1   Diminished warming tolerance and plasticity in low latitude populations of a marine gastropod

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7   **Lay Summary**

8   The physiology of populations within species can determine sensitivity to climate change. Experiments

9   on marine snails indicate that southern populations are most susceptible to warming because they have

10   minimal physiological flexibility and are most threatened by extreme heat events. Management of this

11   species depends on the specific population in question.

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Abstract

22

23   Models of species response to climate change often assume that physiological traits are invariant

24 across populations. Neglecting potential intraspecific variation may overlook the possibility that some

25 populations are more resilient or susceptible than others, creating inaccurate predictions of climate

26 impacts. In addition, phenotypic plasticity can contribute to trait variation and may mediate sensitivity to

27 climate. Quantifying such forms of intraspecific variation can improve our understanding of how climate

28 can affect ecologically important species, such as invasive predators. Here, we quantified thermal

29 performance (tolerance, acclimation capacity, developmental traits) across seven populations of the

30 predatory marine snail *Urosalpinx cinerea* from native Atlantic and non-native Pacific coast populations

31 in the United States. Using common garden experiments, we assessed the effects of source population and

32 developmental acclimation on thermal tolerance and developmental traits of F1 snails. We then estimated

33 climate sensitivity by calculating warming tolerance (thermal tolerance – habitat temperature), using field

34 environmental data. We report that low latitude populations had greater thermal tolerance than their high

35 latitude counterparts. However, these same low latitude populations exhibited decreased thermal tolerance

36 when exposed to environmentally realistic higher acclimation temperatures. Low latitude native

37 populations had the greatest climate sensitivity (habitat temperatures near thermal limits). In contrast,

38 invasive Pacific snails had the lowest climate sensitivity, suggesting that these populations are likely to

39 persist and drive negative impacts on native biodiversity. Developmental rate significantly increased in

40 embryos sourced from populations with greater habitat temperature, but had variable effects on clutch

41 size and hatching success. Thus, warming can produce widely divergent responses within the same

42 species, resulting in enhanced impacts in the non-native range and extirpation in the native range.

43 Broadly, our results highlight how intraspecific variation can alter management decisions, as this may

44 clarify whether management efforts should be focused on many or only a few populations.

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Introduction

48   Understanding the sensitivity of species to climate change is a primary aim of global change

49   ecology (Calosi *et al.*, 2008; Williams *et al.*, 2008; Bennett *et al.*, 2019). Ecological forecasts are a suite

50   of modeling tools that can aid conservation practitioners in determining species sensitivity to climate

51   change by correlating occupied distribution environments or known physiological limits with predictions

52   of future climate scenarios (Pearson and Dawson, 2003; Helmuth, 2009; Chown *et al.*, 2010; Cacciapaglia

53   and van Woesik, 2018). In a conservation and management context, ecological forecasts can be used to

54   identify species at risk and prioritize efforts and management actions on species and ecosystems of

55   concern (Payne *et al.*, 2017; Tulloch *et al.*, 2020). However, these models often use physiological

56   measures from a single population to infer the capacity of a species to respond to environmental change

57   (Pearman *et al.*, 2010; D'Amen *et al.*, 2013; Valladares *et al.*, 2014; Lecocq *et al.*, 2019) and implicitly

58   assume that physiological niches are homogenous across populations within a species (Peterson, 1999,

59   2011; Bennett *et al.*, 2019). However, populations within species often exhibit physiological variation that

60   reflects heterogeneity in environmental conditions and potential local adaptation (Moran *et al.*, 2016;

61   Peterson *et al.*, 2019). Ignoring the potential for such locally-adapted variation greatly risks under- or

62   over-estimating species sensitivity to climate change (Pearman *et al.*, 2010; Valladares *et al.*, 2014;

63   Cacciapaglia and van Woesik, 2018). For example, populations of widely distributed species can differ in

64   thermal tolerance by up to 1.5-3.8°C (e.g., Fangue *et al.*, 2006; Pereira *et al.*, 2017). In contrast, thermal

65   tolerance may be invariant across a species range, a pattern that is described as niche conservatism (Lee

66   and Boulding, 2010; Pearman *et al.*, 2010; Gaitán-Espitia *et al.*, 2017). If populations are niche

67   conserved, then modeling a species as a single unit is appropriate. However, the management implications

68   of assuming niche conservatism or local adaptation can be starkly divergent; when modelled as having

69   homogenous physiology throughout its range, a *Porites* coral species was expected to increase its range

70   by 5-6% by 2100, while when modelled as five distinct populations the range was forecasted to decrease

71   by 50% (Cacciapaglia and van Woesik, 2018). Thus, intraspecific variation in thermal performance may

72 be crucial to understanding species sensitivity to climate change, but our understanding of mechanisms

73 underlying such variation remains incomplete.

74   Climate sensitivity may also be mediated by phenotypic plasticity. Acclimation is one form of

75 plasticity that is defined as within generational phenotypic change in response to an altered environmental

76 change and may allow an organism to rapidly adjust physiology to changing environmental conditions

77 (Seebacher *et al.*, 2012; Beaman *et al.*, 2016). For example, higher acclimation temperatures tend to

78 increase thermal tolerance, primarily due coordinated molecular adjustments such as increased heat shock

79 protein expression to maintain or regain homeostasis (Hofmann, 1999; Basu *et al.*, 2002; Guy *et al.*,

80 2008). The majority of these studies examine plasticity within a focal life stage (Marshall, 2008; Moore

81 and Martin, 2019). However, organismal life stages do not act as 'firewalls' past which the effects of

82 thermal challenge cannot penetrate (Marshall and Morgan, 2011). The effects of marine climate change

83 will impact all life stages of marine organisms and exposure to thermal stress in one life stage can result

84 in latent or carry-over effects to future life stages (Pechenik, 2006; Hettinger *et al.*, 2012). Developmental

85 acclimation should increase adult thermal tolerance to a point, beyond which we expect a reduction in

86 adult tolerance when acclimation temperature exceeds the thermal optima of organismal performance

87 (Overgaard *et al.*, 2011; Scharf *et al.*, 2015; Truebano *et al.*, 2018). Therefore, identifying the potential

88 effects of developmental acclimation are critical to understanding actual organismal reactions in later life

89 stages.

90   Even though plastic trait expression is often linked to environmental exposure, the extent of

91 plasticity capacity itself can be adapted to local conditions (De Jong, 2005; Valladares *et al.*, 2014).

92 Under the latitudinal variability hypothesis, which predicts how thermal phenotypic plasticity might vary

93 between latitudinally separate populations, high-latitude but non-polar populations should have higher

94 plasticity in response to seasonally variable temperatures (Bozinovic *et al.*, 2011; Gunderson and

95 Stillman, 2015; Barria and Bacigalupe, 2017). In contrast, tropical and polar species that experience

96 minimal seasonality are expected to have lower plasticity in response to limited environmental

97 fluctuations (Tewksbury *et al.*, 2008; Overgaard *et al.*, 2011; Peck *et al.*, 2014). It has also been suggested

98   that lower plasticity in warm adapted populations may reflect a trade-off between plasticity and greater

99   overall tolerance (trade-off hypothesis; Stillman, 2003; Magozzi and Calosi, 2015; Sasaki and Dam,

100   2019; Heerwaarden and Kellermann, 2020). Plasticity can buffer species' susceptibility to warming

101   temperatures, and thus it is important to quantify this trait in order to fully assess warming sensitivity

102   (Palumbi *et al.*, 2014). However, among species variation in plasticity means warming sensitivity will

103   also vary, requiring study on a species-by-species basis to accurately understand warming sensitivity

104   (Seebacher *et al.*, 2012). Considering the role of plasticity, in addition to potential local adaptation, are

105   critical to determining organismal susceptibility to thermal stress (Valladares *et al.*, 2014).
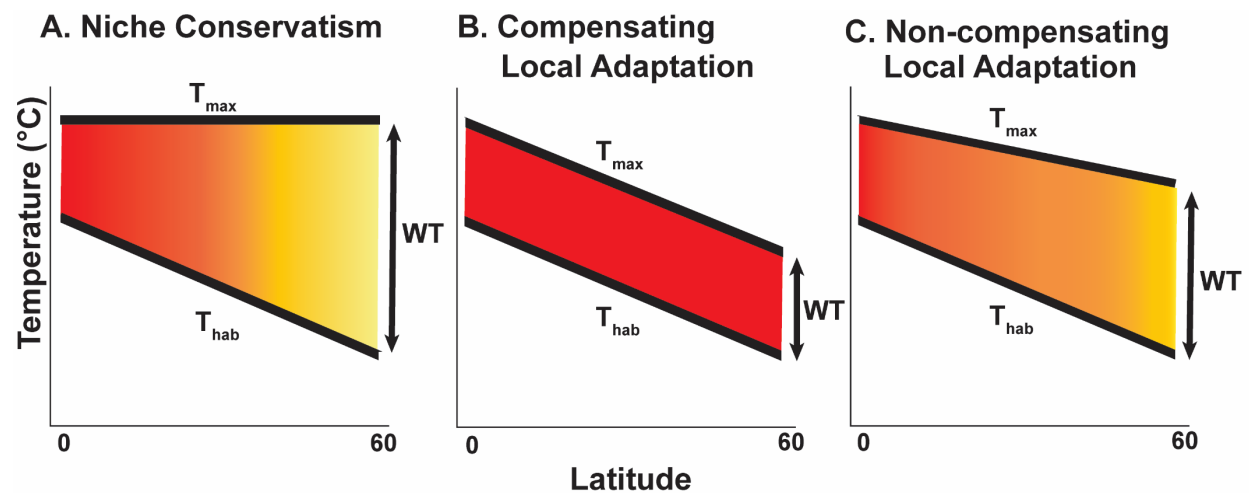
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Figure 1. Conceptual diagram of how thermal tolerance (T_{max}) and habitat temperature (T_{hab}) interact under niche conserved thermal tolerance (A), 'compensating' locally adapted thermal tolerance (B), and 'non-compensating' local adaptation (C) to result in differing expectations of warming tolerance (WT) with latitude. Color shading refers to WT magnitude, with yellow indicating large WT and red indicating small WT values.

113   Understanding geographic variation in thermal performance is central to identifying which

114   populations may be at the greatest risk of extinction caused by climate change. Both across species and

115   populations, evidence suggests that upper thermal tolerances increase with decreasing latitude (e.g.

116   Stillman and Somero, 2000; Sgrò *et al.*, 2010; Zippay and Hofmann, 2010; Sunday *et al.*, 2011; Pereira *et*

117   *al.*, 2017; Jensen *et al.*, 2019; Sasaki and Dam, 2019). However, quantifying thermal tolerance alone does

118   not reveal climate sensitivity, as it does not factor in the 'environmental distance' between thermal

119   tolerance and the *in situ* temperature regime. It is therefore necessary to integrate habitat temperature with

120   organismal tolerance. An organism's 'warming tolerance' (WT) quantifies this buffer by calculating the

121   difference between thermal tolerance and habitat temperature (e.g., mean annual temperature; Deutsch *et*

122   *al.*, 2008). In the absence of rapid thermal adaptation, populations at greatest risk of warming are those

123   with diminished warming tolerance (Deutsch *et al.*, 2008; Bennett *et al.*, 2019). In populations with

124   invariant thermal limits (niche conservatism), warming tolerance may be greater at high latitudes, as the

125   difference between habitat temperature and the conserved thermal tolerance will be large (Fig. 1A;

126   Bennett *et al.*, 2019). In contrast, low latitude populations would be most sensitive because of the small

127   difference between habitat temperature and thermal tolerance, assuming habitat temperatures decrease

128   more or less linearly from the equator to the poles (Tewksbury *et al.*, 2008; Diamond *et al.*, 2012; Bennett

129   *et al.*, 2019; Pinsky *et al.*, 2019). However, if thermal tolerance varies across populations ('compensating'

130   local adaptation), warming tolerance may actually be similar across populations, suggesting sensitivity

131   across the entire species range (if warming tolerance is low) or resilience to changing temperatures (if

132   warming tolerance is high; Fig. 1B; Bennett *et al.*, 2019). Finally, local adaptation in thermal tolerance

133   may exist, but may not track perfectly with habitat temperature ('non-compensating' local adaptation),

134   resulting in greater sensitivity to climate warming in populations with greater thermal exposure (Fig. 1C).

135   Thus, integrating intraspecific measures of physiological performance with environmental data is a

136   promising approach that can clarify population sensitivity to climate change. For conservation

137   stakeholders, this integration can better inform whether management needs to be focused on a few

138   sensitive populations, many populations throughout a species range, or none.

139   In a management and conservation context, knowledge of physiological performance can also

140   clarify our understanding of impacts of invasive species under climate change (Zerebecki and Sorte,

141   2011; Sorte *et al.*, 2013; Lennox *et al.*, 2015). Greater thermal tolerance breadths and plasticity are traits

142   that can contribute to the success of invasive species, particularly in the face of climate change (Chown *et*

143   *al.*, 2007; Slabber *et al.*, 2007; Sorte *et al.*, 2010; Zerebecki and Sorte, 2011; Seebacher *et al.*, 2012;

144   Kelley, 2014). These adaptations may allow invasive species to survive challenging transport conditions

145   and to rapidly colonize habitats with thermal conditions that differ from their native range (Diez *et al.*,

146   2012). These same traits are also predicted to confer climate resilience to invasive species as habitats

147   experience elevated and increasingly variable temperatures (Dukes and Mooney, 1999; Stachowicz *et al.*,

148   2002; Diez *et al.*, 2012; Sorte *et al.*, 2013). Forecasting the impacts of invasive species under climate

149   warming may be informed by knowledge of thermal physiology in both the native and invasive ranges

150   because adaptation in the native range provides the standing genetic material that founds invasive

151   populations. For invasive populations, thermal tolerance and plasticity may be locally adapted to novel

152   environments, even those that are warmer or colder than their native range environment (Beaumont *et al.*,

153   2009; Griffith *et al.*, 2014; Tepolt and Somero, 2014; Wesselmann *et al.*, 2020). Altogether, there exists a

154   range of possible climate sensitivies of invasive populations that may not be accurately described by

155   native range thermal physiology. Neglecting the potential for novel trait performance in invasive

156   populations can decrease the accuracy of ecological forecasts to climate change that are solely based on

157   the native range (Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Loo *et al.*, 2007; Beaumont *et al.*,

158   2009). Thus, evaluating the range of thermal physiology across native and invasive populations of single

159   species can shed light on the range of current adaptations within a species and thus clarify the extent of

160   current sensitivity, as well as the potential for future evolutionary adaptation to climate change

161   (Beaumont *et al.*, 2009; Henkel *et al.*, 2009; Hill *et al.*, 2013; Wesselmann *et al.*, 2020).

162   To address the roles of local adaptation and plasticity in determining thermal sensitivities across

163   native and invasive ranges, we quantified intraspecific variation in thermal performance of invasive and

164   native populations of an ecologically important predatory marine snail (Atlantic oyster drill, *Urosalpinx*

165   *cinerea*). We used split-brood common garden experiments to assess thermal performance of laboratory

166   reared F1 juveniles sourced from native and invasive populations across a latitudinal gradient on the

167   Atlantic (32.7° – 43.1° N) and Pacific (38.1° – 40.8° N) coasts of the United States, respectively. Our

168   specific objectives were to: 1) determine if variation in thermal tolerance and developmental traits occurs

169   among native and invasive populations, 2) quantify plasticity in thermal tolerance and developmental

170 traits by manipulating temperature during embryonic incubation, and 3) estimate climate sensitivity of

171 each population using warming tolerance (Deutsch *et al.*, 2008). We hypothesized that 1) thermal

172 tolerance would increase with environmental temperature, thereby suggesting local adaptation, 2)

173 elevated acclimation temperature during development would result in greater juvenile thermal tolerance,

174 and 3) plasticity would be highest in cold origin populations. Because latitude itself is not a perfect

175 predictor of the actual environmental temperatures experienced by populations, particularly across coastal

176 latitudinal gradients, we also evaluated the correlation between a suite of environmental metrics (e.g.,

177 maximum and mean temperature) and thermal and warming tolerance (Helmuth, 2009; Kuo and Sanford,

178 2009). Our broader goal was to quantify intraspecific thermal performance across a species' native and

179 invasive ranges to determine what populations are likely most sensitive to climate warming, and therefore

180 identify which populations of *Urosalpinx* are likely to persist in the long term without management

181 intervention.

182

183   **METHODS**

184 Species Selection

185 We used the snail *U. cinerea* (hereafter *Urosalpinx*) as our focal species because of its limited dispersal

186 that drives a high potential for local adaptation, its wide range across latitude and thermal regimes, and its

187 tractability in the egg and juvenile life stages (Cheng *et al.*, 2017). *Urosalpinx* undergoes direct

188 development, laying benthic egg cases that each contain 4-16 embryos that develop for 26-56 days after

189 which they emerge as hatchlings (Carriker, 1955). Because of this direct development, dispersal and gene

190 flow are likely limited among populations, suggesting a high potential for local adaptation (Kawecki and

191 Ebert, 2004). Further, we sampled populations from both the invaded and native ranges of *Urosalpinx*

192 with the goal of understanding if trait performance differs between invaded and native populations under

193 different thermal regimes (Zerebecki and Sorte, 2011). *Urosalpinx* is native on the Atlantic coast of North

194 America from south Florida to Massachusetts and cryptogenic (of unknown origin) north to Nova Scotia

195 (Fofonoff *et al.*, 2020). In the late 1800s, *Urosalpinx* was introduced to multiple locations on the Pacific

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196 coast of North America, ranging from San Francisco Bay north to Puget Sound, via importation of

197 Eastern oysters (*Crassostrea virginica*; (Carriker, 1955; Fofonoff *et al.*, 2020). The high biomass (1.7

198 million kg) and diverse origins of oysters transported to these Pacific sites (Hoos *et al.*, 2010) indicates

199 initial *Urosalpinx* populations were likely large, suggesting limited founder effects. In the invasive range,

200 *Urosalpinx* can virtually eliminate native oysters and other native species via predation (Carriker, 1955;

201 Kimbro *et al.*, 2009; Cheng and Grosholz, 2016).

202 Broodstock Collection

203 We examined physiological performance of F1 offspring in order to ensure a common garden

204 environment for the entire embryonic and juvenile life phases. This approach does not fully account for

205 the possibility of maternal or transgenerational effects but is a reasonable starting point for assessing

206 intraspecific patterns of thermal performance. To produce F1 offspring for experimentation, we collected

207 broodstock adult *Urosalpinx* from seven sites, five from the Atlantic and two from the Pacific that

208 encompassed a wide range of their latitudinal distribution (Fig. 2). All collections were conducted from

209 15 March - 9 June, 2019. We chose collection sites to be within 15 km of *in situ* environmental data

210 loggers (e.g. National Data Buoy Center, National Estuarine Reserve System, NOAA Ocean Observing

211 System, Table S1). At each site, we hand-collected at least 30 adult male and female oyster drills in the

212 extreme low intertidal and subtidal zones from both natural and artificial substrate, including oyster reefs,

213 pier pilings, and boulders, within a 30-meter radius. We then transported snails in aerated coolers of

214 seawater from collection sites, kept cool with ice packs and separated by population. Water conditions

215 within the coolers were monitored to maintain 100% dissolved oxygen saturation and temperature within

216 4° C of collection temperature. Samples from Humboldt Bay and Tomales Bay (Pacific populations) were

217 collected in a similar fashion except that they were overnight mailed in plastic bags with saltwater-

218 moistened paper towels but without seawater. Snails were kept cool with ice packs and upon arrival were

219 immediately placed in holding tanks separated by population at the University of Massachusetts,

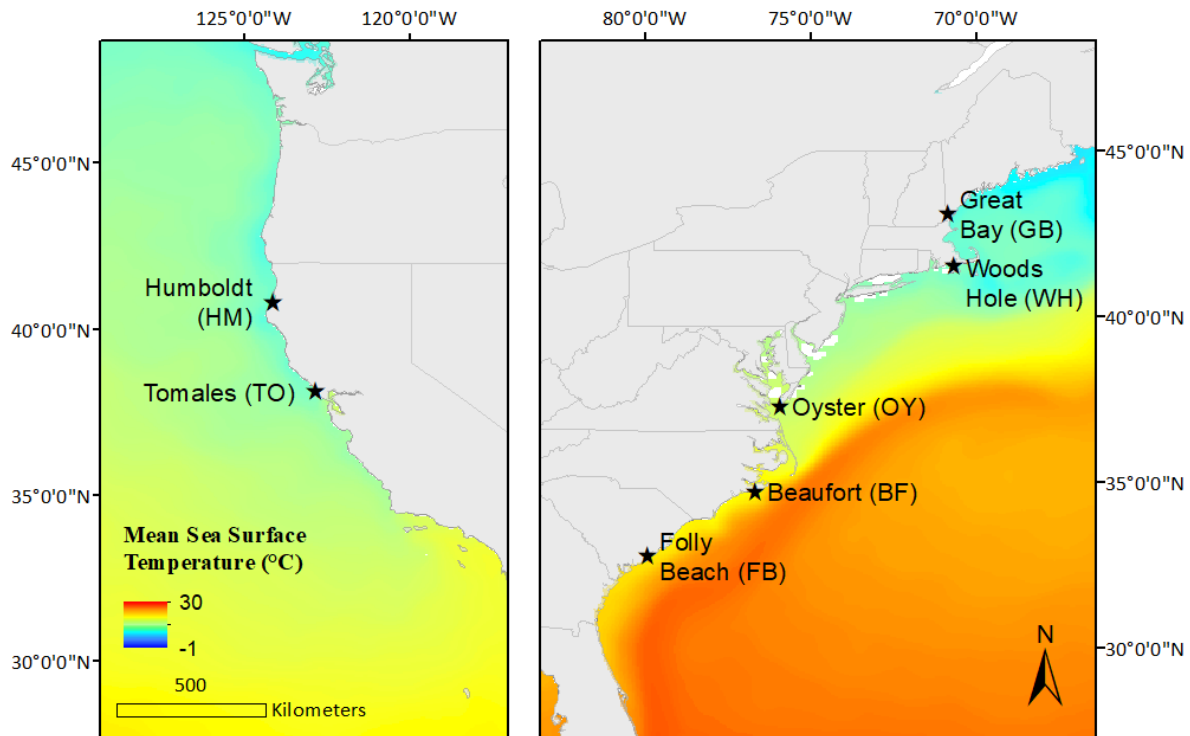220 Amherst. No mortalities occurred as a result of collection or shipping.

Figure 2. *Urosalpinx cinerea* collection sites on the Atlantic and Pacific seaboards of the United States. Mean SST is an annual composite of 2018 5km data (data source: NOAA/NESDIS Geo-Polar (Maturi *et al.*, 2017); annual SST composite data from NOAA Coral Reef Watch 2018 v3.1).

We maintained *Urosalpinx* populations in a recirculating seawater system at 12 °C (salinity 30 PSU) until they were needed for experimentation and as other populations were collected. Populations were kept separate in plastic aquaria with aeration. We fed broodstock *Urosalpinx* with blue mussels (*Mytilus edulis*), acorn barnacles (*Semibalanus balanoides*), and eastern oyster flesh (*Crassostrea virginica*) *ad libitum*. To initiate egg case laying, we raised the system water temperature by 1°C/day until 20°C was reached and then moved all broodstock to an identical recirculating seawater system at the Gloucester Marine Station (UMass Amherst). We performed daily water changes on the broodstock recirculating system using ambient coastal seawater maintained at 20°C. We also monitored ammonia levels (API Mars Fishcare, Inc., Chalfont, PA) to ensure levels stayed below 0.25 ppm. Ammonia varied

235   between 0-0.25 ppm with one spike to 0.5 ppm caused by overfeeding, remedied with daily water

236   changes.

237   Egg case collection and developmental acclimation

238   Our primary goal was to quantify thermal tolerance and plasticity (measured as developmental

239   acclimation capacity at 20 and 24 °C) across populations. We selected 20°C to enable comparison with

240   prior work on *Urosalpinx* (Cheng et al. 2017) and chose 24°C to represent a warmer temperature that

241   *Urosalpinx* likely already experiences during summer and is below a previously recorded juvenile thermal

242   optima (26.5°C; Cheng *et al.*, 2017). Thus, we hypothesized that an increase in acclimation temperature

243   from 20 to 24 °C would result in an increase in thermal tolerance. We performed daily inspections for egg

244   cases from July 5th - 31st, 2019, and collected a total of 122 egg cases. Mothers typically laid eggs in

245   clusters of 5-8 cases. In cases where a mother was discovered laying the egg cluster, we affixed a plastic

246   numbered tag to the mother with cyanoacrylate glue to track the identity of egg laying mothers. We

247   tracked mother identity, as well as unique clutches (group of egg cases found together), to differentiate

248   egg cases laid by different individual mothers. Because some eggs were laid by unidentified mothers

249   (n=21), we used unique clutches to control for maternal effects.

250   We collected eggs the day they were laid and incubated them using two methods to facilitate

251   collection of different data types. For development time, we placed single eggs into plastic tea strainers

252   (Tops Permabrew, Darien, CT) that were divided in half with nylon fabric. Each tea strainer therefore

253   held two eggs from a single egg cluster and allowed us to track time to hatching of individual egg cases.

254   For thermal tolerance, the remaining eggs were housed in undivided tea strainers separated by population

255   (20 - 30 egg cases per strainer) until hatchling emergence. Both types of strainers were submerged in

256   seawater maintained at 20 or 24 °C (salinity = 30 PSU), which served as our developmental acclimation

257   for the egg stage. In each aquarium, we monitored temperature at least twice daily; temperature within the

258   aquaria never varied by more than ± 0.4°C for the duration of egg development.

259   Immediately after hatching, we combined F1 snails from different mothers and of the same

260   population and acclimation temperature into strainers and fed F1 snails *C. virginica* oyster spat *ad libitum*

261   (3 mm shell diameter; Muscongus Bay Aquaculture, Bremen, Maine). F1 snails were housed in strainers

262   between 8 and 16 days submerged within a tank (39 L) maintained at 20°C or 24°C before they were

263   placed in the thermal tolerance experiment, and thus acclimation extended post-hatch. The mass of

264   juvenile snails as recorded immediately before the thermal tolerance experiment was not significantly

265   different between both acclimation temperature treatments (GLM , $F_{1,649} = 2.90$, $P = 0.0892$). The egg

266   cases acclimated at 24°C from Great Bay, NH and Woods Hole, MA, did not produce enough juveniles to

267   enter in a heat bar trial, and so were not included in our analysis.

268   Thermal Tolerance

269   We quantified thermal tolerance and developmental acclimation across populations using LT_{50}

270   methodology with an aluminum heat bar (Kuo and Sanford, 2009; Cheng *et al.*, 2017). The heat bar is

271   drilled to accommodate 5 ml centrifuge tubes that can house individual snails that are then exposed to a

272   gradient of temperatures along the length of the heat bar. This heat bar was constructed with a solid

273   aluminum block similar to Kuo and Sanford (2009), but heat was applied with a silicone heating element

274   (Omega SRFGA-406/2-P 60 watt, Omega Engineering, Norwalk, CT, USA) and adjusted with a

275   proportional integral derivative (PID) controller (ITC-100, Inkbird, Shenzhen, PRC). Cooling was

276   maintained by circulating 3-5 °C water through the opposing end of the heat bar. Although *Urosalpinx*

277   experiences aerial and aquatic thermal stress, this species is commonly found in both subtidal and low-

278   intertidal habitats with limited aerial exposure (Carriker, 1955; Cheng and Grosholz, 2016; Cheng et al.,

279   2017). Thus, we chose to quantify thermal tolerance in water to avoid the confounding effect of aerial

280   desiccation (Stillman and Somero, 2000).

281   In heat bar trials, individual snails were placed in 5 ml centrifuge tubes filled with 5 ml of aerated

282   seawater at the same acclimation temperature the snail experienced during development. We inserted a 2

283   x 2 cm 200 μm nitex mesh square into the tube using a plastic collar so that approximately 0.5 ml of the

284   tube's water was above the mesh. This prevented the snail from crawling out of the water, ensured free

285   exchange of oxygen with the water in the tube, and enabled us to record water temperature without

286   disturbing the snail. We randomly assigned one of the three possible row positions along the heat bar, so

287   that each population was represented in a column but in a random row. Thus, we tested up to three

288   different population-acclimation treatments(each of which was defined as a "trial") at a time on the heat

289   bar array (Fig. S1). Each heat bar "run" was defined as a ramping of three trials in the heat bar with 18-30

290   snails from three populations and a single acclimation temperature. We quantified wet weight of each live

291   snail (Ohaus Pioneer PX Scale, Ohaus Corporation, Parsippany, NJ) prior to the run to account for age

292   and size effects, as age and age-linked size can affect thermal tolerance (Nyamukondiwa and Terblanche,

293   2009; Truebano *et al.*, 2018). However, there was little evidence that age (as measured by body mass)

294   predicted thermal tolerance (Table S2). Therefore, we removed body mass as a predictor from our

295   models. The shell length of these juvenile snails ranged approximately from 1-2 mm.

296   We used the PID controller to control the temperature ramp along the heat bar, increasing the

297   controller setpoint by 5 °C every 30 minutes in steps from 25 °C to 60 °C for a total period of four hours.

298   In the final hour, we held the heat bar at 60 °C, so each snail was exposed to a heat ramp lasting five

299   hours (Table S3, Fig. S2). We measured the temperature in each column every hour using a

300   thermocouple. After the heat ramp, we removed the centrifuge tubes from the heat bar and allowed them

301   to recover in aerated seawater at the appropriate acclimation temperature (20 or 24°C) overnight. After

302   the recovery period, we evaluated snails for mortality using a stereomicroscope and a probe classifying

303   snails that did not retract their foot upon stimulus as dead and those that reacted as alive (Cheng *et al.*,

304   2017). In total, we conducted 22 independent heat bar trials (20°C $n = 14$, 24°C $n = 8$) for seven

305   populations using a total of 652 juvenile snails (Table S4). Individual snail sample sizes between

306   acclimations were uneven, with $n = 418$ at 20°C and $n = 234$ at 24°C, due to egg case availability.

307   Developmental Metrics

308   In addition to thermal tolerance, we quantified the effects of temperature on development across

309   populations by measuring: 1) hatching success, 2) clutch size, and 3) developmental rate. To assess

310   embryo hatching success over the incubation period, we counted the number of successfully hatched

311   snails and compared this to the number of unsuccessful embryos using a microscope (Leica S9i, Leica

312   Microsystems, Inc, Buffalo Grove, IL. USA). We also counted the number of initial embryos per egg case

313   to evaluate clutch size. To measure developmental rate of embryos within egg cases, we noted the lay

314   date of each case within two days of laying and checked egg cases daily for hatching. We classified an

315   entire egg case as hatched when the first hatchling snail emerged from the opening at the top of each egg

316   case, allowing hatchlings to crawl freely out of the egg case.

317   Environmental Metrics

318   While latitude is a commonly used metric of the types of environmental conditions experienced by a

319   population (e.g. Sunday *et al.*, 2014), we chose to evaluate multiple site level environmental temperature

320   metrics as potential predictors of thermal tolerance and developmental traits because latitude may not be

321   an accurate predictor of local scale temperatures experienced by organisms (Kuo and Sanford, 2009).

322   Moreover, while latitude can be a useful predictor that is correlated with environmental conditions,

323   habitat temperatures can differ at the same latitude based on ocean (Pacific vs. Atlantic) and local (inner

324   estuary vs. outer estuary) conditions, and is thus another potential direct driver of environmentally

325   adapted traits (Kuo and Sanford, 2009; Baumann and Conover, 2011; Sunday *et al.*, 2011). Thus, we

326   extracted a series of environmental temperature predictors with the goal of understanding what aspect of

327   habitat temperature (e.g. mean vs. maximum temperature) best predicted patterns in thermal tolerance.

328   From these temperature data, we calculated five environmental predictors: 1) mean annual temperature, 2)

329   summer mean temperature, 3) upper 25th percentile of the summer period, 4) the upper 10th percentile of

330   the summer period, and 5) the maximum summer temperature (Table S5). We used each environmental

331   predictor by itself in each model to evaluate which predictor best explained trait performance patterns

332   using model selection, including a null model. We selected site temperature data based on the

14

completeness of the record in 2018, the proximity of the temperature data to the collection site (no more

than 15 km; Table S1), and from locations representative of collection sites (e.g. environmental data was

collected from buoys in tidal creeks if the collection site was in a tidal creek). When available, we

selected only continuous 2018 temperature records, but the two data sources from the Pacific only had

continuous data from 2015 (Table S1, Fig. 3). Summer was classified as between June 1 and September

30.
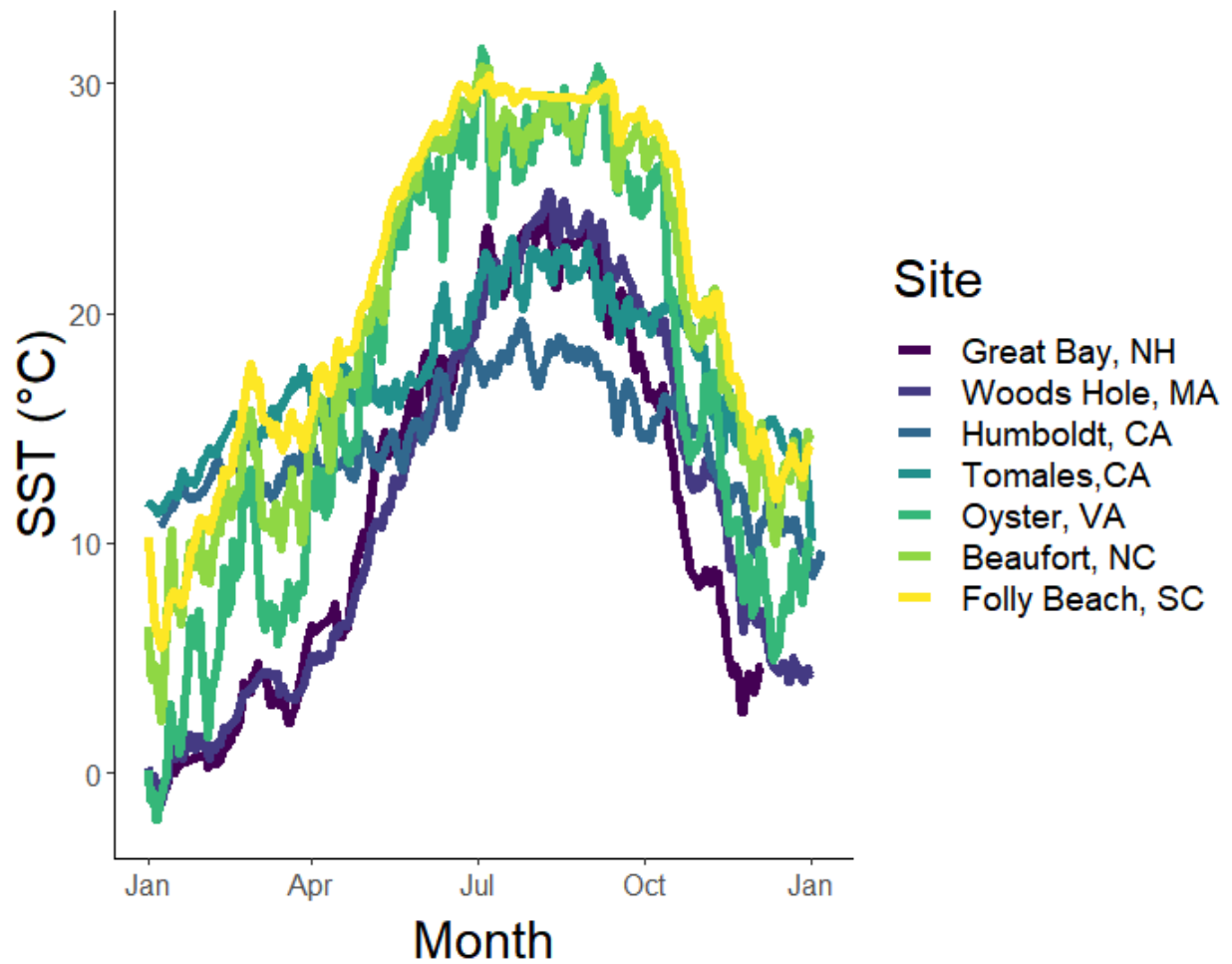
Figure 3. Sea surface temperature (SST) from sources near broodstock collection sites. Each time series
represents one year of data from January 1 to December 31, 2018 (except for Pacific sites, where data
ranged between January 1 to December 31, 2015) for comparison of thermal regime across populations.
Lines represent the daily mean temperature at each site. Sites are presented in order of annual mean
temperature. See Table S1 for source list and sampling dates.

Statistical Analysis

Thermal Tolerance

To evaluate thermal tolerance across populations we used a two-step approach. First, we extracted LT_{50} estimates for each heat bar trial ("trial" = 18-30 snails from a population-acclimation treatment in the heat bar) using Firth's bias-reduced logistic regression (Heinze and Schemper, 2002) due to complete separation of the survival data. Complete separation occurs when a predictor perfectly discriminates between binomial states. In our case, survival in each trial was consistent up to a certain temperature threshold after which all individuals died, and thus was completely separated (Fig. 4; Cheng et al. 2017). This lack of variation is problematic for traditional model estimation, thus necessitating the alternate approach. For these analyses we used the *brglm2* package in R (Kosmidis, 2021) to model the effect of final heat bar temperature on survival for each population and acclimation temperature treatment. Thus, each "run" of the heat bar produced three LT_{50} measurements for the three "trials" of population-acclimation treatments.

Second, as opposed to modeling LT_{50} as a function of population (e.g. using ANOVA), we used a regression-based approach using five environmental variables from each population to understand drivers of thermal tolerance over an environmental cline (Table S5). Once we extracted the LT_{50} from each trial, we then tested for geographic patterns in thermal tolerance by pairing each population's environmental data (Table S5) with their extracted LT_{50} estimates. These environmental data were then used as a suite of predictors, in addition to the acclimation temperature of each trial, in a model-selection framework. We constructed generalized linear models with gaussian error distributions using this set of environmental and acclimation predictors, and used small sample adjusted Akaike's Information Criterion (AICc) to select models which had the greatest support against a null model. We chose our cut-off of well-supported models for model selection throughout as $\Delta AICc < 2$ (Burnham and Anderson, 2002).

369   We further examined the difference between calculated thermal tolerances (LT_{50}) and the habitat

370   temperature of each population (hereafter referred to as warming tolerance; Deutsch *et al.*, 2008). We

371   calculated warming tolerance as $WT = LT_{50} - T_{hab}$, with T_{hab} as the maximum summer temperature. This

372   method accounts for maximum water temperatures an organism could experience, which is likely to be a

373   selective force across populations (Kingsolver *et al.*, 2013; Sunday *et al.*, 2014). We calculated separate

374   warming tolerance estimates using LT_{50} values from the 20 and 24°C acclimation temperatures to assess

375   how thermal history may influence thermal sensitivity estimates. While we included the two Pacific sites

376   in the data, we did not model an effect of invasion status because there was no overlap in T_{hab} values

377   between oceans and due to limited population replication in the Pacific.

378   Developmental Traits

379   We used generalized linear mixed models to assess the fixed effects of acclimation temperature and

380   environmental predictors, and their interaction on developmental traits (hatching success, clutch size,

381   development time). We included clutch as a random effect. For clutch size, we used a Conway-Maxwell

382   Poisson error distribution because of initial overdispersion in the data (Chanialidis *et al.*, 2018). For

383   hatching success of snails, we used a binomial error distribution with logit link function. For development

384   time, we used a gaussian distribution. For all development analyses, we used environmental predictors as

385   defined in Table S5. For these analyses we used the *glmmTMB* package (Brooks *et al.*, 2017). We

386   performed all thermal tolerance and developmental trait statistical analyses in R (v. 3.5.1, R Core Team,

387   2018).

388

389   **RESULTS**

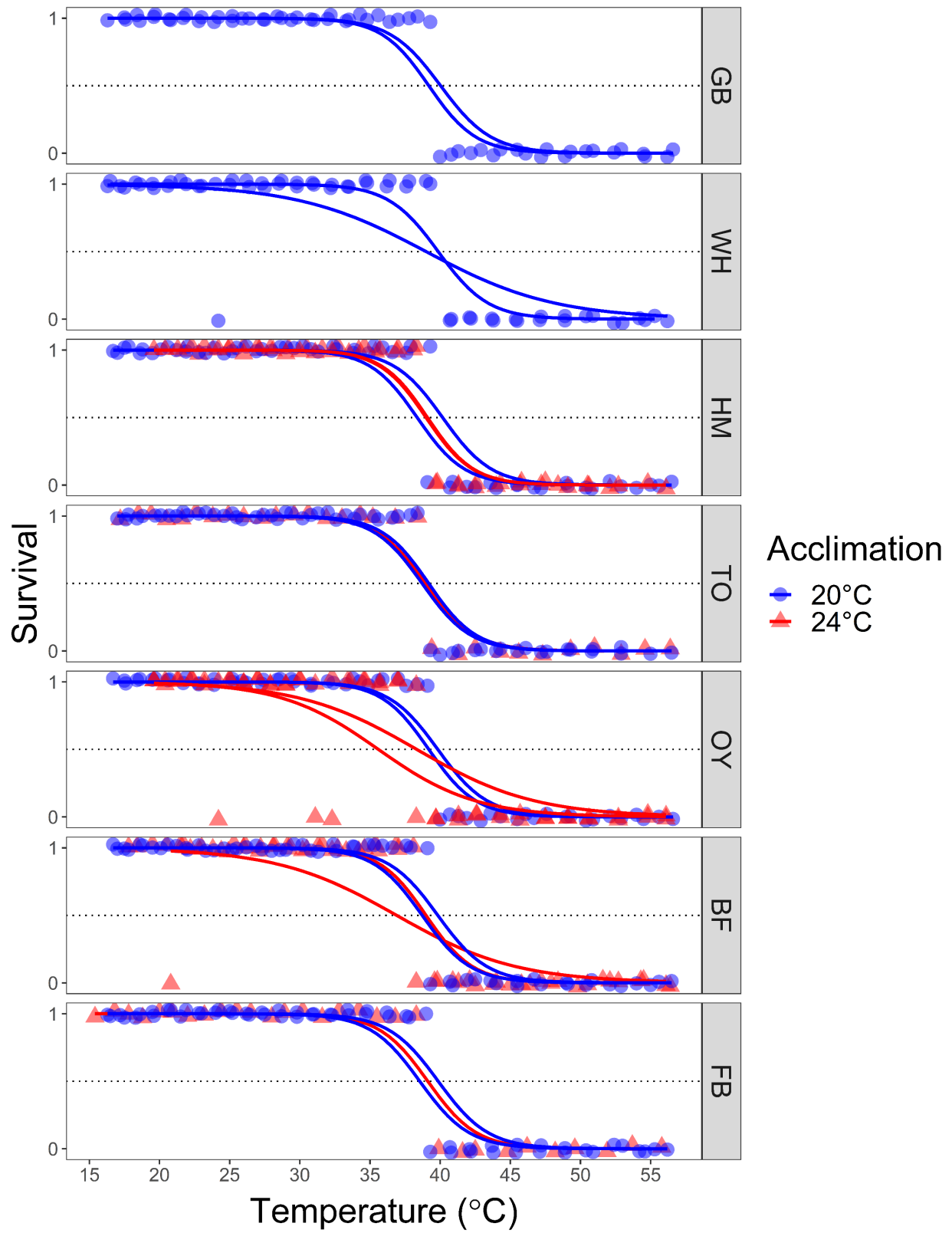390   Thermal Tolerance

391

393   Figure 4. Survivorship of *Urosalpinx* hatchlings (survival = 1, mortality = 0) as a function of final
394   temperature within the heat bar array, separated by acclimation temperature. Model estimates represent
395   independent heat bar trials. Dotted line represents the threshold for calculating LT_{50}. Populations are
396   ordered by ascending mean temperature within the native and invasive (HM and TO) range. Site codes
397   are defined as in Fig. 1. Points jittered for visual clarity.

398

399   The most supported model describing spatial patterns of thermal tolerance in *Urosalpinx*

400   contained habitat temperature (T_{hab}) as measured by the maximum summer habitat temperature at each

401   site with an interactive effect with acclimation temperature (T_{acc}). When acclimated at 20°C, thermal

402   tolerance increased with habitat temperature significantly but with high variability (GLM, $F_{3,18} = 4.51$, *P*

403   = 0.0417; Fig. 5, Table 1). When acclimated at 24°C, thermal tolerance decreased significantly with

404   habitat temperature (GLM, $F_{3,18} = 4.51$, $P = 0.0352$; Fig. 5, Table 1). *Urosalpinx* acclimated at 20°C and

405   24°C had a cross-population mean thermal tolerance of 39.3 ± 0.61 °C (*n* = 14) and 38.3± 1.22 °C (*n* =
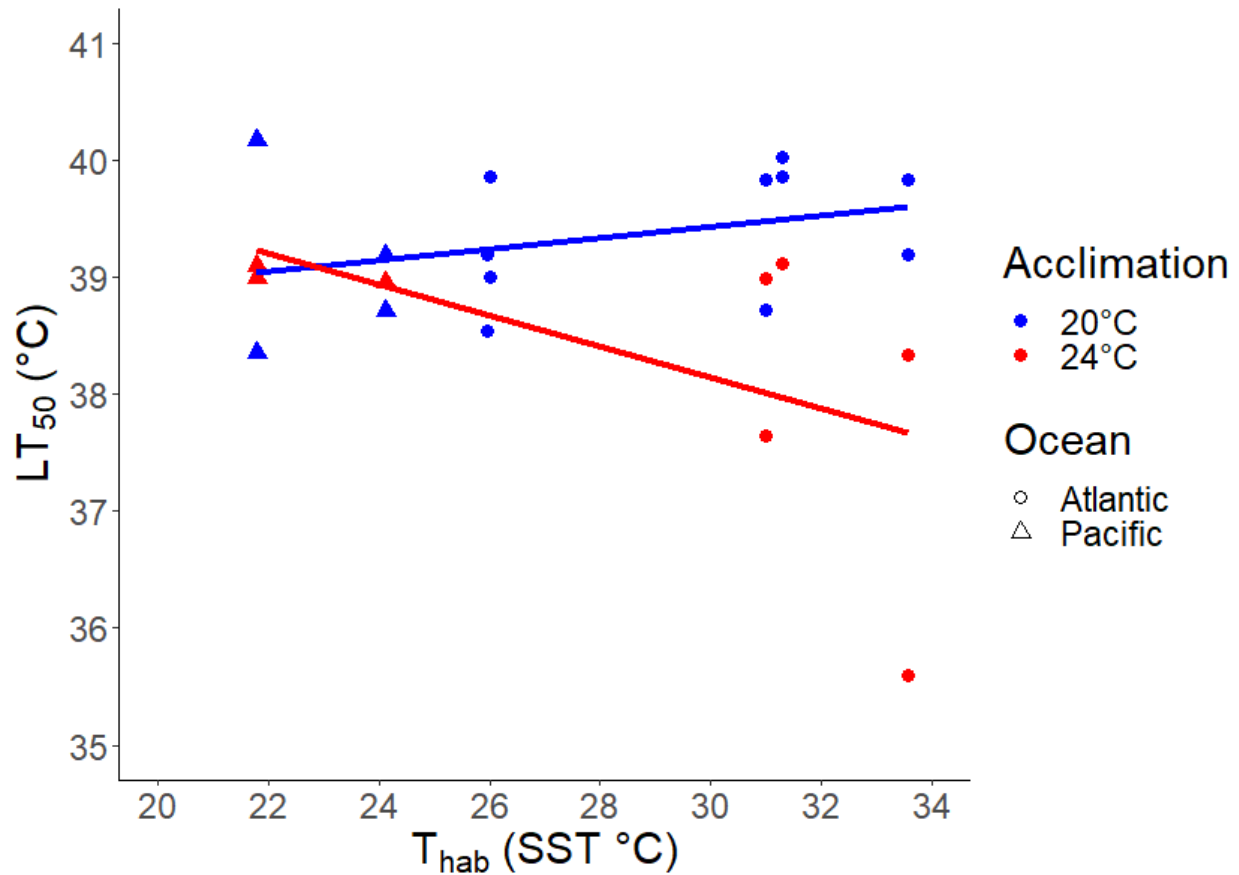
406   8; mean ± SD), respectively.

Figure 5. LT_{50} estimates of *Urosalpinx* hatchlings over their habitat maximum summer temperature and two experimental acclimation temperatures. T_{hab} is the maximum summer temperature.

Table 1. Parameter estimates for thermal tolerance, warming tolerance, and developmental rate models. Bold text denotes significance levels of $P < 0.05$. Multiple and adjusted R-squared values are presented for model-averaged and single-model GLMs. For mixed-effect models (developmental rate), the marginal and conditional R-squared values are given, which estimate model explanatory power between fixed effects and fixed and random effects combined (Nakagawa and Schielzeth, 2013). T_{hab} as determined via AICc model selection, are maximum summer temperature for both thermal tolerance and warming tolerance, and mean annual temperature for developmental rate.

Parameter	Estimate	SE	t/z	*P*
Thermal Tolerance				
R^2 T_{hab}*Acc (multiple/adjusted): 0.429/0.334				
Acc_{20} (Intercept)	17.2	12.4	1.39	0.182
Acc_{24}	1.04	0.568	1.83	0.0838
T_{hab}* Acc_{20}	0.956	0.436	2.19	**0.0417**
T_{hab} * Acc_{24}	-0.0454	0.0199	-2.28	**0.0352**
Warming Tolerance				

20

R^2 T$_{hab}$*Acc (multiple/adjusted): 0.975/0.971

Acc$_{20}$ (Intercept)	38.0	1.49	25.5	**<0.001**
Acc$_{24}$	4.16	2.27	1.83	0.0838
T$_{hab}$ * Acc$_{20}$	-0.951	0.0533	-17.9	**<0.001**
T$_{hab}$ * Acc$_{24}$	-0.182	0.0797	-2.28	**0.0352**

Developmental Rate

R^2$_{GLMM}$ (marginal/conditional): 0.906/0.935

Acc$_{20}$ (Intercept)	46.143	1.756	26.283	**<0.001**
Acc$_{24}$	-15.430	1.844	-8.368	**<0.001**
T$_{hab}$ * Acc$_{20}$	-0.463	0.105	-4.397	**<0.001**
T$_{hab}$ * Acc$_{24}$	0.286	0.111	2.577	**0.00996**

418

419   Warming Tolerance

420   We found a strong pattern of decreasing warming tolerance (thermal tolerance – maximum habitat

421   temperature) with increasing summer maximum site temperature for both acclimation temperatures (GLM

422    $F_{3,18}$ = 11.4, 20°C: P < 0.001, 24°C: P = 0.0352), but that warming tolerance was not significantly

423   different between acclimations (GLM $F_{3,18}$ = 11.4, P = 0.0838; Fig. 6, Table 1). Invasive pacific

424   populations appeared to have the highest warming tolerance values, although we note that we did not

425   explicitly model invasion status because of the low number of invasive population replicates (n = 2) . The

426   minimum calculated warming tolerance occurred in the Virginia population ("Oyster") at 24°C

427   acclimation (2.03 °C), while the largest warming tolerance occurred in the California ("Humboldt")

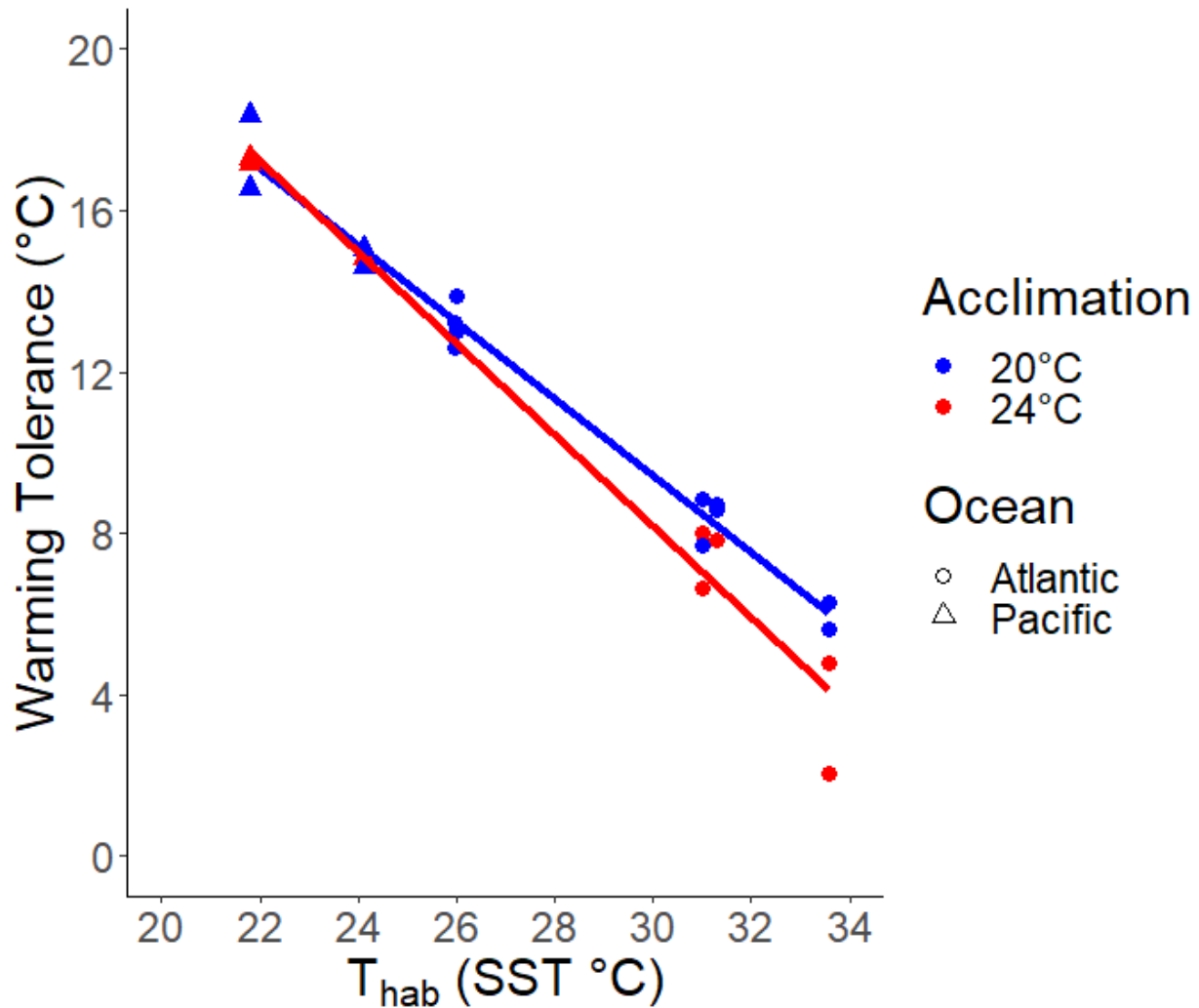428   population at 20 °C acclimation (18.4 °C).

429

Figure 6. Latitudinal and oceanic trends in warming tolerance ($LT_{50} - T_{hab}$), with T_{hab} being the maximum site summer temperatures. Trendline depicts the significant relationship between warming tolerance and T_{hab} at the 20°C and 24°C acclimations. Note that we include Pacific site data, but omitted invasion status as a predictor from analysis because of low sample size. T_{hab} is the maximum summer temperature.

434

Developmental Traits

The hatching time of *Urosalpinx* egg cases decreased with greater mean annual habitat temperature of the source population (GLMM *n* = 39, P < 0.001) for egg cases reared at a common temperature of 20°C (Fig. 7, Table 1). At 20°C acclimation, the shortest developmental time occurred in egg cases from the southernmost Atlantic site (Folly Beach, 36.5 ± 3.53 days (SD)), while the greatest

440   development time occurred in the northernmost Atlantic site (Great Bay, 41.8 ± 2.59 days). When

441   acclimated at the higher temperature of 24 °C, hatching time decreased across all sites (GLMM n = 46, P

442   = 0.00996; Fig. 7, Table 1). The shortest development time at 24°C occurred in North Carolina (Beaufort;

443   26.8 ± 1.28 days), and despite the significant negative trend between habitat temperature and time to

444   hatching, the slowest development rates occurred at both the northernmost and southernmost Atlantic

445   sites (South Carolina; 29.3 ± 0.577 days and New Hampshire; 29.2 ± 1.47 days). Random effects of

446   clutch gave intercept variance of 0.955 ± 0.977 (SD), and little difference between marginal (0.906; fixed

447   effects only) and conditional (0.935; fixed and random effects) R^2_{GLMM} (Nakagawa and Schielzeth, 2013).

448   Multicollinearity was low (VIF < 2.5) for all well-supported developmental trait models. Both clutch size

449   and hatching success metrics had multiple well-supported models, so we model averaged top models of

450   clutch size and hatching success. None of the best-supported models were overdispersed (deviance <

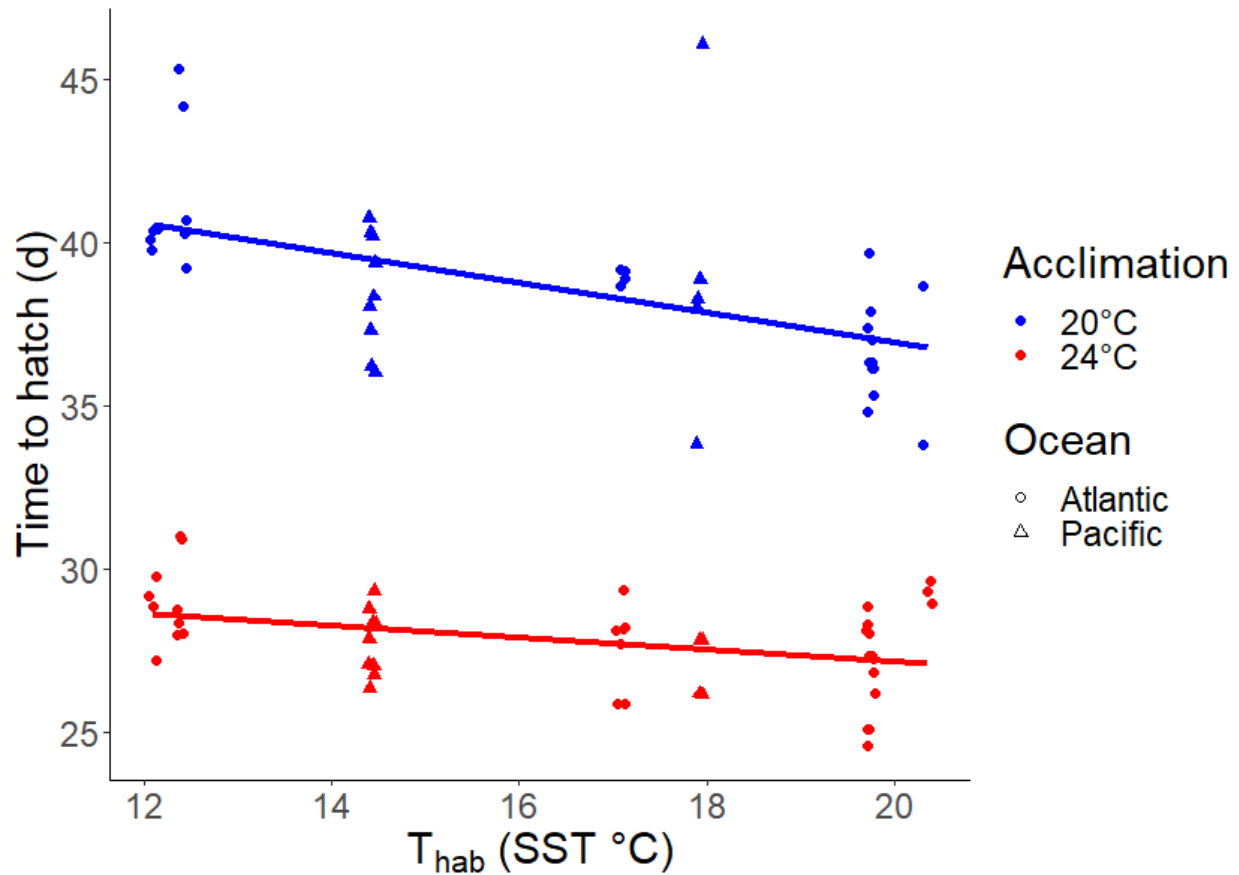451   degrees of freedom).

452

453

Figure 7. Developmental rate of *Urosalpinx* egg cases when acclimated at 20°C and 24°C. T_{hab} is the
mean annual temperature. Points jittered for visual clarity.

456

457   Clutch size showed a significant but highly variable relationship with environmental predictor

458   parameters (GLMM $n = 85$, $P = 0.0086$, maximum summer temperature; Table S6, Fig. S3), such that

459   warm-origin populations had a larger number of embryos per egg case than their cold-origin counterparts.

460   Hatching success increased with habitat temperature (GLMM $n = 85$, $P = 0.0172$, 75th percentile summer

461   temperature), although there was considerable variation (Table S6, Fig. S3). Elevated acclimation

462   temperature had no effect on hatching success (Table S6, Fig. S3). The random intercept of clutch for

463   clutch size had a variance of 0.0557 ± 0.236 (SD), and each egg case's hatching success had a variance of

464   0.373 ± 0.610 (SD). Taken together, the developmental metrics (particularly developmental rate and

465   hatching success) indicate an increase in performance with increasing habitat temperature.

DISCUSSION

466

467   Thermal performance has often historically been assumed to be homogeneous within species, an

468   assumption that can generate inaccurate forecasts of species response to climate change if there is

469   adaptive differentiation across populations. There is increasing recognition that intraspecific variation

470   may be common in the ocean (Kuo and Sanford, 2009; Zippay and Hofmann, 2010; Kelly *et al.*, 2012;

471   Hong and Shurin, 2015; Pereira *et al.*, 2017; Sasaki and Dam, 2019). However, observations supporting

472   this view are generally limited, particularly across populations of a species' native and invasive ranges

473   (but see: Henkel *et al.*, 2009; Yu *et al.*, 2012; Hill *et al.*, 2013; Tepolt and Somero, 2014; Wesselmann *et*

474   *al.*, 2020). Here, we found evidence for greater thermal tolerance in southern populations of oyster drills

475   that experience higher habitat temperatures, in support of our hypothesis of local adaptation. However,

476   when developmental acclimation temperature was increased, thermal tolerance decreased in southern

477   populations (2.1-6.4% decrease), contrary to expectations of greater thermal tolerance with higher

478   acclimation. Further, we found diminished warming tolerances of low latitude Atlantic populations as

479   compared to high latitude Atlantic (native) and Pacific (invasive) populations, consistent with the non-

480   compensating local adaptation model of warming tolerance (Fig. 1C). This follows our conceptual

481   framework of how variation in thermal tolerance may be inverse to variation in warming tolerance (Fig.

482   1); thermal tolerance that compensates well with changes in the environment results in low variance in

483   warming tolerance. In this study, we show that because thermal tolerance does not scale strongly with

484   environmental temperature, variation in calculated warming tolerance is high between populations. These

485   results suggest a striking contrast. Low latitude native populations appear to exhibit high climate

486   sensitivity and may become extirpated if warming continues ultimately resulting in range contraction. In

487   contrast, the two Pacific (invasive) populations of *Urosalpinx* studied may be more likely to persist in a

488   warming future because of a large buffer between current habitat temperatures and their thermal

489   tolerance. *Urosalpinx* has well-documented impacts on native, foundational species such as Olympia

490   oysters, and therefore will likely continue to drive cascading negative effects on native biodiversity into

491   the future (Kimbro *et al.*, 2009; Cheng and Grosholz, 2016).

492   We found interactive effects of source population environment and acclimation temperature on

493   thermal tolerance (Fig. 5). Populations reared at 20°C displayed a positive relationship between thermal

494   tolerance and habitat temperature, consistent with other studies on marine invertebrates (Zippay and

495   Hofmann, 2010; Sunday *et al.*, 2011; Kelly *et al.*, 2012; Pereira *et al.*, 2017; Sasaki and Dam, 2019).

496   Although the differentiation in thermal tolerances appears small (~1.0 °C across the range tested), this

497   effect size is similar to other studies testing intraspecific variation in thermal tolerance (Fangue *et al.*,

498   2006; Kuo and Sanford, 2009; Jensen *et al.*, 2019). Interestingly, higher developmental acclimation

499   temperature (24 °C) resulted in a negative relationship between habitat temperature and thermal tolerance,

500   or what we define as 'negative plasticity'. At first glance, these results are counterintuitive given the

501   tendency of higher acclimation to result in elevated thermal tolerances (Angilletta Jr., 2009; Pereira *et al.*,

502   2017; Sasaki and Dam, 2019). However, evidence of a negative response to higher acclimation

503   temperature has been demonstrated in nudibranchs (Armstrong *et al.*, 2019) and salmonids (Blair and

504   Glover, 2019; Del Rio *et al.*, 2019) in both developmental and within stage acclimations, albeit not

505   between multiple populations. This negative plasticity in thermal tolerance from southern populations is

506   suggestive of a tradeoff between elevated thermal tolerance and plasticity (Stillman, 2003; Armstrong *et*

507   *al.*, 2019; van Heerwaarden and Kellermann, 2020). Southern populations have evolved elevated thermal

508   tolerance in response to warm environmental conditions but have done so at the cost of plasticity extent.

509   Because northern/invasive populations have lower evolved thermal tolerances, they do not exhibit such

510   trade-offs with plasticity. It should be noted that our scope of inference is limited here because we were

511   not able to quantify thermal tolerance of northern Atlantic sites at 24°C (Great Bay and Woods Hole)

512   because we were not able to obtain enough juveniles from each treatment to run a heat bar trial.

513   Furthermore, an acclimation of 24°C itself may be stressful for embryonic and newly hatched *Urosalpinx.*

514   We originally chose 24°C as the higher acclimation temperature because it is below the measured

515   thermal optima of juvenile, invasive range *Urosalpinx* (26.5°C, Cheng *et al.*, 2017), and hatchling

516   survivorship, while invariant with acclimation temperatures in our study, has previously been shown to

517   peak at 20°C and decrease at 25°C (Ganaros, 1958). However, because early life stages are often the

518   most vulnerable to thermal stress, it is further possible that physiological stress is incurred in embryos and

519   hatchlings at 24°C (Truebano *et al.*, 2018; Dahlke *et al.*, 2020; McKenzie *et al.*, 2020). Thermal stress can

520   accumulate over time with heightened sublethal temperatures, resulting in reduced survivorship in what

521   has been described as a tolerance landscape (Rezende *et al.*, 2020). These developmental acclimation

522   effects are tested less often, but are important because ocean warming is occurring across seasonal cycles

523   and can impact early development when many organisms are the most sensitive (Pechenik, 2006;

524   Marshall and Morgan, 2011; Dahlke *et al.*, 2020). Our results point to the importance of carefully

525   considering how seasonality of environmental exposure and ontogeny may affect thermal sensitivity

526   across life stages. This is a critical consideration when designing experimentation tracking local

527   adaptation across generations, especially with complex life stage organisms from environments with

528   strong seasonal thermal fluctuations. Models that predict population persistence using adult thermal

529   optima or tolerance may overpredict potential ranges by not considering heightened sensitivity of early

530   life stages and the carry-over effects of warming during development.

531   Among environmental correlates, maximum habitat temperature best explained variation in

532   thermal tolerance. Most studies use mean annual temperature in predicting variation in thermal tolerance,

533   perhaps because these data are readily available and explain some variation in tolerance (e.g. Deutsch *et*

534   *al.*, 2008; Hughes *et al.*, 2018). However, maximum habitat temperature is expected to be the main driver

535   of thermal tolerance both within and across species (Hoffmann, 2010; Kelley, 2014; Pinsky *et al.*, 2019).

536   Maximum temperatures should act as a 'filtering' agent such that a locally adapted population will have

537   thermal tolerances selected for from standing genetic variation that allow it to persist in that environment

538   (Bennett *et al.*, 2019; Pinsky *et al.*, 2019). Local thermal heterogeneity, driven by processes such as

539   upwelling, tides, and currents also mean that environmental metrics like latitude or mean temperature are

540   not necessarily correlated with maximum habitat temperature (Baumann and Doherty, 2013). We found

541   that maximum habitat temperature consistently drove variation in thermal tolerance spanning native and

542   invasive ranges (Fig. 4). Our temperature records, obtained from buoys within 15 km and of similar

543   habitat type of collection sites, offer a general view of the environmental conditions experienced by

544   populations. However, given organismal body temperature itself may vary as a function of microhabitat

545   and behavior (Helmuth *et al.*, 2010), the exact maximum temperature each *Urosalpinx* population

546   experiences may differ from those obtained via buoy data. As a result, we suggest future work consider

547   testing relationships between upper thermal tolerance and maximum habitat temperatures along with

548   mean temperature and/or latitude, as well as deploying collocated temperature loggers to refine these

549   environmental parameters. By not directly correlating thermal tolerance with a major selective

550   environmental force (i.e. maximum habitat temperature), patterns of local adaptation may be ignored or

551   overstated, potentially wasting resources by managing populations that are not actually sensitive to

552   climate change.

553   Diminished warming tolerance at warm-origin sites indicates that southern populations are closer

554   to their thermal limit than their northern counterparts (Fig. 6), and that population origin has a stronger

555   effect on climate sensitivity than does acclimation temperature. Interestingly, this result sets up a third

556   potential pattern of thermal tolerance, habitat temperature, and warming tolerance (see Fig. 1). Despite

557   thermal tolerance being locally adapted, warming tolerance was not constant across populations,

558   indicating that a third model of warming tolerance (what we call here 'non-compensating' local

559   adaptation, Fig. 1C) between niche conserved (Fig. 1A) and locally adapted populations (Fig. 1B) are

560   possible. This is likely a result of thermal tolerance not being 1:1 correlated with decreasing habitat

561   temperature. This decreasing relationship between warming tolerance and habitat temperature is

562   consistent with studies that have examined intraspecific sensitivity to climate in crabs, nudibranchs, and

563   leaf miner moths (Gaitán-Espitia *et al.*, 2014; Pincebourde and Casas, 2015; Armstrong *et al.*, 2019), as

564   well as studies of interspecific climate sensitivity (Deutsch *et al.*, 2008; Sunday *et al.*, 2011; Allen *et al.*,

565   2012; Diamond *et al.*, 2012; Vinagre *et al.*, 2016; Comte and Olden, 2017; Janion-Scheepers *et al.*, 2018).

566   Taken together, this evidence supports the view that low latitude populations appear to have high climate

567   sensitivity (Tewksbury *et al.*, 2008; Pinsky *et al.*, 2019). In contrast, temperate populations have greater

568   warming tolerance despite reduced thermal tolerance, perhaps because of exposure to lower

569   environmental temperatures (Deutsch *et al.*, 2008; Janion-Scheepers *et al.*, 2018). Reduced warming

570   tolerance at the warm edge of a population's range also highlights the potential role of thermal tolerance

571   in driving extirpation and range contractions at the trailing edge (Sunday *et al.*, 2012; Cahill *et al.*, 2014;

572   Hardy *et al.*, 2014). Depending on the management goal for a species exhibiting this pattern of warming

573   tolerance (control for *Urosalpinx*, conservation for others), this potential for local extinction and species

574   range contraction at the warm trailing edge is of critical interest and may call for resource reallocation

575   away from warm, trailing-edge populations.

576   We found strong evidence for faster developmental rates for populations sourced from warm

577   habitats, and higher developmental acclimation at 24°C resulting in overall faster growth than at 20°C

578   (Fig. 7). Warm, southern populations developed the fastest at all acclimation temperatures, as expected by

579   biogeographic theory of embryonic development rate in marine ectotherms (Lonsdale and Levinton,

580   1985; Collin, 2003; Weydmann *et al.*, 2015). Increased development rate at lower latitudes may result

581   from simple increases in metabolic rate with habitat temperature (Lonsdale and Levinton, 1985), or

582   potentially because of selection arising from heightened risk of predation in tropical low latitude systems

583   (Schemske *et al.*, 2009). Interestingly, the fastest development rate occurs at the acclimation temperature

584   (24°C) and populations (low latitude Atlantic) that had the lowest thermal tolerance, suggesting potential

585   trade-offs across life stages (Stillman, 2003). While both were highly variable, hatching success increased

586   with habitat temperature, such that warm populations develop faster and have higher survivorship, and

587   clutch size decreases with higher habitat temperature. Therefore, warm-origin populations spawn smaller

588   egg case clutches, which develop quicker, and have a greater chance of developing successfully. As

589   juveniles, these warm-origin populations show higher thermal tolerance (Fig. 5), but only at a lower

590   acclimation temperature. Additionally, the reduced number of embryos per egg case (low "embryo

591   packing") in warm populations may be a product of a tradeoff between embryo density and oxygen

592   availability within each egg case in warm waters (Lee and Strathmann, 1998; Fernández *et al.*, 2007).

593 These results indicate the potential for rapid embryonic development to result in trait performance trade-

594 offs in later life stages as a result from increased metabolic demand during embryonic growth (Van Der

595 Have, 2002; Pörtner *et al.*, 2006; Del Rio *et al.*, 2019). If development rate is maximized at each

596 acclimation temperature, then enzymatic activity may itself be maximally efficient at these temperatures,

597 and thermal tolerance is reduced due to inefficient enzymatic reactions at elevated temperatures (Somero,

598 1995; Van Der Have, 2002) . One caveat of our findings is that we quantified embryonic performance in

599 July in order to synchronize experimental treatments. It is possible that the variation in hatching success

600 and clutch size may reflect phenological shifts in spawning seasons (Carriker 1955). Future efforts should

601 quantify these aspects of spawning and development across the spawning seasons in order to fully resolve

602 the potential range of intraspecific variation and plasticity in *Urosalpinx*. Our results point to the

603 mechanistic importance of early life stage experiences on trait performance and tradeoffs in subsequent

604 life stages, and the need for future research to characterize trait performance and optima across life stages

605 (Pechenik, 2006; Slotsbo *et al.*, 2016).

606 We found invasive and high latitude native *Urosalpinx* populations to be the least sensitive to

607 climate impacts based on their large warming tolerance values, suggesting that these populations will

608 persist in their environments. We acknowledge that sampling in the invasive region was limited to two

609 populations and that current data is unable to determine whether greater warming tolerance of these

610 populations is due to population genetics (e.g., founder effect or population bottleneck from introduction)

611 or due to the environment alone (i.e., a large buffer from current habitat temperatures and thermal

612 tolerance). Current efforts are underway to resolve genetic differences among populations in the native

613 and invasive range. Nonetheless, the high warming tolerance observed at the California sites is a concern

614 for native biodiversity because near term warming is likely to increase the predatory impact of *Urosalpinx*

615 on native species, including consumption of Olympia oysters (*Ostrea lurida*) that are the focus of

616 conservation and restoration efforts (Cheng *et al.*, 2017). Further, heightened development rate at greater

617 acclimation suggests that embryos will develop faster with potentially higher metabolic rates, increasing

618   the consumption of newly-hatched juveniles on oysters. From a community ecology perspective, these

619   differing climate sensitivities between *Urosalpinx* throughout native and invasive ranges demonstrates the

620   potential for indirect impacts of climate change on native biodiversity. Interactions between *Urosalpinx,*

621   climate, and humans highlights "trophic skew", the reorganization of biological communities with species

622   loss from extinction and species gain from invasion (Grosholz, 2002; Duffy, 2003; Byrnes *et al.*, 2007).

623   As marine environments warm, native species will experience both abiotic pressure from warming as well

624   as pressure from the persistence and proliferation of invasive, warm-origin predators like *Urosalpinx*

625   (Cheng and Grosholz, 2016). Early eradication and control of these resilient invasive predators may assist

626   native species by removing a biotic pressure as natives adapt or migrate in the face of climate change,

627   thereby potentially reducing of trophic skewness (Byrnes *et al.*, 2007; Grosholz and Ruiz, 2009; Cheng *et*

628   *al.*, 2017).

629   In conclusion, our work demonstrates the importance of taking an intraspecific approach to

630   examining thermal performance and sensitivity to climate. Such variation can have large implications for

631   forecasts of species responses to climate change that often assume homogeneity across populations,

632   thereby missing the possibility of more resilient populations under climate change. We found largely

633   negative effects of developmental acclimation on thermal tolerance, a crucial consideration given that

634   climate change occurs across temporal scales (e.g. seasons) and will result in biological effects both

635   within and across life stages. We also show that integrating environmental data can provide a more

636   complete picture of population-level sensitivity that may drive geographic range contractions. Taken

637   together, this approach can be useful for developing an understanding of climate impacts on populations

638   across their native and invasive ranges. Such a perspective is useful for clarifying potential interactions

639   between climate and biological invasions that can erode native biodiversity. The variation in thermal

640   physiology we demonstrate here supports the necessity of using data from multiple populations when

641   making ecological forecasts of climate change.

642   **Funding**

31

650 **Acknowledgements**

656

657

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