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Predicting climate-induced changes in population dynamics of invasive species in a marine epibenthic community

Marcy L. Cockrell [a,*], Cascade J.B. Sorte [b,1]

[a] Northeastern University Marine Science Center, 430 Nahant Road, Nahant, MA 01908, USA
[b] Bodega Marine Laboratory, University of California, Davis, P.O. Box 247, Bodega Bay, CA 94923, USA

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ABSTRACT

As climate change and invasive species, both individually and in concert, continue to elicit responses in native communities, we are challenged with finding strategies for predicting the strength of such impacts. The effects of invasive species are often determined by their abundance, and warming temperatures can alter species' demographic rates and, thus, population growth rates. Here, we combined lab experiments, field experiments and observations, and population modeling to predict the population dynamics of three marine invaders in response to climate warming. We projected population growth rate at an ambient and an increased temperature predicted by climate-change scenarios (+4 °C) for three invasive species in the epibenthic fouling community of Bodega Harbor, California, USA: the tunicates *Botrylloides violaceus* and *Botryllus schlosseri* and the bryozoan *Watersipora subtorquata*. There was a positive effect of temperature on population growth rate for *B. schlosseri*, and further analysis revealed that this predicted increase was driven by warming effects on settler growth rate and adult fecundity. Increases indicated for non-native marine fouling species are especially pertinent when considering the potential cascading effects on community composition and functioning that can result from species invasions. Our results highlight the potential for marked increases in an invasive species in response to climate change, as well as the promising role that population modeling can play in elucidating the mechanisms of such responses.

1. Introduction

Climate change and biological invasions are among the most serious threats to marine ecosystems, as they can both have dramatic impacts on the structure and function of native communities (Dukes and Mooney, 1999; Occhipinti-Ambrogi, 2007; Stachowicz et al., 2002; Vitousek et al., 1996; Walther et al., 2002). In addition, climate change may alter the effects of invasive species given the role of environmental conditions in determining demographic rates such as fecundity (Adler and HilleRisLambers, 2008), survival (Coulson et al., 2001; Oro et al., 2010), and growth (Gooding et al., 2009). Demographic shifts could lead to increases or decreases in invasive species' population sizes, which are related to their levels of success and impact (Parker et al., 1999; Strayer et al., 2006). Because climatic changes can influence demography, and these effects are likely to vary between species, we took a population-dynamics approach to predict impacts of increasing temperatures on invasive species.

There is increasing evidence that invasive species may be favored by warmer temperatures in some communities (Dijkstra et al., 2011; Dukes and Mooney, 1999; Occhipinti-Ambrogi, 2007; Sorte et al., 2010; Stachowicz et al., 2002). Population demographic methods can be effective tools both for determining the strength of climate change impacts and for understanding and managing biological invasions (Sakai et al., 2001; Walther et al., 2002). In order to accurately predict the ecological consequences of climate change, we need detailed information on the environmental sensitivity of life-history parameters and other population-intrinsic mechanisms that ultimately affect community and ecosystem-level processes.

We examined the effects of climate change on population dynamics in the marine epibenthic community of Bodega Harbor, California, USA. Epibenthic communities are composed largely of sessile invertebrate species that settle on hard substrata such as docks, pipelines, boat hulls, and natural rocky reefs. Previous studies have revealed that temperature can strongly influence the recruitment, growth, and survival rates of species in epibenthic communities (Epelbaum et al., 2009; Stachowicz et al., 2002; Yund and Stires, 2002), including the Bodega Harbor community (Sorte and Stachowicz, 2011; Sorte et al., 2010). We focused on three common species in the community: the tunicates *Botrylloides violaceus* Oka, 1927 and *Botryllus schlosseri* Pallas, 1766, and the encrusting bryozoan *Watersipora subtorquata* d'Orbigny, 1852. All three of these species are non-native to Bodega

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[*] Corresponding author at: University Of South Florida, College of Marine Science, 140 Seventh Ave South, St. Petersburg, FL 33701, USA. Tel.: +1 973 943 6121.
E-mail address: Marcy.Cockrell@gmail.com (M.L. Cockrell).
[1] Current address: University of Massachusetts, Department of Environmental, Earth and Ocean Sciences, 100 Morrissey Boulevard, Boston, MA 02125-3393, USA.

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Harbor, with *B. schlosseri* introduced prior to, and *B. violaceus* and *W. subtorquata* introduced since, the year 1970 (Boyd, 1972). Bodega Harbor has experienced increases in both water temperature and abundance of invasive species over the past ~35 years, and the community currently is comprised of ~70% invasive species (Sorte and Stachowicz, 2011; Sorte et al., 2010).

We addressed the effects of increased temperature associated with climate change on these three invasive species by developing stage-structured population models to project population growth rate at ambient and increased water temperatures. We defined three life stages (settler, recruit, and adult; Fig. 1) and used field and laboratory experiments and field observations to calculate stage-transition probabilities and parameterize population models (one for each species at each temperature). In addition, to examine the mechanisms of our predicted responses to climate warming, we conducted a life table response analysis (Caswell, 2001; also see Boyce et al., 2006) and quantified the contribution of each life stage and demographic process to the projected differences in population growth rates between temperatures. Our results indicate likely species-specific shifts in population dynamics in this system under warming, in addition to highlighting stage-structured population modeling as a tool for examining the responses (and potential underlying mechanisms) of invasive populations to climate change.

2. Materials and methods

2.1. Experimental design

We projected population growth for three common species in the epibenthic fouling community of Bodega Harbor, California, at two water temperatures: (1) 13.8 °C, the approximate ambient temperature in the Harbor when the experiment was performed in July and August 2009 (Sorte and Stachowicz, 2011), and (2) 17.8 °C, equivalent to a 4.0 °C temperature increase, which represents an upper estimate of likely ocean warming by the year 2100 according to A1B scenario predictions presented by the Intergovernmental Panel on Climate Change (IPCC, 2007). We did this by: (1) performing a laboratory mesocosm experiment to determine survival and growth of the three species at 13.8 °C and 17.8 °C, (2) parameterizing a population model based on results of the mesocosm experiment, supplemented with data from field observations and experiments (as presented in Sorte and Stachowicz, 2011), and (3) using the population model to calculate population growth rate at each temperature. Finally, we (4) used a life table response analysis to determine the contribution of each stage transition to the temperature effect on population growth rate.

2.2. Temperature effects on demographic rates

A laboratory mesocosm experiment was used to determine the effect of temperature on survival and growth of all three species. To obtain colonies (i.e., "individuals" for the purpose of our study), 100-cm^2 PVC plastic plates were hung from docks 1-m below the water surface at Spud Point Marina in Bodega Harbor (38.3292°N, 123.0584°W). Organisms were allowed to settle naturally (on the undersides of the horizontally-oriented plates) for up to two weeks, after which plates were transported to the lab and maintained at ~14 °C for 24 h of acclimation to lab conditions. After individuals were counted and identified, plates were randomly assigned to either an 'ambient' or 'increased' temperature treatment (n = 12 per treatment) with the requirement that plates with the least common species, *B. schlosseri*, be assigned equally to each treatment. Six additional plates were assigned to a 'field' treatment to evaluate potential laboratory effects on survival and were returned to their initial collection location in Bodega Harbor for the duration of the experiment.

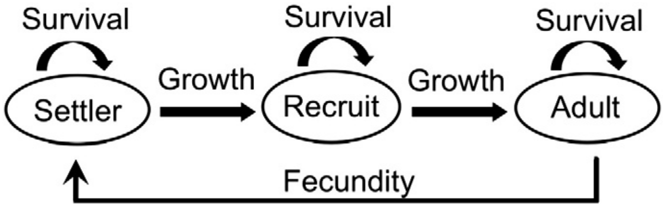

Fig. 1. *Conceptual diagram*. Conceptual diagram showing the life stages and transitions included in the population model. Individual colonies could stay in a stage (survival) or move to the next stage (growth). Adults contributed new settlers to the population through fecundity.

Lab plates were suspended horizontally in separate 2.5-L aquaria (i.e., mesocosms), which were bubbled to provide vigorous air supply and water flow. During the experiment, mesocosm temperatures were measured daily and were maintained within 0.5 °C of the treatment temperature. Mesocosm temperatures (average ± SEM) recorded during the experiment were 13.8 ± 0.2 °C (ambient) and 17.8 ± 0.2 °C (increased). Water in the static mesocosms was replaced daily with temperature-equilibrated, unfiltered seawater that contained natural levels of phytoplankton as a food source. Individuals on lab and field plates were counted with a dissecting microscope and photographed every five days. Survival and growth rates were determined by analyzing photographs in ImageJ v.1.42 (National Institutes of Health, USA; http://rsbweb.nih.gov/ij/). Cumulative survival was calculated as the percent of colonies from the initial cohort alive at the end of each five-day interval. Temperature effects on percent survival were analyzed using a repeated-measures ANOVA in SAS v.9.1 (SAS Institute, Inc., Cary, NC, USA) on arcsine-transformed data, including 100% survival at day zero. Temperature effects on growth were analyzed using a repeated-measures ANOVA in JMP v.5.0.1 (SAS Institute) on square-root transformed surface area data (with growth measurements averaged across individuals on a plate). For both survival and growth analyses, time, temperature, and time × temperature were the model factors, and the most conservative degrees of freedom (d.f. = 1) was used for the time factor.

2.3. Population model parameterization

We used results from our mesocosm experiment to parameterize a stage-based population model for *B. violaceus*, *B. schlosseri*, and *W. subtorquata*. Our model included three stages: settler, recruit, and adult (Fig. 1). For all species, the settler stage started when individuals attached to the substratum, the recruit stage started when settlers became established (i.e., survival stabilized based on cumulative survival curves; Fig. 2), and the adult stage started when sexual maturity was reached (based on published sources; Table 1). Digital photographs were used to follow the stage state (settler, recruit, or adult) based on presence and size (Table 1) of each individual in the initial cohort of the mesocosm experiment for 40 days in 10-day intervals. During each interval, individuals could remain in the same stage (survival), grow into a new stage (growth), or die (mortality). The probability of moving into a stage (i.e., stage-transition probability) for each plate (replicate) was averaged to calculate the mean probability of each stage transition in each of the two temperature treatments (Table 2). All growth was assumed to be positive, with recruit-to-settler and adult-to-recruit transition probabilities set to zero.

Because individuals reached the adult stage only at the end of the mesocosm experiment, we used field data to estimate temperature effects on adult survival and fecundity (i.e., sexual reproduction; asexual budding was considered growth). Adult survival was determined by tracking adults in photographs of plates that were in the field from June 2006 through October 2006 (n = 8, over 10–15 day intervals), and linear regression was used to relate survival to natural temperature variation (which ranged from 13.8 °C to 17.3 °C; Sorte and Stachowicz, 2011). Adult fecundity was estimated using settlement data collected from May 2005 to June 2009 (presented in

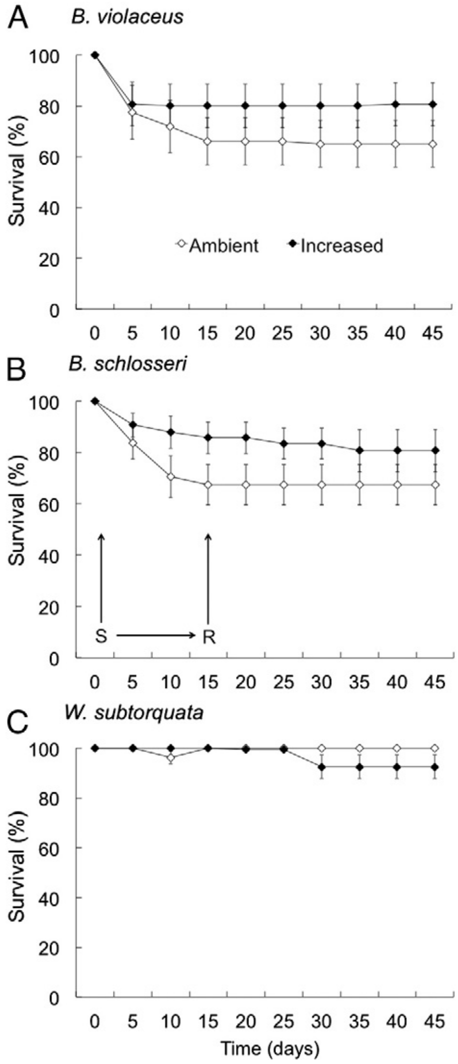

Fig. 2. *Mesocosm survival.* Cumulative survival (±SEM) of (A) *B. violaceus*, (B) *B. schlosseri*, and (C) *W. subtorquata* at ambient (open symbols) and increased (closed symbols) temperatures. Values are cumulative percent survival from the initial cohort at each 5-day interval. The vertical arrows in (B) denote the setter (S) and recruit (R) stages and the horizontal arrow marks the direction of the stage transition.

Sorte and Stachowicz, 2011). In addition, adult abundance was quantified in 0.0625-m^2 quadrats (n = 20) during five dock surveys conducted between October 2006 and June 2009 (see Appendix A1 and Sorte, 2010 for additional methodological details). The per-capita fecundity value for each treatment was calculated as the predicted number of settlers (as determined from a regression of Bodega Harbor temperature to settlement; Appendix A1; Sorte and Stachowicz, 2011) divided by the number of reproductive adults (sensu Ripley and Caswell, 2008). Since dispersal in this system is extremely localized (Grosberg, 1987; Grosholz, 2001; Worcester, 1994; also see Yund and Stires, 2002), we assumed that larvae settling on the plates were produced by adults in an adjacent 1-m^2 area on the dock.

Table 1

Age and size of stage thresholds. Average age and size associated with the start of each stage. Recruit thresholds were calculated from digital photographs of plates and cumulative survival curves in the mesocosm experiment. Published work was used to estimate the size at sexual maturity. *W. subtorquata* individuals at the adult threshold size were measured in digital photographs to estimate average surface area after determining the size in number of zooids (surface area shown in parentheses). Note that *B. schlosseri* values were used for both Botryllids due to lack of available data on *B. violaceus*.

Species	Stage	Age (days)	Size (cm^2) ± SEM	References
B. violaceus	Recruit	10	0.12 ± 0.02	Grosberg (1988); Harvell and Grosberg (1988); Yund et al., (1997)
	Adult	35	0.69 ± 0.15	
B. schlosseri	Recruit	15	0.06 ± 0.02	Grosberg (1988); Harvell and Grosberg (1988); Yund et al. (1997)
	Adult	35	0.24 ± 0.09	
W. subtorquata	Recruit	10	2 ± 1 zooids	Hyman (1940)
	Adult	40	16 ± 2 zooids (0.14 ± 0.02)	

Table 2

Transition probability matrices. Stage transition probabilities and stage-specific mortality (q_x) values used in the population model for (a) *B. violaceus*, (b) *B. schlosseri*, and (c) *W. subtorquata*. Transitions follow from 'states' (columns) to 'fates' (rows), with estimates for settlers and recruits from the mesocosm experiment and those for adults from field plates. The adult-to-settler transition represents fecundity. Values without parentheses are ambient (13.8 °C) temperature parameters, and values in parentheses are increased (17.8 °C) temperature parameters. Because of our assumption of only positive growth, the recruit-to-settler and adult-to-recruit transitions were set to zero for both treatments. Values of '0.00' indicate that the transition was possible but not observed.

	Settler	Recruit	Adult
(a) *B. violaceus*			
Settler	0.58 (0.67)	0	0.69 (1.24)
Recruit	0.29 (0.20)	0.80 (0.90)	0
Adult	0.00 (0.00)	0.20 (0.06)	0.67 (0.37)
q_x	0.13 (0.14)	0.00 (0.04)	0.33 (0.63)
(b) *B. schlosseri*			
Settler	0.64 (0.50)	0	5.82 (28.95)
Recruit	0.27 (0.47)	0.33 (0.39)	0
Adult	0.00 (0.00)	0.67 (0.61)	0.70 (0.44)
q_x	0.09 (0.06)	0.00 (0.00)	0.30 (0.56)
(c) *W. subtorquata*			
Settler	0.61 (0.43)	0	0.05 (0.14)
Recruit	0.38 (0.55)	0.97 (0.74)	0
Adult	0.00 (0.00)	0.03 (0.25)	0.78 (0.37)
q_x	0.01 (0.03)	0.00 (0.11)	0.22 (0.63)

2.4. Population model projections

We estimated the maximum potential rate of population increase (lambda; λ) for each species at ambient and increased temperature. Lambda represents the proportional increase in the population such that $\lambda > 1$ indicates a growing population, and $\lambda < 1$ indicates a shrinking population (Gotelli, 2001). First, lambda estimates for each replicate were determined by calculating the dominant eigenvalue of each replicate transition matrix. Only replicate plates for which we were able to measure values for all possible transitions were used to calculate lambda (i.e., plates with 100% mortality before reaching the adult stage were not used). All λ estimates were calculated using the "primer" package available for the statistical software R (R Core Development Team, 2008; Stevens, 2009). Replicate λ estimates (n = 4-11 plates; Fig. 3) were then used to calculate a mean λ for each species × temperature combination, and a general linear model (GLM) was used to asses the effect of species, temperature, and species × temperature on λ. Tukey-adjusted p-values from the GLM were used to compare the effect of temperature treatment on λ estimates for each species.

2.5. Life table response analysis

We conducted a life table response analysis (sensu McMurray et al., 2010) for each species (Table 3) to determine the relative contribution of each transition to the overall temperature effect on λ (see Caswell, 1996 for more detail). A matrix was constructed for each species × temperature combination using the mean stage transition values (Table 2). An 'average transition matrix' was then calculated

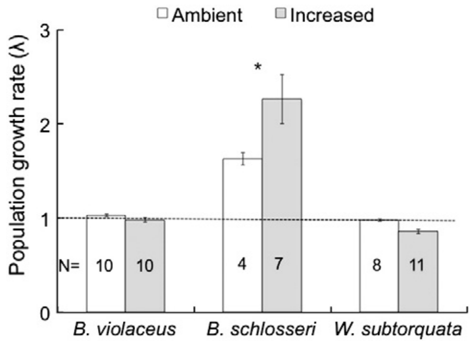

Fig. 3. *Population growth rate*. Predicted mean population growth rate (±SEM) of *B. violaceus*, *B. schlosseri*, and *W. subtorquata* at ambient (13.8 °C; light bars) and increased (17.8 °C; dark bars) temperature. The dotted line at $\lambda = 1$ indicates the threshold for constant population size; values > 1 indicate a growing population while values < 1 lead to a population decline. N values are the number of replicate plates, and asterisks (*) denote significant differences between temperature treatments.

for each species by taking the average of corresponding elements in the ambient and increased temperature matrices. A sensitivity analysis was run on the average transition matrix using PopTools v.3.1.0 (CSIRO, Canberra, Australia; http://www.cse.csiro.au/poptools), giving a 'sensitivity matrix' ($[A^s]$). Using the ambient temperature matrix as a baseline ($[A^{13.8}]$), the difference between the mean ambient and increased matrices was calculated ($[A^{17.8} - A^{13.8}]$). This 'difference matrix' was then multiplied by the sensitivity matrix to give the final matrix of contributions:

$$A^s * \left[A^{17.8} - A^{13.8}\right].$$

All calculations between matrices were performed on corresponding elements.

The values in the matrix of contributions indicated the relative importance of survival, growth, and fecundity to the temperature effect on population growth of each species. Positive values indicate parameters that led to an increase in projected population growth with an increase in temperature, and negative values indicate those that contributed to a decrease in population growth with an increase in temperature. The sum of all matrix elements ($\sum$) indicates the overall temperature effect on population growth.

Table 3
Life table response analysis. Contributions of stage transitions for (a) *B. violaceus*, (b) *B. schlosseri*, and (c) *W. subtorquata*, with each value representing the transition's contribution to projected differences in λ between ambient (13.8 °C) and increased (17.8 °C) temperatures. There are no data (nd) for transitions set to zero in the model.

	Settler	Recruit	Adult
(a) *B. violaceus*			
Settler	0.02	nd	0.05
Recruit	−0.04	0.06	nd
Adult	0.00	−0.10	−0.06
$\sum$	−0.06		
(b) *B. schlosseri*			
Settler	−0.05	nd	0.71
Recruit	0.28	0.02	nd
Adult	0.00	−0.05	−0.09
$\sum$	0.82		
(c) *W. subtorquata*			
Settler	−0.02	nd	0.04
Recruit	0.01	−0.18	nd
Adult	0.00	0.06	−0.05
$\sum$	−0.14		

2.6. Literature review

To assess the generality of our results across populations adapted to different ambient conditions, we conducted a systematic literature review of studies that examined changes in survival, growth, and fecundity under ambient and increased temperatures for these three species. Using ISI Web of Knowledge, we ran topics searches using the following string of search terms: TS = (*Botryllus* OR *Botrylloides* OR *Watersipora*) AND (population OR demograph* OR mortality OR survival OR growth OR fecundity OR reproducti*). We also conducted two broader searches using the terms: TS = (foul* community OR epibenth* community) AND (grow* OR surviv* OR cover OR fecund* OR reproducti* OR mortality). Our searches returned a total of approximately 500 studies of which 19 included appropriate comparisons.

3. Results

Predicted population growth rate (λ) differed between species ($F_{2,44} = 72.2$, $p < 0.001$) and temperatures ($F_{1,44} = 3.94$, $p = 0.05$), with a significant species × temperature interaction ($F_{2,44} = 7.55$, $p = 0.002$) indicating that warming responses were species-specific. In particular, there was a 44% increase in λ at the increased temperature for *B. schlosseri* (Tukey-adjusted $p = 0.005$; Fig. 3) whereas population

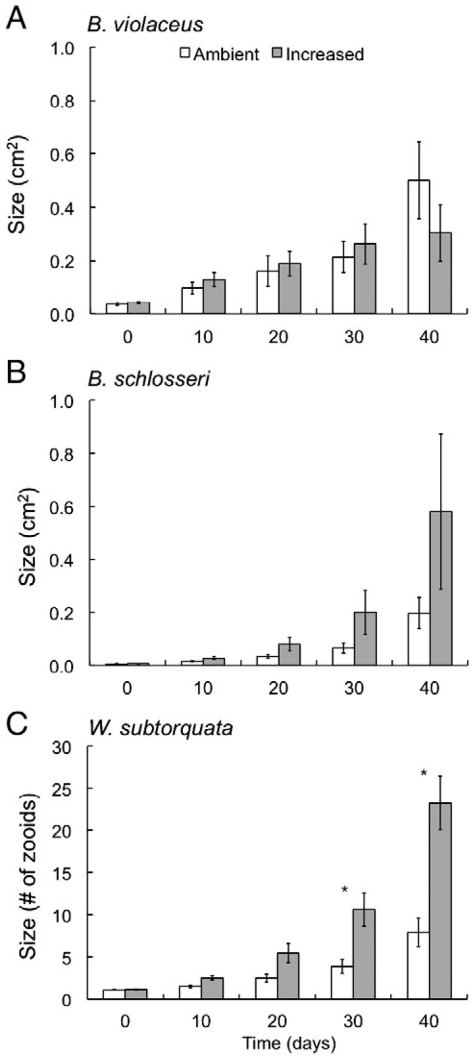

Fig. 4. *Mesocosm growth*. Colony size (surface area in cm^2 or zooid no.; ±SEM) of (A) *B. violaceus*, (B) *B. schlosseri*, and (C) *W. subtorquata* at ambient (white bars; N = 8–10 plates) and increased (shaded bars; N = 9–11 plates) temperature. Asterisks (*) denote significant differences between temperatures at a given time point.

growth rate did not change across this temperature range for *B. violaceus* ($p=0.99$) or *W. subtorquata* ($p=0.92$). Based on the life table response analysis, the overall effect of increased temperature was positive for *B. schlosseri* (0.82), whereas the effects on *W. subtorquata* (−0.14) and *B. violaceus* (−0.06) were extremely small and slightly negative (Table 3). The positive overall effect of increased temperature on *B. schlosseri* population growth was primarily due to changes in settler growth (0.28) and adult fecundity (0.71), while the slightly negative effect on *B. violaceus* appeared to be driven by recruit growth (−0.10) and that on *W. subtorquata* by recruit survival (−0.18).

In contrast to the strong influence of temperature on population growth rates via changes in growth and fecundity, we did not detect a significant effect of temperature ($p>0.10$) or a time × temperature interaction ($p>0.11$) on survival of these three species during the mesocosm experiment (Fig. 2). These ANOVA results are consistent with the relatively low contributions of survival to the temperature effect based on the life table response analysis (absolute values across species and stages were ≤0.18; Table 3). We did, however, detect an effect of temperature ($p<0.01$), time ($p<0.01$), and a time × temperature interaction ($p=0.01$) on growth for *W. subtorquata* during the mesocosm experiment (Fig. 4). In general, *W. subtorquata* individuals were larger in the increased treatment, and size in both treatments increased over time. Differences between treatments emerged as significant at days 30 and 40. This result is reflected in the greater growth transition probabilities for settlers and recruits of *W. subtorquata* in the increased treatment (Table 2). However, these effects were not strong enough to contribute to an overall increase in population growth rate for *W. subtorquata*. There was also an effect of time detected for *B. violaceus* and *B. schlosseri* ($p<0.01$), indicating that size increased over time in both treatments. There was a pattern of greater size in the increased treatment for *B. schlosseri*, but this pattern was non-significant.

Overall, we detected no negative effects of laboratory conditions on survival: instead, mortality was higher on field plates than lab plates for *W. subtorquata* ($F_{1,105}=48.88$, $p<0.001$) whereas lab and field mortality did not differ for *B. violaceus* ($F_{1,104}=2.17$, $p=0.144$); field mortality was not assessed for *B. schlosseri* due to low recruitment.

4. Discussion

Based on our population models, which were parameterized with values derived from laboratory and field experiments, we predict an increase in the population growth rate (λ) of *B. schlosseri* at increased water temperature in Bodega Harbor, California. In contrast, demographic responses of *B. violaceus* and *W. subtorquata* were either in opposing directions or not of sufficient magnitude to drive differences in λ estimates. When comparing the demographic responses to warming observed in this study to those for the same three species inhabiting locations across a wide range of temperatures, we found responses measured here largely paralleled those from earlier studies (Appendix A2). However, there were many variations in these qualitative responses across populations, and the direction of response did not seem to be a simple function of temperature (i.e., studies showing negative effects of warming were not necessarily at the extremes of ambient temperatures).

The life table response analysis allowed for further examination of the mechanisms contributing to the positive overall temperature effect on *B. schlosseri*: changes in fecundity and settler growth rate were both important contributors to the temperature effect. In contrast, settler and recruit growth in *B. violaceus* and survival in *W. subtorquata* showed slightly negative responses to warming. Although there were small positive effects on settler and recruit survival for *B. violaceus*, growth for *W. subtorquata*, and fecundity for both species, they were not strong enough to elicit an overall positive effect of temperature on λ. Thus, beyond projecting species-specific responses to temperature increases, this demographic modeling approach gives insights into the mechanisms underlying warming impacts.

Differences in λ estimates between temperatures for *B. schlosseri* could lead to large potential increases in population sizes over time. For example, if substrate was not limiting, increases in population growth rate due to increased temperature (as predicted by our model) could lead to an over 19-fold increase for *B. schlosseri* after just 90 days. However, space availability would likely prevent this rapid an increase, as the success of invasive species is controlled largely by fluctuations in resource availability and the ability of an invader to access resources without intense competition from resident species (Davis et al., 2000). In epibenthic communities, space is known to be a major limiting factor (Buss and Jackson, 1979; Osman, 1977; Stachowicz et al., 1999), and competitive overgrowth is common. Thus, the amount of available space, and opening of space through disturbance events, can play an important role in the success of invaders in epibenthic communities (Altman and Whitlatch, 2007; Clark and Johnston, 2005; Clark and Johnston, 2011; Davis et al., 2000). At the same time, the acquisition of space through recruitment can be affected by temperature, with climate warming driving shifts in recruitment timing and magnitude (Stachowicz et al., 2002). Given the importance of fecundity and growth of early life stages detected in our analysis, warming-driven demographic changes might give *B. schlosseri* an initial advantage in space occupation; however, the effects of competition would in part determine subsequent community composition. Although competition was included in our demographic model as an agent of adult mortality, outcomes of competition may be species- and context-specific, leading to differences in competitive pressure as community composition and temperature change. For example, at ambient temperatures, *W. subtorquata* is a strong competitor whereas *B. violaceus* and *B. schlosseri* are weak competitors (Edwards and Stachowicz, 2010), and the competitive abilities of *W. subtorquata* and *B. violaceus* appear to increase in warming conditions (C. Sorte and W. White, Unpublished manuscript). Future research, both with experimentation and modeling, should focus on incorporating more specificity in density-dependent processes such as overgrowth competition. Furthermore, adding detail on the size-dependence of demographic rates (including changes in fecundity as adult colonies grow), multiple environmental variables (e.g., salinity, food availability), and seasonal variability would help to further refine our predictions. The benefits of increasing the number of parameters will eventually, however, need to be weighed against the benefits (and lower costs) of more general demographic models (see Anderson et al., 1994).

Our predictions of increasing population growth rate for *B. schlosseri* have serious implications given that it is recognized as a highly invasive species worldwide (Epelbaum et al., 2009). *B. schlosseri* population sizes appear to have been relatively constant in Bodega Harbor over the past ~40 years (Boyd, 1972; Sorte and Stachowicz, 2011), although our results indicate the potential for a sizeable increase in population abundance and dominance as oceans continue to warm. In contrast, although we did not detect an effect of increased temperature on *W. subtorquata*, in Bodega Harbor *W. subtorquata* has been present for only ~20 years but has quickly become a dominant species, inhabiting ~38% of the occupied space in the community (Boyd, 1972; Sorte and Stachowicz, 2011). Determining whether or not an impending increase in these species is a worldwide phenomenon will require further study, particularly given the location-specific idiosyncrasy of responses to warming evident from our literature review (Appendix A2). Clearly, all three of these species are able to persist at temperatures higher than the 17.8 °C used in our "increased" treatment: globally, temperature ranges inhabited are −0.6 °C to 29.3 °C for *B. violaceus*, 2.8 °C to 30.6 °C for *B. schlosseri*, and 6.7 °C to 30.6 °C for *W. subtorquata* (Zerebecki and Sorte, 2011). That a 4 °C increase is predicted to elicit such a large response of *B. schlosseri* populations in the Bodega Harbor community speaks to the strong temperature-dependence of demographic rates and the acclimatization and/or adaptation of this population to local temperatures (see Sorte et al., 2011). In comparison, a Massachusetts population of *B. schlosseri* (which occurs at a higher ambient temperature than the California population) had an estimated population growth rate (λ) of 2.05–2.69 (Grosberg, 1988), which is more similar to the California population's growth rate under increased temperature conditions.

Forecasting the outcomes of warming impacts on population growth requires relating demographic and population processes to species' abundances in the field. To some extent, the range of observations currently available support the prediction that *B. schlosseri* will increase as oceans warm. Several studies have reported increased *B. schlosseri* population density (Rinkevich et al., 1998; Yund and Stires, 2002) and abundance (Dijkstra et al., 2007) at increased temperatures. Similar to our result of no great increase in *B. violaceus* population growth with warming, Grey (2011) did not find a clear increase in the growth rate of Washington populations across a spatial gradient in temperature; instead, population growth rate decreased at both the warmest and coldest sites. Such differential responses to warming, which could be explained by local acclimatization or adaptation of populations (or, e.g., differences in experimental methodology), suggest that there may be a need to use location-specific demographic parameters when forecasting changes using a population modeling and life table response approach.

Climate change and biological invasions have both already had drastic impacts on ecosystems around the world (Byers et al., 2002; Chapin et al., 2000; Walther, 2010; Walther et al., 2002). However, studies that attempt to link climate change with shifts in invasive species' abundances or ranges seldom consider the underlying life-history processes and population dynamics contributing to those shifts (Dahlgren and Ehrlén, 2009; but see for example Williams et al., 2007). If we are to understand the responses of populations, and accurately predict the ecological consequences of climate change, we need species- and temperature-specific demographic data, as well as an understanding of the mechanisms linking environmental conditions to population dynamics. We have demonstrated here that predicted population trajectories and the mechanisms of responses to climate change are species-specific. Our model, parameterized for three invasive species in a temperate subtidal community, serves as a starting point for efforts to project warming-related changes in invasive species' population dynamics and, by doing so, explore synergies of biological invasions and climate change.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2012.11.008.

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