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Trophic sensitivity of invasive predator and native prey interactions: integrating environmental context and climate change

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Summary

1. Climate change is predicted to intensify the impacts of invasive species by enhancing their performance relative to their native counterparts. However, few studies have compared the performance of invasive predators and native prey, despite the fact that non-native predators are well known to disrupt native communities.

2. The 'trophic sensitivity hypothesis' suggests that predators are less tolerant of increasing environmental stress than their prey, whereas the 'tolerant invaders hypothesis' suggests that invaders are more tolerant than native species due to selection during the introduction process. It is therefore unclear how invasive predators will respond to increasing climate stressors.

3. We coupled physiological measurements (thermal tolerance, thermal optima, salinity tolerance, predation rate) with environmental time-series data to assess the effects of warming and extreme low salinity events on non-native predators (gastropods) and native prey (oysters) from a coastal ecosystem.

4. In general support of the trophic sensitivity hypothesis, we found that both non-native predators exhibited lower thermal optima relative to native prey, lower salinity tolerance and one predator was less tolerant of warming. However, because warming tolerance was extremely high (i.e. habitat temperature is 7·9–21 °C below thermal tolerance), near-term warming may first increase predator performance (consumption and growth rates), with negative effects on prey. Low salinity will likely produce heterogeneous effects on predator–prey interactions due to varying watershed sizes among estuaries that control the duration of low salinity events.

5. The trophic sensitivity hypothesis may be a useful framework for understanding community responses to extreme climate change, which portends a decoupling of predator–prey interactions. However, we conclude that this hypothesis must be evaluated in environmental context and that coupling physiological metrics with *in situ* environmental data offers the best predictive power of near-term climate change impacts on invaded communities. Within our study system, warming is likely to intensify the impacts of both invasive predators, which may greatly reduce the abundance of the native oyster, a species of conservation and restoration focus.

Key-words: climate change, invasion, predator–prey, salinity, thermal optima, thermal performance curve, thermal safety margin, warming tolerance

Introduction

Climate change is predicted to increase the impacts of many invasive species by facilitating the introduction of new invaders or by favouring already established non-native species (Dukes & Mooney 1999; Stachowicz *et al.* 2002; Rahel & Olden 2008; Diez *et al.* 2012). For example, invaders may be more tolerant of warming, drought, desiccation and ocean acidification than their native counterparts, potentially leading to competitive dominance by invaders under changing environmental conditions (Chown

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et al. 2007; Lenz *et al.* 2011; Bates *et al.* 2013; Sorte *et al.* 2013). However, this understanding of climate change effects on native and introduced species is largely based on comparisons of closely related, functionally similar or competing species (e.g. Chown *et al.* 2007; Sorte *et al.* 2013). Few studies have evaluated the climate change responses of non-native predators and their native prey, despite the well-known impacts of invasive predators on native biodiversity and ecosystem function (e.g. Blackburn *et al.* 2004; Croll *et al.* 2005). In addition, experiments typically evaluate the effect of one stressor on species interactions, although climate change generally involves multiple physical drivers that can produce nonlinear and complex effects on species responses (Bonebrake & Mastrandrea 2010; Todgham & Stillman 2013; Cheng *et al.* 2015). Accurately predicting the impacts of climate change and species invasions requires an understanding of how multiple climate change drivers influence the physiology of individual species as well as the interactions among them.

Predators may be more sensitive to changing environmental conditions than their prey, a concept we refer to as the 'trophic sensitivity hypothesis' (Petchey *et al.* 1999; Voigt *et al.* 2003; Vasseur & McCann 2005). Trophic sensitivity may arise if predators are more mobile than prey and respond to environmental stressors via emigration rather than by evolving tolerance of environmental stress (Menge & Sutherland 1987). In contrast, prey (particularly sessile species) may have limited behavioural mechanisms to cope with stress and may evolve greater tolerance via biochemical adaptation (e.g. Petes *et al.* 2008). Predators also generally exhibit greater body size and lower abundance, which may decrease population persistence in response to increasing environmental stress (Purvis *et al.* 2000). In addition, climate change may differentially affect predator and prey trait performance, which will alter their subsequent interactions (Kordas, Harley & O'Connor 2011; Dell, Pawar & Savage 2014). For example, predator body velocities (e.g. attack or strike speeds) exhibit lower thermal optima (T_{opt} – temperature at which a trait is maximized) relative to herbivore body velocities (e.g. avoidance or escape speeds; Fig. 1a). If warming moves current habitat temperature (Fig. 1a, T_{hab0}) to a new state (T_{hab1}) and closer to predator T_{opt}, then encounter and predation rates could increase due to an enhanced predator performance relative to their prey (Fig. 1a; Öhlund *et al.* 2015). In contrast, if warming moves current temperature (T_{hab0}) to a more extreme condition (T_{hab2}) and beyond predator T_{opt}, encounter and predation rates could diminish due to the decreased predator and increased prey performance (Fig. 1a; Englund *et al.* 2011; Grigaltchik, Ward & Seebacher 2012). Both of these scenarios represent 'trophic sensitivity' because predator thermal optima (or tolerance) are lower than prey optima and they highlight the importance of linking the current and forecast environmental conditions to organismal physiology.

In contrast to trophic sensitivity, invasive predators may have greater thermal optima than their prey if the process of invasion selects for environmentally tolerant and plastic species (Davidson, Jennions & Nicotra 2011; Bates *et al.* 2013; Sorte *et al.* 2013). We refer to this case as the 'tolerant invaders hypothesis' (Fig. 1b). To date, no study has investigated the trophic sensitivity and tolerant invaders hypotheses in a naturally occurring predator–prey system.

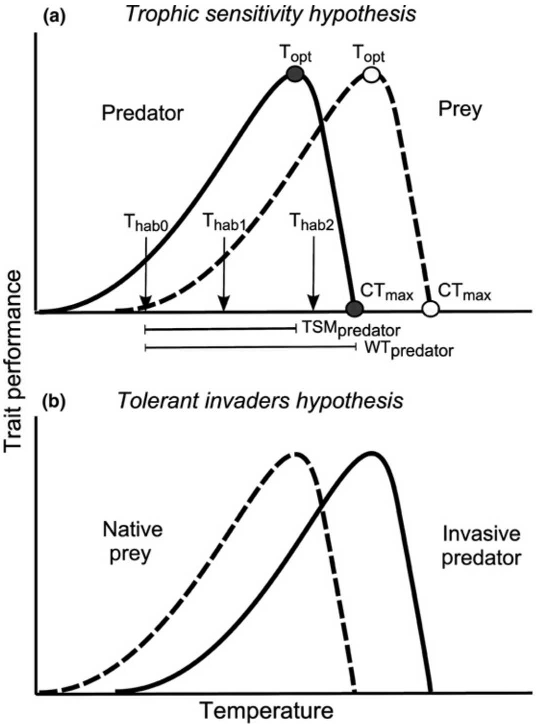


Fig. 1. Conceptual diagram of trait performance (e.g. growth rate) across temperature. (a) The 'trophic sensitivity hypothesis' predicts that predators are less tolerant of increasing stress than their prey. Thermal optima (T_{opt}) represent the temperature at which a trait is maximized. Critical thermal maximum ($\mathrm{CT}_{\mathrm{max}}$) is the maximum temperature tolerance. T_{hab} is a measure of habitat temperature (e.g. median), represented here as single points for clarity, but is often variable in nature. Thermal safety margin (TSM) is $T_{\mathrm{opt}}-T_{\mathrm{hab}}$ and warming tolerance (WT) is $\mathrm{CT}_{\mathrm{max}}-T_{\mathrm{hab}}$ (denoted for the predator given T_{hab0}). In this example, the predator (solid line, grey circles) is predicted to be less tolerant of warming than the prey (dashed line, open circles). (b) The 'tolerant invaders hypothesis' predicts that invasive predators are more tolerant of environmental stress than native prey due to selection during the process of invasion.

In order to understand how climate change may affect interacting species, common metrics are needed to compare the physiology of predator and prey. In addition to T_{opt}, metrics such as critical thermal maxima ($\mathrm{CT}_{\mathrm{max}}$ – maximum temperature tolerance; Fig. 1a) can define an organism's response to environmental drivers. These responses can be combined with *in situ* environmental data to generate new sensitivity metrics that describe a species' ability to cope with changing conditions. For example, the difference between $\mathrm{CT}_{\mathrm{max}}$ and T_{hab} is the 'warming tolerance' (WT, Fig. 1a; Deutsch *et al.* 2008). A high WT suggests that a species can withstand substantial warming before the lethal effects are observed. The difference between T_{opt} and T_{hab} is the 'thermal safety margin' (TSM, Fig. 1a; Deutsch *et al.* 2008), where positive values suggest that warming will increase organismal performance and negative values suggest a decrease in performance. Using these common indices among predators and prey (as well as invasive and native species) allows for the direct comparison of how environmental conditions may be expected to affect each species and their biotic interactions. However, to date, this approach has rarely been applied to predator–prey systems and we suggest that this may be a useful framework for using individual species responses to predict the outcome of species interactions under a changing climate.

Here, we employed this framework of linking physiological metrics to environmental data to examine the impacts of climate change on a community of interacting species. We focused on a California estuary, Tomales Bay, where native oysters are preyed on by two predatory gastropods known as oyster drills (Kimbro *et al.* 2009a). Oysters provide numerous ecosystem services such as filtration and habitat provisioning (e.g. Coen *et al.* 2007), and globally, oysters have suffered major declines due to numerous factors including invasive predators (Beck *et al.* 2011; Zu Ermgassen *et al.* 2012). First, we assessed the thermal tolerance (CT_{max}), thermal optima (T_{opt}) and salinity tolerance (S_{crit} – critical salinity; Braby & Somero 2006) of oysters and oyster drills using laboratory trials. Secondly, we integrated these metrics with environmental time-series data to derive ecologically relevant sensitivity metrics (WT – warming tolerance, TSM – thermal safety margin, and ST – salinity tolerance) that indicate each organism's potential for coping with environmental change. In addition to warming, we examined low salinity tolerance because climate change is expected to increase the frequency and severity of storms and extreme precipitation within coastal ecosystems such as California (Allan & Soden 2008; Min *et al.* 2011; Yoon *et al.* 2015). Although multiple stressors often occur simultaneously, we did not test for the combined effects of temperature and salinity in these experiments, because stressful values of low salinity and high temperatures do not co-occur in this system and are typically offset by many months in low-inflow estuaries (i.e. Mediterranean climates with warm dry summers and cool wet winters; Largier, Hollibaugh & Smith 1997; Cheng & Grosholz 2016). Our overarching goal was to understand how invasive predators and their native prey conform to predictions of the trophic sensitivity and the tolerant invaders hypotheses and to assess the current and future environmental context under which these predator–prey interactions occur in nature.

Materials and methods

We compared the trophic sensitivity and tolerant invaders hypotheses using two introduced species, the Atlantic oyster drill (*Urosalpinx cinerea*) and the Japanese oyster drill (*Ocenebra inornata*), and the native Olympia oyster (*Ostrea lurida*), which co-occur in multiple estuaries along the western coast of the United States. We collected experimental broodstock from Tomales Bay, CA, USA (38·153°, −122·909°), a Mediterranean climate estuary located approximately 50 km north-west of San Francisco Bay. For thermal trials, we acquired experimental animals by rearing juveniles of all species in the laboratory (i.e. spawning oysters and hatching oyster drills from egg capsules). We used juveniles because they exhibit high growth rates and develop during the late spring and summer when thermal stress is high. For salinity trials, we used field-collected adult oysters and oyster drills because low salinity stress in this system occurs in the winter and early spring when only adults are present. We then compared physiological metrics against time-series data collected from Tomales Bay as well as nearby San Francisco Bay. Both estuaries contain oysters and oyster drills, but contrast greatly in their extent of freshwater input. A tabular summary of the experiments and further methodological details are provided online (see Appendices S1–S5, Supporting Information).

THERMAL TOLERANCE – CT_{MAX}

To assess CT_{max}, we exposed laboratory-raised juvenile oyster drills and oysters (Appendix S2) to a thermal challenge using an aluminium heat bar (Kuo & Sanford 2009). The heat bar creates a temperature gradient with a warming element on one end and a cool water bath at the other. The heat bar accommodates 2·0-mL microcentrifuge tubes that were filled with 1·5 mL of aerated seawater and one individual of each species (Atlantic drill shell height, hereafter SH, mean SH ± SD = 8·6 ± 1·8 mm; Japanese drill mean SH ± SD = 8·7 ± 1·3 mm; oyster mean SH ± SD = 7·4 ± 1·2 mm). We tested thermal tolerance in seawater to avoid the confounding effects of desiccation under aerial heat exposure (Stillman & Somero 2000). Furthermore, these predators and prey interact within the low intertidal and subtidal zone (Cheng & Grosholz 2016), and in Tomales Bay, aerial temperatures do not deviate greatly from water temperatures (Appendix S4). Upon insertion into the heat bar, the animals were allowed to rest for 30 min after which the temperature of the warming element was increased 4 °C every 30 min for 4 h. In the fifth and final hour of the experiment, we held the temperature constant (5·5 hr of total duration where final water temperatures ranged from 18·7 to 44·9 °C; Appendix S3). After the heat ramp, individuals were transferred to aerated 18 °C seawater and assessed for mortality the following day (Appendix S2).

SALINITY TOLERANCE – S_{CRIT}

To assess S_{crit}, we exposed adult oyster drills and oysters to an osmoregulatory challenge. Individual field-collected oysters ($N = 40$, mean SH ± SD = 42·2 ± 4·2 mm), Atlantic drills ($N = 80$, mean SH ± SD = 22·2 ± 2·3 mm) and Japanese drills ($N = 50$, mean SH ± SD = 23·2 ± 4·0 mm) were acclimated in the laboratory for 14 days at 12 °C and 33 psu. All organisms were randomly assigned to one of five salinity treatments (4, 8, 12, 16 and 33 psu) in individual 1-L aerated containers in a spatially interspersed design. The animals were gradually exposed to their target salinity with daily water changes (seawater diluted with distilled water) over 5 days until they reached target salinity (Appendix S3). After 4 days of exposure to the target salinity, test organisms were brought to 16 psu for 24 h and then 33 psu. We provided animals with food and allowed them to recover for 7 days to account for delayed mortality. Each day of the trial, we assessed the survival and conducted 100% water changes.

THERMAL PERFORMANCE – T_{OPT}

To assess oyster drill growth T_{opt}, we subjected drills to six temperatures (16, 20, 24, 26, 28 and 30 °C; Appendix S2) for a 27-day growth period. The animals were held at 20 °C prior to the experiment and temperatures were ramped to reach targets over 5 days. Each temperature treatment was replicated across three aquaria (38 L) with submerged heating elements and aeration. In each tank, three oyster drills of each species were kept in 20-mL plastic tea strainers (one predator per strainer and six strainers per tank) with mesh sides (Perma Brew tea strainers, Upton Tea Imports, Hopkinton, MA, USA) for a total of 108 oyster drills (2 species × 3 individuals × 3 tank replicates × 6 temperatures = 108). We gave oyster drills an *ad libitum* supply of juvenile oysters (three to five prey oysters per predator, depending on temperature) every 3 days in conjunction with 100% water changes. Prior to the experiment, there were no differences in oyster drill sizes across temperatures (within species), but Japanese drills were slightly larger (mean SH ± SD = 4·3 ± 0·8 mm) than Atlantic drills (mean SH ± SD = 3·7 ± 1·3 mm). After the experiment, we calculated growth as $\mathrm{SH}_{\mathrm{final}} - \mathrm{SH}_{\mathrm{initial}}$.

We measured the oyster growth T_{opt} under high and low ration conditions, because oysters in Tomales Bay experience resource limitation (Kimbro, Largier & Grosholz 2009b). In the high ration experiment, oysters were housed in the same aquaria (38 L) as oyster drills described above, except that we omitted the 28 °C treatment due to the limited recruitment onto experimental tiles. Each tank housed three PVC tiles with attached oysters (10–25 individuals per tile) that we standardized to 50 oysters per tank (initial shell area, hereafter SA, mean SA ± SD = 0·04 ± 0·01 cm^2). In the low ration experiment, oysters were grown over 60 days at 16, 20, 24, 26, 28 or 30 °C treatments using the temperature-controlled water baths. Each experimental unit (2 L) contained a PVC tile with three oysters (mean initial SA ± SD = 0·4 ± 0·2 cm^2). At the beginning and end of both experiments, we photographed the oysters and measured the growth as $\mathrm{SA}_{\mathrm{final}} - \mathrm{SA}_{\mathrm{initial}}$ using image analysis software (IMAGEJ, National Institutes of Health, version 1.46, Bethesda, MD, USA). For the low ration oyster experiment, we calculated the total oyster growth from each experimental unit because there was evidence for intraspecific competition for limited food resources (oysters of larger size appeared to monopolize available phytoplankton). Because the oyster experiments differed in duration and stocking densities, we standardized the growth measurements by duration and then centred and scaled the data prior to analysis.

To estimate Atlantic drill predation T_{opt}, we housed three Atlantic drill recruits within aerated plastic containers (1 L) and exposed animals to temperature treatments identical to the previously described oyster drill growth experiment for 25 days (8 containers × 6 temperatures = 48). Oyster drills (mean SH ± SD = 6·0 ± 1·1 mm) were offered an *ad libitum* supply of oyster recruits (as above, oyster mean SA ± SD = 0·07 ± 0·02 mm). On the 22nd and 25th day of this experiment, we quantified the prey consumed over the previous 3 days by examining prey oysters for drill holes with a dissecting scope, which allows us to differentiate predation by oyster drills from handling stress. We then averaged the predation rate between the two time points and calculated a daily per capita oyster consumption rate for each temperature.

STATISTICS

For the $\mathrm{CT}_{\mathrm{max}}$ experiments, we used Firth's bias reduced logistic regression (Heinze & Schemper 2002) to model the effect of species and temperature on survival. We used this approach because the data exhibited 'complete separation'. This occurs when the values of a binary response variable are identical (e.g. $y = 1$) for all values of a predictor variable above (or below) some threshold (e.g. 30 °C) and then the opposite value (e.g. $y = 0$) for values of the predictor variable below (or above) that threshold value. This lack of overlap in values of the response variable across a continuous predictor results in 'complete separation', which complicates the estimation of model coefficients. Firth's logistic regression addresses this problem by using a penalized maximum-likelihood estimation procedure (Heinze & Schemper 2002). For the S_{crit} experiments, we used logistic regression with a binomial error distribution and logit-link function. Due to the complete separation, we treated species, temperature and salinity as additive predictors, which tests for shifts in the location of each logistic curve among species, but assumes that the shape of the curve is the same. Using model predictions, we then calculated $\mathrm{CT}_{\mathrm{max}}$ and S_{crit}, defined here as the temperature or salinity that resulted in 0·5 probability of mortality. Because of high oyster tolerance to low salinity in the 4-day trials, we extracted an oyster S_{crit} estimate from a concurrent study that exposed oysters to a broader range of low salinity exposure (1 to 8 days; Cheng *et al.* 2015). For these models, we did not evaluate overdispersion because the data modelled were in the form of zeroes and ones (i.e. binomial with one trial, Bernoulli distribution), and therefore, overdispersion cannot occur (McCullagh & Nelder 1989).

Thermal performance data are often analysed within the universal temperature dependence framework (UTD, Gillooly *et al.* 2001), which integrates enzyme kinetics and temperature to predict trait performance (e.g. metabolism, attack speed). However, evidence suggests that predator–prey interactions do not conform to UTD predictions and often exhibit hump-shaped responses (Englund *et al.* 2011; Rall *et al.* 2012). Therefore, we modelled thermal performance using temperature as linear and quadratic predictors. For the T_{opt} oyster drill growth experiment, we used linear mixed models (LMM) to assess the fixed effect of temperature and species with a random tank effect. Oysters were analysed separately from oyster drills due to differing units of growth (SH vs. SA) and differing random-effect structures. Low ration oysters were modelled with a random tank effect and high ration oysters were modelled with a random effect of tile nested within tank. Due to obvious differences in the shape of oyster growth between high and low ration experiments and because our primary interest was in extracting T_{opt}, we also modelled each oyster growth experiment separately. For all T_{opt} experiments, we evaluated temperature as a linear and second-order polynomial predictor and compared models using *F*-tests or likelihood ratio tests (LRT). For LMM, we used the Satterthwaite approximation for denominator degrees of freedom and graphically examined estimates vs. residuals and $\log_{10}$-transformed data as necessary to meet variance and normality assumptions.

ENVIRONMENTAL METRICS

We calculated WT and TSM because these metrics integrate physiological measures with environmental exposure (Deutsch *et al.* 2008). Although operative body temperatures have recently been used in ecologically realistic measures of thermal safety margins (Sunday *et al.* 2014), the organisms within our system have limited capacity to behaviourally thermoregulate. Therefore, we utilized water temperature to index thermal exposure, which is a reasonable proxy for body temperature during inundation and emersion within the low intertidal zone (i.e. $T_{\mathrm{hab}} \approx$ body temperature, Appendix S4). To provide ecological context for physiological measurements, we collected *in situ* environmental data (temperature and salinity; 15-min sample interval) at the 'Middle Bay' site, Tomales Bay, CA, from 2010 to 2013. Middle Bay is located at the seaward range boundary of both oyster drills within Tomales Bay and is a location with high oyster density (Cheng & Grosholz 2016). Data were acquired with a water-quality sonde (YSI 6920 V2, Yellow Springs, OH, USA) mounted at 0·5 m depth and within 15 m of oyster habitat. We supplemented these data with temperature time series from another site within Tomales Bay ('Inner Bay') that was collected with a thermistor deployed on the shore at 0·0 m depth (60-min sample interval). Inner Bay is a useful site to compare with Middle Bay because of thermal gradients that occur along the axis of Tomales Bay and because both sites bookend the spatial extent of predator–prey interactions (Cheng & Grosholz 2016). We calculated WT and TSM using CT_{max}, T_{opt} and the median, 95th and 99th percentile of May–August temperatures at both sites because oyster drills appear to cease feeding and burrow during the winter (B. Cheng, personal observation).

Our physiological data showed a substantial effect of low salinity duration and magnitude that differed among organisms; therefore, we examined salinity time series from Tomales Bay as well as China Camp State Park, San Francisco Bay (2006–2013; National Estuarine Research Reserve System, NERRS). We chose to compare Tomales Bay to China Camp, San Francisco Bay, for several reasons. Environmental data have been collected at this site by the NERRS since 2006, creating one of the most robust time-series data sets in the region. San Francisco Bay also drains a watershed much larger than Tomales Bay, which suggests that low salinity events could be more frequent and extreme. China Camp also contains significant oyster populations, but has not yet been invaded by oyster drills, although Atlantic drills are established nearby in Richardson Bay (12 km south of China Camp). To evaluate salinity exposure, we examined the prevalence of lethal low salinity events by quantifying the length of time (continuous days) that an event remained below a given salinity threshold value (Cheng *et al.* 2015). This approach was necessary because low salinity exposure elicits threshold organismal responses that are a function of both low salinity magnitude and duration (Cheng *et al.* 2015). All analyses and graphs were conducted in R (R Core Team 2016) with the packages: 'ggplot2', 'lme4', 'lmerTest', 'logistf', 'piecewiseSEM' and 'pROC'.

Results

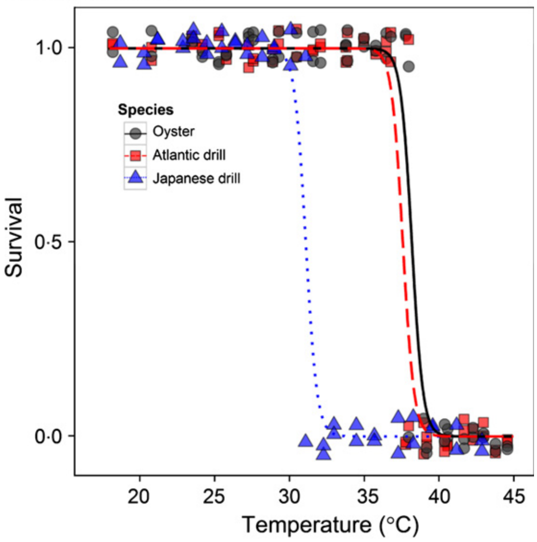
THERMAL TOLERANCE – CT_{MAX}

At the highest temperatures tested, survival decreased for all species (Fig. 2a; Table 1). Japanese oyster drills were least tolerant of warming (CT_{max} = 31·1 °C; Table 1), whereas Atlantic oyster drills and Olympia oysters were more tolerant (CT_{max} = 37·6 °C, 38·2 °C, respectively). There was no statistical difference between Atlantic oyster drill and oyster CT_{max} (Fig. 2a; Table 1).

SALINITY TOLERANCE – S_{CRIT}

Low salinity exposure of 4 days resulted in an increased mortality for all species, but oyster drills were more sensitive than oysters (Fig. 2b). Atlantic drills experienced mortality beginning at a salinity of 12 psu with an estimated $S_{crit(4d)}$ = 7·5 psu (Fig. 2b, Table 1). Japanese drills also began to experience mortality at 12 psu with an estimated $S_{crit(4d)}$ = 10·9 psu (Fig. 2b, Table 1). Oysters exhibited slightly increased mortality at low salinity (Fig. 2b, Table 1), but only 2 of 40 oysters perished in this experiment (one individual at 4 and 8 psu each). Because of this high survival, we extracted tolerance estimates from another experiment over a broader low salinity duration (>2000 oysters tested from 1 to 8 days; Cheng *et al.* 2015), which estimates an S_{crit} of 6·3 psu for 8 days. We also provide oyster drill S_{crit} measurements for 1- and 2-day low salinity exposures (Appendix S5).

(a) *Thermal tolerance*



(b) *Salinity tolerance*

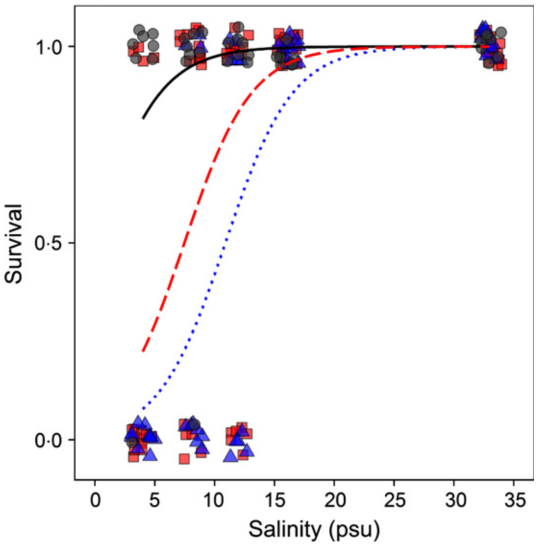


Fig. 2. Organismal tolerance to (a) high temperature and (b) low salinity. Data points are plotted as 1 (survival) or 0 (mortality) for oysters (grey circles, solid line), Atlantic drills (red squares, long dash line) and Japanese drills (blue triangles, dotted line). Each point represents an individual experimental animal with a slight random jitter applied for clarity. For thermal tolerance, data exhibited the complete separation, where temperature perfectly discriminates survival (see text for further explanation). For the salinity tolerance experiment, only two oysters perished (at 4 and 8 psu).

THERMAL PERFORMANCE – T_{OPT}

Thermal performance varied greatly by species (Fig. 3, Table 1). Both Atlantic and Japanese drills exhibited a

Table 1. Statistical results from experiments testing thermal/salinity tolerance and thermal performance. Each experimental analysis is denoted in boldface with the extracted physiological metric in parentheses. Parameter estimates represent slopes and intercepts (i.e. betas) from analyses. For analyses with multiple predictors, the additional slope/intercept terms are in relation to the reference group within each analysis. We report goodness-of-fit metrics, except for the thermal tolerance data that are perfectly discriminated by temperature (i.e. they exhibit complete separation). R^2_{GLMM} is given as marginal/conditional R^2, which estimate model explanatory power due to fixed effects alone and fixed and random effects combined, respectively (Nakagawa & Schielzeth 2013)

Parameter	Estimate	SE	Test statistic*	*P*
Thermal tolerance (CT_{max})				
Oyster (reference)	102·5	33·68	>100	<0·001
Temperature	−2·683	0·883	>100	<0·001
Atlantic drill	−1·618	1·371	1·55	0·213
Japanese drill	−19·03	6·396	51·8	<0·001
Salinity tolerance (S_{crit})				
Oyster (reference)	0·067	0·851	0·079	0·937
Salinity	0·357	0·067	5·326	<0·001
Atlantic drill	−2·731	0·851	−3·211	0·001
Japanese drill	−3·955	0·927	−4·265	<0·001
ROC Area Under Curve – 0·91				
Oyster drill (high ration T_{opt})†				
Atlantic drill (reference)	4·016	0·137	29·39	<0·001
Temperature	9·009	1·277	7·058	<0·001
Temperature^2	−4·268	1·281	−3·331	0·002
Japanese drill	−1·381	0·185	−7·454	<0·001
Japanese drill * Temperature	−14·92	1·773	−8·416	<0·001
Japanese drill * Temperature^2	−4·562	1·776	−2·570	0·012
R^2_{GLMM} – 0·65/0·66				
Oyster (high ration T_{opt})				
Intercept	−2·769	0·621	−4·461	<0·001
Temperature	0·125	0·026	4·747	<0·001
R^2_{GLMM} – 0·31/0·53				
Oyster (low ration T_{opt})†				
Intercept (reference)	0·000	0·123	0·000	1·000
Temperature	−3·308	0·853	−3·876	<0·001
Temperature^2	−1·814	0·853	−2·126	0·039
Adjusted R^2 – 0·27				
Atlantic oyster drill (predation T_{opt})†				
Intercept (reference)	1·947	0·091	21·28	<0·001
Temperature	4·436	0·634	6·996	<0·001
Temperature^2	−1·674	0·634	−2·640	0·011
Adjusted R^2 – 0·68				

*Test statistics are as follows: χ^2 (thermal tolerance), *Z* (salinity tolerance), *t* (oyster drill and oyster thermal performance and Atlantic oyster drill predation rate).

†Model contains a second-order polynomial predictor.

thermal response with parabolic shape (Fig. 3a) and were best fit by a second-order polynomial function (Table 1; LRT; χ^2 = 32·6, d.f. = 2, P < 0·001). Based on model estimates, Japanese oyster drills had a lower growth T_{opt} than Atlantic oyster drills (T_{opt} = 21·4 vs. 26·5 °C, respectively). Oyster T_{opt} depended on available food ration. In the high ration experiment, the selected temperatures only encapsulated the rising region of thermal response and their growth model fit was not improved with a polynomial model (LRT; χ^2 = 0·09, d.f. = 1, P = 0·758). Therefore, we fit native oyster growth with a linear model, which estimated the maximum growth at the highest temperature tested (Fig. 3b, Table 1, $T_{opt} \geq$ 30·0 °C). In contrast, oyster T_{opt} under low food ration was best fit by a quadratic model (LRT; χ^2 = 3·98, d.f. = 1, P = 0·046; Table 1). Oyster T_{opt} was reduced under low rations (Fig. 3b, Table 1, T_{opt} = 19·3 °C). Atlantic oyster drill predation rates exhibited a parabolic shape where consumption increased with warming until a slight decline at high temperatures (Fig. 5). Data were $\log_{10}$-transformed and best fit by a quadratic function (Table 1; *F*-test, F_1 = 23·0, P < 0·001), which estimated an Atlantic drill predation T_{opt} of 26·7 °C, near the previously estimated growth T_{opt} of 26·5 °C.

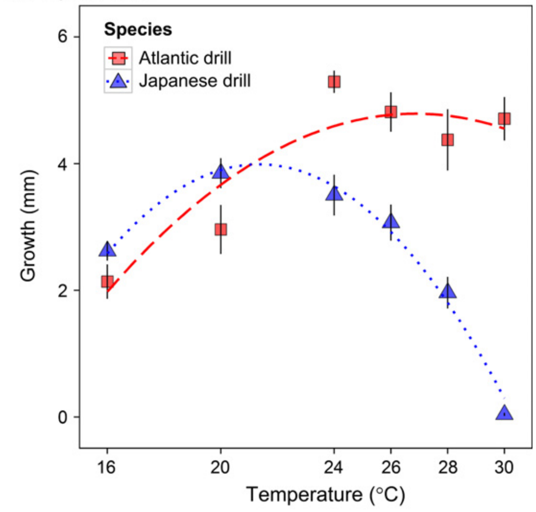
ENVIRONMENTAL METRICS

Median, 95th and 99th percentile of T_{hab} at Tomales Middle Bay was 16·6, 19·3 and 20·2 °C, respectively. The Tomales Inner Bay site was warmer and median, 95th and 99th percentile of T_{hab} was recorded at 18·8, 21·7 and 23·7 °C, respectively. These temperatures resulted in positive WT ($CT_{max} - T_{hab}$) for all species across all quantiles (Table 2, Fig. 4a). TSM ($T_{opt} - T_{hab}$) estimates were positive for all species and quantiles at both sites except for Japanese drills at the Inner Bay site for the 95th and 99th percentile of water temperature (Table 2, Fig. 4a).

Environmental time-series data indicate that within Tomales Bay, salinity events were insufficient to result in mortality for all species (Fig. 4b). In contrast, salinity time series from San Francisco Bay (China Camp) revealed extreme low salinities of sufficient duration and magnitude to result in Atlantic and Japanese drill mortality (Fig. 4b; points well above oyster drill S_{crit}), whereas oyster salinity tolerance is approached, but not exceeded (Fig. 4b).

Discussion

It has been proposed that climate change may intensify the effects of many non-native species (Dukes & Mooney 1999; Rahel & Olden 2008), but most studies of climate change impacts comparing native and invasive species have focused on competitors or closely related species (e.g. Bates *et al.* 2013; Sorte *et al.* 2013). Here, we utilize physiological tools in the context of *in situ* environmental data to demonstrate that invasive predators in this system are generally less tolerant of environmental stress. Predators exhibited lower salinity tolerance and lower thermal tolerance (for one predator) than prey (Fig. 2). Under high resource availability, predators also responded with a lower T_{opt} (Fig. 3). Our results provide partial support for the 'trophic sensitivity hypothesis', which proposes that higher trophic levels are more sensitive and less tolerant of environmental change than lower trophic levels (Fig. 1a, Petchey *et al.* 1999; Voigt *et al.* 2003). Although many invasive competitors exhibit greater tolerance than their


(a) *Oyster drills*

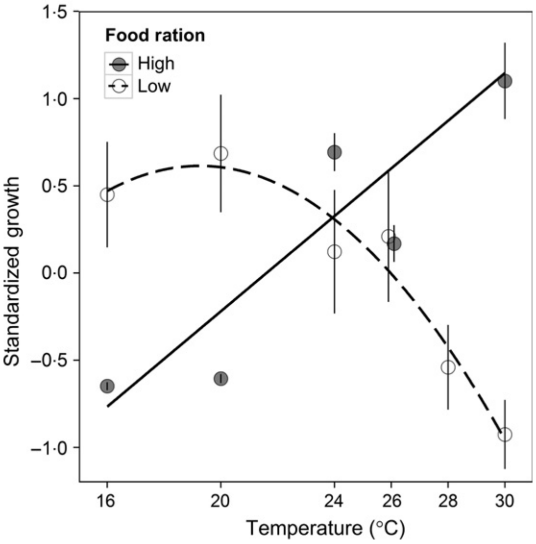

(b) *Oyster*

Fig. 3. Thermal performance curves for (a) oyster drills (high ration only) and (b) oysters under high and low rations. Data points are mean shell growth ± SE. Oyster growth data are standardized by experimental duration and then centred and scaled.

native counterparts (Bates *et al.* 2013; Sorte *et al.* 2013), invasive predators may not be more tolerant than native prey. Additional information is needed to resolve the potential for systematic differences in physiology among invasive and native species and how this relates to trophic position. Our work highlights the importance of contextualizing physiological metrics with current and forecasted environmental conditions to understand climate change impacts on biological communities. For example, if predators are generally found to be less tolerant of environmental stress than their prey, this would have different implications for species currently inhabiting ecosystems closer to their thermal limits (i.e. predators may be at greater risk in some habitats, but have a significant thermal buffer in other habitats; Deutsch *et al.* 2008; Sunday *et al.* 2014; Vasseur *et al.* 2014).

Upon first inspection, support for the 'trophic sensitivity hypothesis' would appear to indicate that warming and low salinity events may attenuate invasive predator impacts by reducing the predator survival and performance. However, we suggest that climate change may first intensify the impacts of these non-native predators for several reasons. First, temperature data reveal that WT ($\mathrm{CT}_{\mathrm{max}} - T_{\mathrm{hab}}$) is positive and high among all species (Table 2, Fig. 4a; consistent with other mid-latitude ectotherms; Deutsch *et al.* 2008), suggesting that lethal responses in predators will require exceptionally extreme heating events, which are unlikely in the near future (IPCC 2014). In contrast, TSM ($T_{\mathrm{opt}} - T_{\mathrm{hab}}$) data reveal that near-term warming may enhance the growth and consumption of both oyster drills, increasing their predatory impacts on native oysters (Table 2, Figs 3 and 5). Two negative TSMs (indicating the decreased performance under warming) are noted for Japanese drills at the Inner Bay site (Table 2). However, the presence of Atlantic drills with greater tolerance suggests a degree of redundancy in non-native impacts. Finally, although oyster drills are less tolerant of low salinity than oysters, time-series data indicate that low salinity events sufficient to result in oyster drill mortality have yet to be recorded within Tomales Bay (Fig. 4b), supported by the observation that Tomales Bay sites nearest to freshwater input actually exhibit the greatest oyster drill abundance and highest rates of oyster mortality from predation (Cheng & Grosholz 2016).

The mechanism for trophic sensitivity remains unknown, but could be related to one or several contributing factors. Predators may be less tolerant of environmental stress if they exhibit greater mobility than their prey, thus relying upon behavioural responses (e.g. emigration or sheltering) to manage their microclimate (Menge & Sutherland 1987). In nature, oyster drills could exhibit small movements in response to thermally stratified or brackish waters that reside on top of dense seawater. In contrast, particularly when sessile, prey may possess limited behavioural mechanisms to deal with stress and may rely upon biochemical adaptations to a greater extent than their predators (e.g. heat shock response, metabolic depression; Petes *et al.* 2008; Pörtner & Farrell 2008). Additionally, environmental change (e.g. warming) can affect the relative balance between acquiring and losing energy. Ectotherm consumption rates generally increase with warming to match greater metabolic rates. However, predator metabolic rates tend to be more sensitive to warming than ingestion rates, leading to decreased energetic efficiency and eventually starvation, even under resource-rich conditions (Vucic-Pestic *et al.* 2011; Iles 2014). If predator efficiency peaks at lower temperatures relative to prey efficiency, this could drive the decreased predator performance predicted by the trophic sensitivity hypothesis (as is seen for predator vs. prey body velocity; Dell, Pawar & Savage 2014). However, the relative energetic efficiency of predators and prey across temperatures has yet to be tested and could provide further insight into a mechanism for trophic sensitivity.

Table 2. Warming tolerances (WT; $CT_{max} - T_{hab}$) and thermal safety margins (TSM; $T_{opt} - T_{hab}$) for invasive oyster drills and native oysters. Positive WT is indicative of thermal buffer before lethal temperatures are reached. Positive TSM indicates that warming will result in an increased organismal performance, whereas negative TSM indicates the decreased performance. Metrics are calculated using several estimates of thermal exposure (median, 95th, 99th percentile) at two sites within Tomales Bay from May to August 2012. The Middle Bay and Inner Bay sites encapsulate the geographic extent over which oyster drills and oysters interact within this estuary. Middle Bay has few oyster drills, but many oysters. In contrast, Inner Bay has many oyster drills, but few oysters (Cheng & Grosholz 2016). Atlantic drill = *Urosalpinx cinerea*, Japanese drill = *Ocenebra inornata*, Olympia oyster = *Ostrea lurida*. Negative values are in boldface.

	Warming tolerance			Thermal safety margin		
Site/Species	Median	95th percentile	99th percentile	Median	95th percentile	99th percentile
Middle Bay						
Atlantic drill	21·0	18·3	17·4	9·9	7·2	6·3
Japanese drill	14·5	11·8	10·9	4·8	2·1	1·2
Oyster	21·6	18·9	18·0	13·4	10·7	9·8
Inner Bay						
Atlantic drill	18·9	15·9	14·4	7·8	4·8	3·3
Japanese drill	12·4	9·4	7·9	2·7	**−0·3**	**−1·8**
Oyster	19·5	16·5	15·0	11·3	8·3	6·8

Generalizing the results of climate change experiments on individual as well as interacting species will require knowledge of how organisms are resource limited in nature. High resource availability can completely offset the effects of environmental stressors (e.g. Thomsen *et al.* 2013), whereas reduced resource availability is expected to shift T_{opt} to lower temperatures, so that the acquisition of resources is in line with the metabolic expenditure of energy (Brett, Shelbourn & Shoop 1969). This point is demonstrated by the greater oyster T_{opt} in resource-rich conditions and reduced T_{opt} under resource limitation (Fig. 3b). In the inner region of Tomales Bay, water temperatures are highest (likely driving higher metabolic rates) and phytoplankton productivity is diminished due to the reduced nutrient concentrations, which results in lower oyster growth as compared to the cooler (Middle Bay) region that exhibits higher phytoplankton availability and higher oyster growth (Kimbro, Largier & Grosholz 2009b). This pattern is maintained by the interaction of tidal flows with upwelling-driven nutrient supply (Hearn & Largier 1997), where warm Inner Bay waters are not recharged with nutrient-rich coastal upwelled water. In contrast, it is unknown whether oyster drills are resource limited. Oyster drills are generalists that can feed upon a variety of prey (e.g. oysters, barnacles and mussels; Carriker 1955), suggesting that they are capable of prey switching if the preferred resources are unavailable. Therefore, it is possible that warming may ultimately have negative effects on resource-limited oysters by increasing metabolic costs, decreasing energetic efficiency and increasing predation rates by oyster drills.

Climate change is expected to increase the variability of precipitation with the subsequent impacts on the salinity regime within estuaries (Min *et al.* 2011; Yoon *et al.* 2015). Our data highlight the potential for regional-scale (~100–1000 km) dependence of climate change impacts on interacting species. The absence of significant low salinity events within Tomales Bay is likely due to its small watershed size (561 km^2) and suggests that low salinity may not be a potent driver of species responses within many coastal estuaries of California with smaller watersheds (e.g. Elkhorn Slough, San Diego Bay, etc.). By comparison, San Francisco Bay drains almost 40% of the state of California (~153 000 km^2; Conomos, Smith & Gartner 1985) resulting in pronounced low salinity events that likely prevents oyster drills from invading north San Francisco Bay (Fig. 4b). Atlantic oyster drills can be abundant in the high salinity central and south San Francisco Bay, which are less influenced by river inputs (Conomos, Smith & Gartner 1985). Thus, extreme but periodic low salinity events could mitigate invader impacts in San Francisco Bay by excluding oyster drills. In contrast, we suspect that warming will be the dominant driver of oyster drill and oyster interactions in Tomales Bay as a result of limited freshwater input. This complex spatial component of species responses to climate change reveals the importance of evaluating the effects of multiple climate drivers on interacting species within the context of their environments.

Adapting a standardized, comparative approach across species that interact ecologically provides a framework to compare the relative species responses under current and future environmental conditions. For future studies utilizing this approach, it may be most appropriate to modify experimental conditions or physiological response metrics to match the ecology of the system. The measurement of multiple traits to assess physiological performance can also provide independent confirmation of metric robustness, such as the case with the consistent Atlantic drill T_{opt} for growth and predation rate observed in this study. It is important to note that other biological processes, such as acclimation and ontogeny, can influence CT_{max}, T_{opt} and must be considered when using laboratory results to reach an ecological interpretation (e.g. Schulte, Healy & Fangue 2011; Komoroske *et al.* 2014, Seebacher, White & Franklin 2015). For example, we exposed animals to thermal stress while fully submerged in seawater. For organisms that occupy both subtidal and intertidal habitat, testing thermal stress in water avoids the confounding effects of

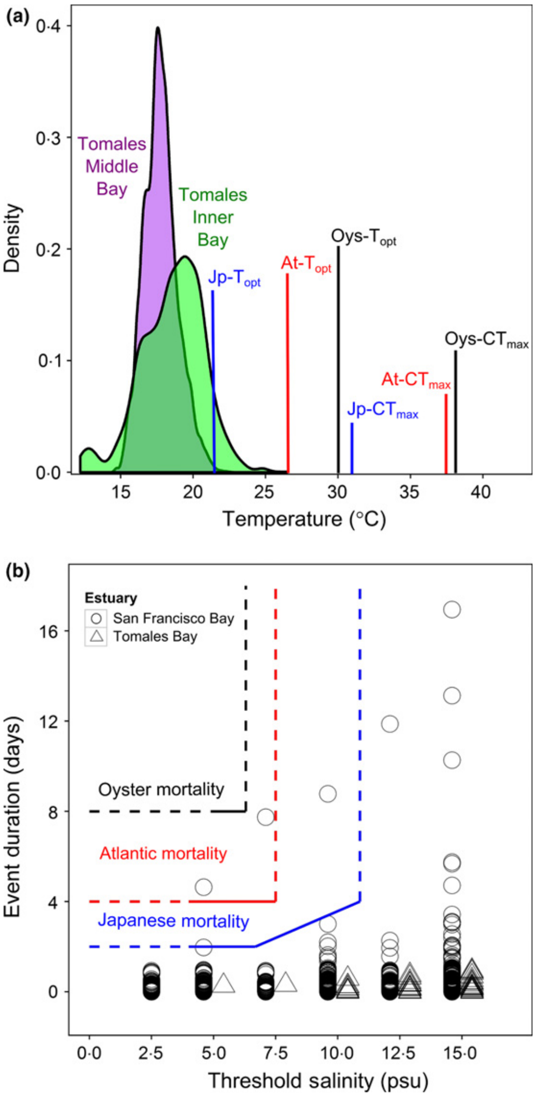


Fig. 4. The integration of physiological metrics with temperature and salinity time-series data. T_{opt} is calculated from growth experiments, whereas CT_{max} and S_{crit} are calculated from tolerance experiments. (a) Summer (May–August) temperatures (probability density functions) from two sites within Tomales Bay. The Middle Bay site is located 12 km from the mouth of the estuary and is a site with high oyster abundance, but low oyster drill density. The Inner Bay site is located 17 km from the mouth of the estuary and is a site with low oyster abundance, but high oyster drill density (Cheng & Grosholz 2016). Predator and prey T_{opt} and CT_{max} overlaid for a visualization of thermal safety margins and warming tolerances. (b) Salinity tolerance is a function of both magnitude and duration of exposure. Therefore, we index salinity exposure in Tomales Bay and San Francisco Bay using the number of continuous days (y-axis) below a threshold salinity (x-axis). Estimates of S_{crit} are represented for each species with solid lines (data from this study) and dashed lines (approximate). For example, if an oyster died at 5 psu for an 8-day exposure, we assume that the same would occur at 5 psu for 15 days. However, we note that an S_{crit} measured at longer exposure may be at a higher salinity (e.g. S_{crit} = 12·0 psu for oysters exposed for 15 days). Jp, Japanese drill; At, Atlantic drill; Oys, Olympia oyster.

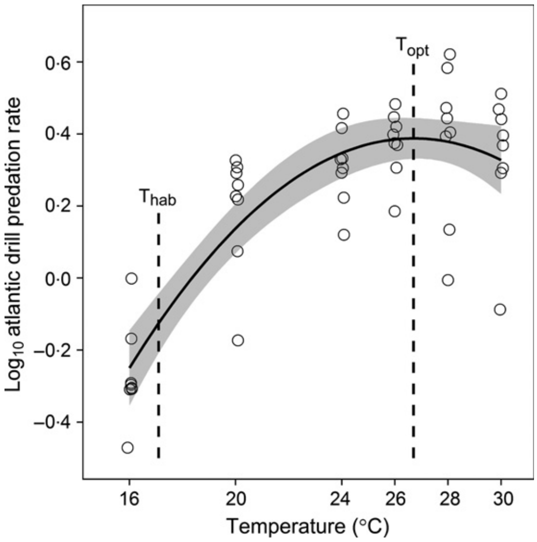


Fig. 5. Atlantic drill predation rate (daily per capita) on oysters across temperature. Model estimate is a second-order polynomial and shaded region refers to 95% CI. T_{hab} is median summer temperature from the Middle Bay site within Tomales Bay. T_{opt} is the temperature at which Atlantic oyster drill predation in laboratory experiments was greatest. Slight random jitter applied for clarity.

desiccation stress and is relevant to the habitat that they occupy (Stillman & Somero 2000). However, testing thermal tolerance and performance in water and air may be important for species that inhabit the high intertidal zone (Yamane & Gilman 2009; Bjelde & Todgham 2013). Environmental variation in stressors may also alter physiological metrics, such as the case with oscillating temperature regimes that can increase performance relative to constant temperatures (Niehaus *et al.* 2012), or in some cases, decrease CT_{max} and T_{opt}, thereby reducing WT and TSM (Paaijmans *et al.* 2013). Variation can also alter the outcome of multiple stressor experiments. Warming is expected to intensify the negative effects of hypoxia in ectotherms (Vaquer-Sunyer & Duarte 2011), but when hypoxia is variable (i.e. diel cycling), warming can offset hypoxia effects (Cheng *et al.* 2015). Integrating such complexity of environmental variation is a next step in advancing our understanding of climate change effects on organismal physiology and community responses.

The comparative physiology framework has long emphasized the study of congeners or confamilial species in order to understand the mechanisms underlying adaptation to past and future change (Prosser 1950). Frequently, congeners or confamilial species do not interact, but are found in different habitats or along biogeographic transitions. Yet, a key challenge to clarifying the impacts of climate change on biological communities is determining how changing environmental conditions will alter biotic interactions (Tylianakis *et al.* 2008; Kiers *et al.* 2010). Adapting comparative physiological approaches into an ecological framework may have great utility in addressing questions regarding sets of interacting species that are unrelated phylogenetically, but are linked ecologically (e.g. predator/prey, parasite/host, mutualists). If proved to be general, trophic sensitivity may underlie the broad-scale response of communities to climate change and suggests that an ultimate effect of stress may be to decouple food web interactions (Winder & Schindler 2004; Voigt, Perner & Jones 2007). However, additional comparisons of interacting predator and prey pairs are needed to evaluate the validity of the trophic sensitivity hypothesis. Furthermore, this hypothesis must be evaluated within environmental context, with knowledge of organismal 'buffer' (e.g. WT or TSM), which can mediate the degree to which consumer interactions are intensified or reduced. Our work suggests that non-native predators may conform to predictions of trophic sensitivity, which indicates that invasive predator effects may be mitigated by extreme climate change (i.e. heat waves, extreme low salinity events). However, near-term climate change (e.g. warming) may first intensify predator effects and potentially increase prey stress if they are resource limited. Physiological metrics that integrate long-term environmental data present a useful approach for understanding the impacts of non-native species, especially when considering the complex interplay of multiple climate change drivers and their relation to species interactions.

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Data accessibility

Data deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.jb85f (Cheng, Komoroske & Grosholz 2016). Environmental time-series data from China Camp State Park are publicly available through the National Estuarine Research Reserve System (http://cdmo.baruch.sc.edu).

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. Summary of experiments examining predator and prey response to temperature and salinity.

Appendix S2. Field collections and recruit rearing.

Appendix S3. Time-series of experimental CT_{max} temperatures along the length of the heat bar (upper panel).

Appendix S4. Time-series of water and air temperature at the Tomales Bay inner station (Site 7 from Cheng & Grosholz 2016) from 10 April–18 August, 2012.

Appendix S5. Oyster drill salinity tolerance as a function of salinity and duration.