used non-parametric case resample bootstrapping on each population-bin model using *rTPC* and (table S5, [49]). Once models were fit to the data, we extracted the thermal optima ( $T_{opt}$ ) and maximum trait performance (MTP) of each thermal performance curve (table S5, figure S3). We then modeled the  $T_{opt}$  and MTP for each population against a suite of environmental metric predictors (table S2) in a model-selection framework using generalized linear mixed models with gaussian error distribution and with population as a random effect using *glmmTMB* [51]. Each environmental predictor was used only once per model to identify which predictor best describes patterns in trait performance and to avoid the issue of multicollinearity in models with multiple correlated predictors (i.e. where  $VIF > 4$ ; table S3). We used Akaike's Information Criterion (AICc) to select the greatest supported model, with a cutoff of  $\Delta AICc < 2$  [52]. For MTP, multiple predictors fell within the model selection criterion, and so we performed model averaging. To evaluate the possibility that analyses were influenced by invasive populations from the Pacific, we conducted a sensitivity analysis by constructing identical models with Pacific populations excluded. Our analyses were not sensitive to the removal of Pacific sites from analysis; both the best-supported environmental parameters and the significance level ( $p < 0.05$ ) were maintained for the MTP and  $T_{opt}$  analyses. We therefore present the full analysis of Atlantic and Pacific sites in the results. For survival, we used type II ANOVA from the *car* package [53] on generalized linear models with a binomial error distribution and logit link to analyze if population, common garden temperature, or the interactive effects of population and temperature affected *Urosalpinx* survival in the common garden experiment.

## Results

We found strong evidence of variation in growth rate across our common garden temperatures that depended largely on population origin (figure 3). Populations from the high-latitude Atlantic tended to express higher maximum growth rates (larger MTP) at a higher optimal temperature (larger  $T_{opt}$ ) compared to populations from the low-latitude Atlantic and the Pacific. Thus, [these high latitude TPCs](#)



are shifted “up and to the right” compared to other TPCs. Great Bay, NH, the site with the greatest MTP and  $T_{\text{opt}}$ , grew 134% faster than the slowest population (Humboldt, CA) and exhibited a  $T_{\text{opt}}$  3.52°C higher than the population with the coldest  $T_{\text{opt}}$  (Folly Beach, SC). Season length 10°C and 12.5°C (number of days Temperature > 10°C and 12.5°C, respectively) were the best predictors of MTP, whereas mean temperature during the initial spawning period was the best supported predictor of  $T_{\text{opt}}$  (figure 4, table S6). Initial spring spawning mean was well-supported under AIC for MTP as well as season length, but its 95% confidence intervals did not deviate from zero and thus was not considered a strong predictor of MTP (table S6). The maximum trait performance for shell growth decreased significantly with increasing season length (table S7, generalized linear mixed-effects model, conditional  $R^2_{\text{GLMM}} = 0.825/0.825$ ,  $p = 0.0138/0.0361$  for model averaged season length  $T > 10^\circ\text{C}$  and  $T > 12.5^\circ\text{C}$ , respectively), indicating that cold-origin populations grew faster than their warm-origin counterparts (figure 4a), which is consistent with countergradient variation. For thermal optima, growth was significantly correlated with the mean temperature during the first month of spawning (table S6 and S7, generalized linear mixed-effects model, conditional  $R^2_{\text{GLMM}} = 0.172$ ,  $p = 0.0288$ ), where increasing thermal optima was correlated with increasing spawning temperature (figure 4b). In other words, sites which had higher spawning temperatures had the highest thermal optima, which is consistent with cogradients variation. Taken together, these thermal performance metrics provide evidence for Mixed Model 2 (figure 1d & 1h), a mixture of countergradient and cogradients variation, between populations of *Urosalpinx*.

Of the initial 432 juvenile *Urosalpinx* that entered the common garden experiment, 394 (91.2%) snails survived. Survivorship in the common garden experiment was not affected by source population ( $\chi^2 = 7.52$ ,  $\text{df} = 7$ ,  $p = 0.377$ ) nor the interaction between population and common garden temperature ( $\chi^2 = 3.47$ ,  $\text{df} = 7$ ,  $p = 0.839$ ). However, survival increased with temperature ( $\chi^2 = 7.61$ ,  $\text{df} = 1$ ,  $p = 0.00581$ , figure S4). At 16°C, 84% of snails survived, while survivorship was maximized at 30°C, where 95% of snails survived.

## Discussion

Our mechanistic understanding of how environmental drivers influence spatial patterns of local adaptation is limited. Here, we report a novel form of mixed cogradient and countergradient variation in growth rate (figure 1*d* & 1*h*) that was driven by multiple aspects of the physical environment. In oyster drills, MTP was greatest in populations exposed to short growing seasons. In contrast,  $T_{opt}$  was greatest in populations with warm spawning periods due to a phenological delay in spawning. While other important work has hypothesized the respective environmental drivers of MTP and  $T_{opt}$  in isolation among different species [6,18,23,29], our work identifies the role of different physical drivers in shaping thermal performance, which was only apparent once we considered the potential for natural history (reproductive phenology) and multiple environmental metrics that influence organismal fitness.

### (a) Demonstration of a novel mixed model of trait performance

Our data supports a mixed model of spatial adaptation in growth rate (figure 1*d* & 1*h*), marked by countergradient variation in MTP and cogradient variation in  $T_{opt}$ . This pattern indicates countergradient variation (figure 1*b* & 1*f*), wherein environment and genotype are opposed to one another [23]. In contrast to CnGV, sites where the mean temperature during spawning was greatest yielded the highest thermal optima ( $T_{opt}$ ). In this context,  $T_{opt}$  exhibits cogradient variation – the genotype and environment are aligned. Northern native range populations tended to express higher this higher  $T_{opt}$ , followed by southern native range and invasive range populations. Interestingly, the Massachusetts population (Woods Hole) expressed lower MTP and  $T_{opt}$  than what would be predicted by the site's season length and spawning temperature. This may be due to a warmer thermal history than indicated by temperature data from the nearby NOAA buoy, as the population was sampled from the mouth of an estuary warmer than the surrounding ocean. It should be noted that our spawning metric was based on observations by multiple sources using different observation methods and frequencies [34,47], and future work may benefit from a standardized methodology to validate our findings of increasing  $T_{opt}$  with spawning temperature. Altogether, this provides support for Mixed Model 2 (figure 1*d* & 1*h*), a novel pattern we describe in this

paper. This pattern may arise because different aspects of the environment can be selective drivers and thus differently shape our expectations of phenotypic responses in different traits. Previous research of trait performance between populations of two silverside species from the Atlantic (*Menidia menidia*) and the Pacific (*Atherinops affinis*) found that growth rate was correlated with mean temperature (*A. affinis*) and season length (*M. menidia*), yielding a pattern of countergradient variation [26]. In contrast, we found season length to decrease with increasing latitude across our two Pacific sites, lending support to the observation that season length may be a stronger driver of CnGV than mean temperature, even in the low-seasonality Pacific. The phenology of important life histories like spawning and development may therefore have a significant impact on trait performance adaptation by regulating the type of environmental exposure among populations [18,30,54]. While we uncovered this novel mixed model of trait performance in *Urosalpinx*, it is entirely possible that other fitness-linked traits not examined in this paper may demonstrate other patterns of trait performance (including Mixed Model 2). Thus, we encourage future research to consider the potential for multiple traits responding to different environmental signals and what the cumulative interactions of these different trait performance models mean for organismal fitness in a changing climate.

We note that the data from the non-native populations must be interpreted with caution, as we cannot fully discount the possibility of effects from demographic history such as bottleneck events that could have influenced adaptive potential and phenotypic constraints. Such effects may arise via reduced genetic diversity of source populations that can confound our assumption that patterns of growth were driven solely by environment. However, we point out that *Urosalpinx* were introduced with eastern oysters (*C. virginica*) that were indiscriminately dredged and transferred in massive quantities over several decades [40], suggesting high propagule pressure and a large inoculating population. Recent molecular work in other gastropods introduced via the same vector in some of the same estuaries that we sampled reveals no evidence of a founder effect [55]. Finally, our sensitivity analysis demonstrated that removing invasive Pacific populations from the analysis did not change the overall results. This evidence

contributes to the notion that founder effects are often not observed in aquatic invasions under high propagule pressure scenarios [56]. Our ongoing molecular studies will clarify if this idea is supported by our study system as well and inform our broader understanding of how such patterns may contribute to adaptive potential.

#### (b) Environmental correlates of spatial adaptation

We found that different environmental metrics drive different aspects of *Urosalpinx* thermal performance. Our results agree with previous work hypothesizing season length and mean spawning temperatures as important environmental mechanisms behind adaptive growth patterns [6,18,57,58]. This suggests that *Urosalpinx* in high latitude environments are selected for rapid growth rates to compensate for a shorter seasonal growth window to achieve greater body size, and thus higher survival, over winter months [59]. In contrast, low latitude populations may be selected for lower growth rates to counteract potential energetic trade-offs with sustained rapid growth, shifting energy to reproductive effort or resistance to disease [25,26]. High thermal optima in high latitude populations with warm spawning periods may also enable these populations to optimize growth during the short seasonal growing window (above 10°C) [30]. Conversely, lower thermal optima in low latitude populations may allow snails to complete multiple spawning events throughout the year [60,61]. This suggests that *Urosalpinx* at high latitudes have evolved to commence spawning in warmer water than low latitude populations. Because mean temperature during spawning period is not correlated with latitude (figure S6;  $\rho = -0.290$ ), our results call attention to the importance of testing multiple environmental metrics that can drive variation in thermal performance [5,30,62]. This highlights the importance of integrating organismal natural history, in context with local environment, as critical considerations for accurately predicting organismal response to climate change.

#### (c) Implications for climate change

Species that range across environmental gradients provide an excellent opportunity to examine the potential for trait evolution in response to climate change [11]. Using this “space for time” approach, we can look to populations adapted to warm environments to build insight into the potential evolutionary trajectory of trait adaptation in cool environments [10]. Climate change studies sometimes assume that greater habitat temperatures will yield greater growth rates (e.g., [63,64]), which would be consistent with cogradient variation. By contrast, countergradient variation suggests that growth rates could actually decline under climate warming because this response is expected for warming across both space and time [26]. Thus, our findings of mixed cogradient and countergradient variation suggest that high latitude populations that experience a warmer climate could exhibit two responses. First, a longer growing season that is expected under climate warming may result in decreased growth rates [65]. Second, if warming results in an advance in spawning phenology at high latitude populations, this could result in adaptation to decreased thermal optima, as observed in low latitude populations [34]. Given that reduced body size is one well-documented result of climate change [66–68], our results of the adaptive growth rate patterns in *Urosalpinx* highlight the potential for evolutionary forces to drive slower growth rates which may contribute to patterns of diminished body size. Indeed, we observe smaller body sizes in low latitude populations of *Urosalpinx* within the native range [69]. As the environment in low latitude populations continues to warm, growth rates may be further reduced and extreme temperatures may even exceed thermal tolerances, potentially driving increased mortality. These populations also have diminished phenotypic plasticity in thermal tolerance, suggesting that extreme climate warming could drive local extinction of low latitude populations of *Urosalpinx*, resulting in range contraction [42]. A final observation is that latitudinal gradients in temperature across the Pacific and Atlantic coasts of North America are weakening, indicating that these populations may display convergent growth performance under climate change [36]. Uncovering the aspects of the environment that act as the strongest selective drivers therefore presents a challenge to ecologists, as assumptions of one parameter over others (i.e. one informed by phenology as we show here) may produce divergent expectations of physiological response to climate change.

#### (d) Conclusion

To accurately predict the effects of climate change on species, there is a clear need to quantify multiple environmental mechanisms driving organismal physiology [62,70]. If different environmental aspects influence unique components of thermal performance, then knowing the impacts of climate change on organisms requires investigating how physiologically relevant environmental parameters such as season length and spawning temperature will influence organismal physiology and evolution. This is an important consideration as TPCs are increasingly integrated into predictions of species distributions under climate change, an important step towards predicting species response to a rapidly changing environment [33,71,72]. Some species distribution and performance models accomplish this through applying trait performance to predictions of mean annual temperature and seasonal variability under different emissions scenarios [71–73]. While species-distribution approaches are increasingly informed by environmental mechanism (e.g. [73,74]), they generally do so among species without accounting for intraspecific variation, thus ignoring the potential for local adaptation [11]. In all cases, TPC-based prediction is only as good as our understanding of how climate links to organismal physiology [75]. Therefore, such models can be further improved by carefully considering the environmental mechanisms behind trait adaptation. Our work supports the need for the full consideration of phenology, natural history, physiology, and climate to provide a framework for increasing the accuracy of forecasts of organismal response to climate change.

#### **Data Accessibility**

R scripts and associated datafiles may be accessed via [https://github.com/villesci/Uro\\_TPC](https://github.com/villesci/Uro_TPC) [76]

#### **Authors' Contributions**

A.R.V., L.M.K., and B.S.C. conceived the study. A.R.V. and B.S.C. designed the experimental framework. A.R.V. collected and analyzed the data. A.R.V., L.M.K., and B.S.C. wrote the paper.

#### **Competing Interests**

The authors declare no competing interests.

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## Figure Captions

Figure 1. Conceptual models of spatial patterns of thermal reaction norms, illustrated using thermal performance curves (TPCs, (a) – (d)) and TPC components ((e) – (h)). Under CoGV ((a) and (e)), thermal optima ( $T_{opt}$ ) increases with environmental temperature whereas maximum trait performance (MTP) is equal. Under CnGV ((b) and (f)),  $T_{opt}$  is equal between populations, while the cool population has higher MTP than the warm population. Under Mixed Model 1 ((c) and (g)),  $T_{opt}$  increases with environmental temperature, while MTP is highest in the cool population. Under Mixed Model 2 ((d) and (h)), both MTP and  $T_{opt}$  are greater in cool populations.

Figure 2. *Urosalpinx* collection sites on the Atlantic and Pacific seabords of the United States. Mean sea surface temperature is an annual composite of 2018 5 km grid data (data source: NOAA/NESDIS Geo-Polar [77]).

Figure 3. Thermal performance (growth rate) of *Urosalpinx* from eight populations as a function of six common garden temperatures. For each population, three curves were produced for each of the three replicate ‘bins’ in the common garden experiment. Colored ribbons represent the confidence intervals (95%) around thermal performance curves, three for each population (one for each replicate).

Figure 4. Relationship between thermal performance metrics and environmental correlates. (a) Scatterplot of maximum growth rate (MTP) and season length (days above 10°C). (b) Scatterplot of thermal optima and mean temperature during the maximum spawning period. Black lines in both plots represent linear model estimate based on best performing model, although season length above 12.5°C was also a well-supported predictor for MTP. Shaded ribbon represents the standard error about the mean of each linear regression. Each population has three data points from the three thermal performance curves constructed for each population. USA state codes are given above each plot in order of ascending environmental parameter (x axis).