Ecology, 91(8), 2010, pp. 2198–2204
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Ocean warming increases threat of invasive species in a marine fouling community

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Abstract. We addressed the potential for climate change to facilitate invasions and precipitate shifts in community composition by testing effects of ocean warming on species in a marine fouling community in Bodega Harbor, Bodega Bay, California, USA. First, we determined that introduced species tolerated significantly higher temperatures than natives, suggesting that climate change will have a disproportionately negative impact on native species. Second, we assessed the temperature dependence of survival and growth by exposing juveniles to an ambient control temperature and increased temperatures predicted by ocean warming scenarios (+3°C and +4.5°C) in laboratory mesocosms. We found that responses differed between species, species origins, and demographic processes. Based on the temperature tolerance, survival, and growth results, we predict that, as ocean temperatures increase, native species will decrease in abundance, whereas introduced species are likely to increase in this system. Facilitation of invasions by climate change may already be underway; locally, invasive dominance has increased concurrent with ocean warming over the past ~40 years. We suggest that the effects of climate change on communities can occur via both direct impacts on the diversity and abundance of native species and indirect effects due to increased dominance of introduced species.

Key words: Bodega Bay, California, USA; bryozoan; climate change; community ecology; fouling community; global warming; introduced species; invasion; nonindigenous species; survival; temperature; tunicate.

Introduction

Global climate change is hypothesized to lead to the increased invasion of communities by nonnative species (Dukes and Mooney 1999), thus compounding threats to biodiversity (Vitousek et al. 1997, Sala et al. 2000). Correlative evidence from terrestrial systems suggests that invasive species have larger latitudinal ranges than native species, which may be indicative of their ability to tolerate a broader range of environmental conditions and their potential for greater success at increased temperatures (see Dukes and Mooney 1999). However, few empirical studies have specifically linked climate change to increasing abundances of nonnative species (Hellmann et al. 2008, Rahel and Olden 2008; but see Stachowicz et al. 2002, Chown et al. 2007, Willis et al. 2010), especially in marine systems. This is in part because it is challenging to separate climate change effects from invasion processes, such as propagule supply, which cannot be controlled in most field studies (e.g., Harris and Tyrrell 2001). We examined the effects of temperature on survival and growth of native and nonnative species in a subtidal community using laboratory mesocosms in which propagule supply was absent. Previous studies indicate that temperature increases similar to those predicted by climate change models can strongly impact marine species (Sanford 1999, Phillips 2005, Harley et al. 2006, Wethey and Woodin 2008), but less is known about responses of marine invaders relative to native species (Carlton 2000; but see Braby and Somero 2006, Fields et al. 2006).

Our study system was the marine fouling community of Bodega Harbor, Bodega Bay, California, USA (see Plate 1). Fouling communities comprise species that colonize human-made structures including ships' hulls, mariculture farms, and seawater pipelines, as well as natural hard substrata (see Harris and Tyrrell 2001, Valentine et al. 2007). Fouling communities have long been models for community assembly studies (Boyd 1972, Sutherland 1974, Sutherland and Karlson 1977), and they can be dominated by nonnative species, especially in ports and marinas where human-mediated colonization is frequent (Lambert and Lambert 1998). For example, at our study site, nonnative species currently represent 71% of cover in the dock fouling community based on annual surveys conducted from 2006 through 2009. The 11 species of sessile invertebrates, including four natives and seven introduced species, considered in our study account for 80% of the occupied space.

Manuscript received 2 February 2010; revised 19 March 2010; accepted 25 March 2010. Corresponding Editor: P. T. Raimondi.

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Space is an important limiting resource in fouling communities (Stachowicz et al. 1999, Dunstan and Johnson 2004), and we therefore focused our experiments on the temperature dependence of the processes most important for allowing juveniles to initally acquire and maintain space. In the early life stages considered here, these processes include survival and growth. Competition becomes important in later stages and is strongly size dependent (Buss 1980, Sebens 1982); thus, there is a direct relationship between initial acquisition of bare space and adult abundance. We first conducted temperature tolerance experiments to address the hypothesis that introduced species are more tolerant of high temperatures than native species. Second, we determined the survival and growth rates of the common space-holders in the fouling community in Bodega Harbor at current (ambient) and future predicted temperatures. Our results indicate that, as ocean temperatures increase, the fouling community is likely to become increasingly dominated by introduced species.

Methods

All field collections were made from a floating dock at Spud Point Marina in Bodega Harbor, California (38.3290° N, 123.0581° W) during peak recruitment season (June–August). Common species included bryozoans (*Bugula californica* Robertson 1905, *Bugula neritina* Linnaeus 1758, *Schizoporella* sp., and *Watersipora subtorquata* d'Orbigny 1842), colonial tunicates (*Botrylloides violaceus* Oka 1927, *Botryllus* sp., *Didemnum* sp., *Diplosoma listerianum* Milne-Edwards 1841, and *Distaplia occidentalis* Bancroft 1899), the solitary tunicate *Ascidia ceratodes* (Huntsman 1912), and the hydroid *Obelia* sp. Of these species, *Bugula californica*, *Distaplia*, *Ascidia*, and *Obelia* are considered to be native to Bodega Harbor, whereas the other seven are introduced species.

Lethal temperature experiment

Individuals ($\leq$5 weeks old) of 10 fouling species (four natives and six invasives) settled on plastic tiles (Duplos; LEGO Group, Billund, Denmark) suspended 1 m below the surface in Bodega Harbor. Tiles were transferred to the laboratory and weeded to contain two individuals (subsamples) of the target species; tiles with one individual were used when necessary. We supplemented tiles of *Bugula californica* with colonies collected manually from the docks. After a 24-h laboratory acclimation in running seawater, tiles were placed in 1-L tanks with constant aeration at ambient temperature (~12°C), and temperature was raised by 1°C every 15 min until the treatment temperature was reached. Individuals were exposed to the treatment temperature for 24 h, and we scored them as "live" or "dead" based on the presence of movement (either autonomous or when probed) immediately after the treatment and after 2 d of recovery at ambient temperature. Values did not vary between these two observations; therefore, the first observation was used in our analyses.

Survivorship of the 10 species was tested at six temperatures ranging from 14° to 32°C (~14°, 16°, 20°, 24°, 28°, and 32°C) for each target species. We ran $N = 5$ replicates for each species × temperature combination, with the following exceptions: for *B. neritina*, $N = 7$ for runs at 20°C and 24°C, and for *Ascidia*, which recruited in low abundance, we evaluated survival at 20°, 24°, and 28°C with $N = 3$, 3, and 2, respectively. Species × treatment combinations were randomly assigned to tank and experimental run (nine runs were completed over 4 weeks). Survivorship values were used to calculate the temperatures lethal to 50% of individuals (LT_{50}) using probit analysis in SAS version 9.1 (SAS Institute, Cary, North Carolina, USA).

Mesocosm experiments

For the survival experiment, fouling species recruits ($\leq$2 weeks old) were collected on 10 × 10 cm PVC plastic plates suspended horizontally at 1-m depth in Bodega Harbor. Initial recruits were counted, and plates were not weeded. The 18 plates were randomly assigned to 2.5-L plastic aquaria ($N = 6$ per temperature). Treatment temperatures were 13.5°C (ambient), 16.5°C (+3°C increase), and 18.0°C (+4.5°C increase; see Appendix A for supplementary methods). Plates were suspended upside down and horizontally, each in a separate tank. Individual counts were repeated after 5 weeks. Survival (percentage of initial individuals surviving) was calculated for seven species for which natural recruitment led to sufficient replication.

Plates for the growth experiment were naturally field-seeded as in the survival experiment. Unlike the survival experiment, growth plates were initially weeded of all but individuals of a single species. In 2008, we ran sequential 6-d experiments on six of our focus species that recruited in adequate abundance. For each species, the experiment was run during its seasonal peak in recruitment, and all individuals were $\leq$1 week of age at the start of the experiment. A total of 72 tanks ($N = 24$ for each of the three temperature treatments) were arrayed in two different seawater tables (blocks), and experimental runs of the two blocks were staggered by 1 d. For most species, we analyzed changes in surface area relative to the initial sizes. Plates were photographed before and after the experiment, and we digitally measured three random, isolated colonies per plate using the average of two measurements per colony (length and width) to calculate their total (roughly circular) surface area. The exception to this method was that, for *Bugula* (arborescent bryozoan) species, we counted individual zooids of all individuals on the plate ($N = 1$–22 subsamples per plate) and calculated growth as relative change in zooid number. In 2009, we used the same methods to measure growth of *B. californica*, except that colonies were $\leq$2 months old, and $N = 7$ for each of two temperature treatments (ambient and

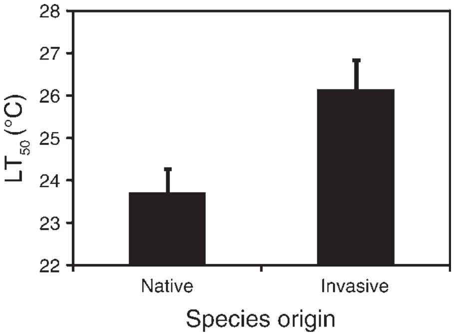

FIG. 1. Temperature tolerance of native and invasive fouling species from Bodega Harbor, California, USA. Values are temperatures at which 50% of individuals died after a 24-h exposure (LT_{50}; mean + SE), based on probit regressions of mortality at 14°, 16°, 20°, 24°, 28°, and 32°C. Each species was treated as an experimental unit, with $N = 4$ native species (*Ascidia*, *Bugula californica*, *Distaplia*, and *Obelia*) and $N = 6$ invasive species (*Botrylloides*, *Botryllus*, *Bugula neritina*, *Didemnum*, *Diplosoma*, and *Watersipora*).

+4.5°C increase). To justify including the 2009 data for *B. californica*, we did a concurrent experimental run of *B. neritina* and confirmed that this species' increase in growth at the +4.5°C relative to the ambient treatment did not differ between the 2008 and 2009 experiments (*t* test, $P = 0.195$).

The effect of temperature on each species in the survival experiment was assessed by ANCOVA using total initial abundance (Init) as a covariate; the interaction term was not included in the model after testing for homogeneity of slopes. For the growth data, relative percentage increase in size was analyzed with a separate ANOVA (growth = temperature, block, temperature × block; with both as fixed effects) for each species. Power transformations were applied to data, as required, to meet the assumptions of normality (using the Shapiro-Wilk test) and homogeneity of variances (using Levene's test). Least-squares means were used for multiple comparisons and for calculating relative change in growth (Appendix B). Data are reported as means ± SE.

Community structure changes

The survival and growth data were used to explore potential species-specific changes in total (assuming no space limitation) and relative cover after 5 weeks for the five species common to both mesocosm experiments. Initial values were from individual cover estimates of these focus species on eight plates collected in August 2008 that had been in the field for 3 weeks. We estimated change in cover using the experimentally determined survival and growth values at +4.5°C relative to the ambient temperature (Appendix B). To calculate each species' relative percent cover, we divided the individual species' cover values by the total of all species. Specifically, the percent cover of species *t* at 5 weeks was calculated as follows:

$$t_{5\text{wk}} = t_{\text{init}} lg / T_{5\text{wk}}$$

where l was survival per 5 weeks, g was growth per 5 weeks, and $T_{5\text{wk}}$ was the total cover of all species at 5 weeks. Predicted values were compared to actual counts on the field plates (at ambient temperature) 5 weeks later.

RESULTS

Introduced species were more tolerant of higher temperatures than native species ($t = 2.45$, $P = 0.040$; Fig. 1). Temperatures lethal to 50% of individuals (LT_{50}) were 23.7° ± 0.6°C and 26.1° ± 0.7°C for native and introduced species, respectively.

The native *Distaplia* exhibited decreased survivorship after exposure to the +4.5°C increase (temperature, $F_{2,14} = 4.41$, $P = 0.033$; Init, $F_{1,14} = 5.63$, $P = 0.033$; Fig. 2A). Survival rate declined >80% between the +4.5°C increase and ambient treatments (Tukey post hoc $P = 0.034$). Survival was unrelated to temperature for the six nonnative species (ANCOVA $P > 0.2$). Survival rates ranged from 2% for *Distaplia* in the +4.5°C treatment to ~100% for *Watersipora*.

Growth was strongly influenced by temperature for five of the seven species examined (ANOVA $P < 0.04$; Fig. 2B). For the five species that exhibited temperature-dependent growth, growth rates increased by 49–136% between the ambient and +4.5°C temperature treatments (see Appendix B). Of these five species, the native *Distaplia* exhibited the smallest increase in growth. Growth rates were not related to temperature for the native *B. californica* or introduced *Watersipora* ($P = 0.965$ and 0.806, respectively). Although there was a significant block effect for three of the species (*Distaplia*, *Didemnum*, and *Watersipora*), the temperature effect was consistent across blocks with the possible exception of *Watersipora* (temperature × block, $P = 0.052$).

Based on the temperature dependence of growth and survival, as increases approach +4.5°C, three of four nonnatives are predicted to increase in abundance, whereas *Distaplia*, the most commonly recruiting native species, is predicted to decrease in abundance (Fig. 3; Appendix B). The abundance of *Distaplia* is predicted to decrease by 74%, whereas the nonnative species *Didemnum*, *Botrylloides*, and *Bugula neritina* are predicted to increase by 4%, 5%, and 19%, respectively (Fig. 3). *Watersipora* is not predicted to increase via this mechanism because it was the only species for which both survival and growth were temperature independent (ANCOVA $P = 0.215$ and ANOVA $P = 0.806$, respectively).

DISCUSSION

To the extent that our findings in the fouling community reflect a general pattern, as mean ocean temperatures increase, introduced species are likely to become more abundant due to their higher survival and greater increase in growth relative to native species.

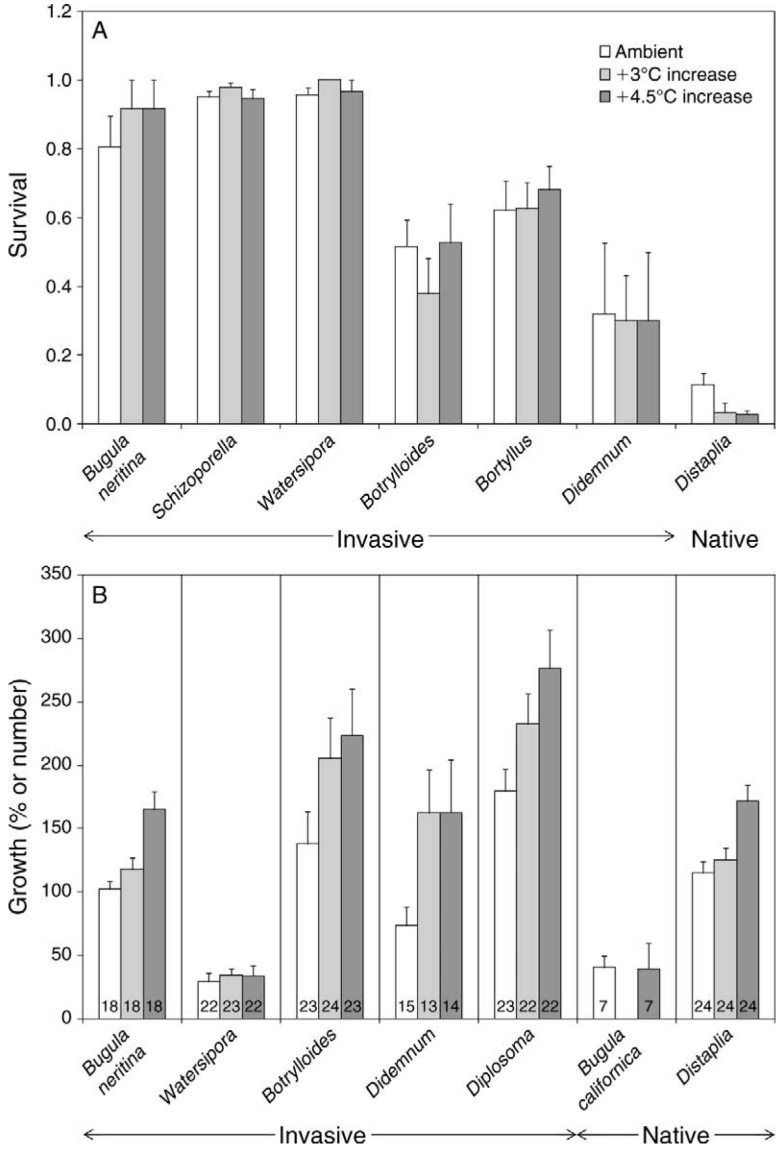

FIG. 2. (A) Survival after five weeks at ambient, +3°C, and +4.5°C temperature treatments for the seven most common species on experimental plates. Survival was calculated as the proportion of individuals present after the experiment relative to initial abundance. $N = 6$ per treatment for all species except *Didemnum* ($N = 5$). (B) Growth (percentage change in surface area or, for *Bugula* species, zooid number) after six days at ambient, +3°C, and +4.5°C temperatures for seven species. Vertical lines signify that individual species experiments were run sequentially, not concurrently. Sample size is noted at the base of each bar. All values are mean + SE.

After making the simplifying assumption that survival and growth are solely responsible for the initial maintenance and acquisition of space, respectively, we used data for the five species included in both the survival and growth experiments to estimate potential changes in abundances. An indication of the model's qualitative explanatory ability is that the trajectory of predicted changes in abundances over time at ambient temperature are the same as those we documented on ambient field plates. We found that as temperature increases approach +4.5°C, three of four nonnative species are likely to become more abundant, whereas abundance of the native species *Distaplia* is predicted to decrease from 2.5% cover at ambient temperature to 0.66% cover at +4.5°C. This decreased abundance of *Distaplia* is predicted in part because of high post-settlement mortality, which, at ambient temperature, was ~80% monthly in the laboratory experiment and 90% in the field (mean on six field plates; M. Cockrell, *unpublished data*). In current ambient temperature conditions, *Distaplia* offsets this high mortality rate by recruiting in high abundances, but it seems unlikely that

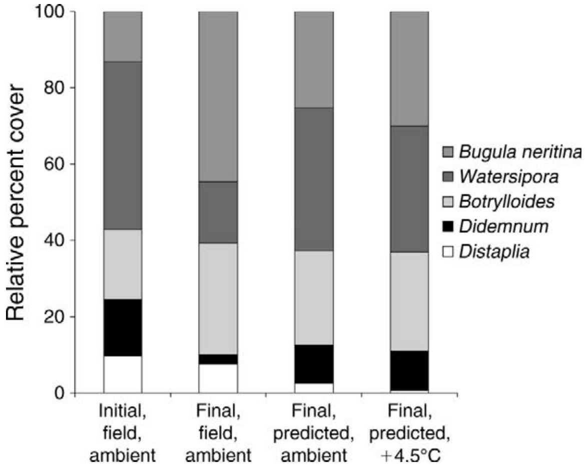

FIG. 3. Actual and predicted change in relative abundance after five weeks. The five common species include one native (*Distaplia*) and four nonnative species. Initial and final field values are from species' abundances on recruitment plates at ambient temperature. Predicted abundances were calculated by starting with initial field plate values and extrapolating ahead five weeks using demographic rates at ambient and +4.5°C temperatures, as measured in the survival and growth experiments.

there will be a fivefold change in reproduction to counteract the temperature-driven decrease in survival.

The decline in relative abundance predicted for *Distaplia* as ocean temperatures increase is also expected for a larger suite of native species in the community. Although only seven species were sufficiently abundant for analyses of survival in our multispecies survival experiment (Fig. 2A), a total of 11 species (four natives and seven nonnatives) were initially present on the plates. At the end of the survival experiment, native species represented a lower proportion of total individuals at higher temperatures (39% of individuals were natives at ambient temperature, 20% at +3°C, and 13% at +4.5°C; Appendix C), and this change in relative proportion of natives was temperature dependent (ANOVA $F_{2,15} = 4.09$, $P = 0.038$). Combined, our results for both dominant and rarer species in the community demonstrate that early post-settlement success of nonnative species is enhanced, whereas success of native species declines, as temperatures increase.

Furthermore, results from the lethal temperature experiment indicate that introduced species are more temperature tolerant than native species. In addition, these six invasives inhabit, on average, broader environmental temperature ranges globally than the four native species (R. A. Zerebecki and C. J. B. Sorte, *unpublished data*). Ocean temperatures approaching the lethal temperatures of these species are currently rare in Bodega Harbor; however, an average of 18.9°C was observed over a 24-h period during a heat wave in July 2006 (C. J. B. Sorte, *unpublished data*). Based on this heat wave temperature and predicted increases in mean temperature and heat wave severity, LT_{50} temperatures for native species, but not invasives, are likely to be exceeded with increasing frequency in the next century (Meehl and Tebaldi 2004, IPCC 2007). Thus, extreme temperature events are also likely to increase invasive dominance by causing widespread mortality that disproportionately impacts native species.

Our results indicate that ocean warming, along with continuing spread and propagule pressure, could have contributed to the increasing dominance of invasive fouling species already evident in both Southern California (Lambert and Lambert 1998) and Bodega Harbor (Boyd 1972). Nonnatives currently represent 67% of the nine most common local species compared to only 33% almost 40 years ago (Boyd 1972), coincident with an increase in ocean temperature (measured at a shoreline station on the outer coast) of >1.0°C between 1957 and 2007 (Bodega Ocean Observing Node; data *available online*).[4] Both *Bugula neritina* and *Botrylloides violaceus* have become more locally abundant than their native congeners, *Bugula californica* and *Botrylloides diegensis*, and comparisons with historical data suggest that relatively rare native species (e.g., *Botrylloides diegensis* and the hydroid *Obelia* sp.) will continue to decrease in abundance (Boyd 1972). However, these patterns may need to be evaluated if *B. diegensis* or *Obelia* are later identified as nonnative in origin (J. Carlton, *personal communication*). Although *Didemnum* is currently the least abundant of the nonnative species considered, we show that it could increase in abundance over four times more rapidly than the other increasing species as oceans warm. In addition, field observations in Bodega Harbor have shown that *Didemnum* outcompetes both *Botrylloides* and *Watersipora* at ambient temperatures (K. Edwards and J. Stachowicz, *unpublished data*). *Didemnum*'s superior abilities to colonize, compete, and resist predators (Osman and Whitlatch 2007, Valentine et al. 2007) will likely be strengthened as temperatures increase. Ocean warming, thus, might help explain why *Didemnum* has recently become an aggressive and actively spreading invader on both coasts of North America (Bullard et al. 2007).

In conclusion, the survival and growth of early life stages of nonnative species increased relative to native species under predicted ocean warming scenarios. This study demonstrates that ocean warming can facilitate species invasions independent of propagule pressure, which cannot be controlled in correlative and field studies. Because survival and growth are responsible for space acquisition and maintenance, they set the stage for subsequent competitive interactions and community development. Strong responses of these two key processes to increased temperature underscore the

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[4] ⟨http://www.bml.ucdavis.edu/boon/⟩

Plate 1. Fouling community from Bodega Harbor, California, USA. After six weeks of community development in the field, species on this experimental plate include the native tunicate (sea squirt) *Distaplia occidentalis*, the invasive tunicates *Botrylloides violaceus* and *Diplosoma listerianum*, and the invasive branching bryozoan *Bugula neritina*; the invasive encrusting bryozoan *Watersipora subtorquata* can be seen to the left of the plate. Photo credit: C. J. B. Sorte.

potential for shifts in community composition. Such shifts seem to be already underway in Bodega Harbor, where dominance of invasive species has approximately doubled over the last 40 years, as sea temperatures have increased. Increasing dominance of fouling communities by nonnative species could influence ecosystem and economic impacts of the community by leading to changes in filtering rates and water clarity (Wilkinson et al. 1996), mobile (e.g., fish) species abundances and diversity (Clynick et al. 2007), and competition with farmed shellfish (McKindsey et al. 2007). In addition, faster growth rates in response to ocean warming indicate that fouling control practices will need to be undertaken with increased frequency and at increased cost. More broadly, our results highlight the need to consider two types of climate change effects on communities: direct impacts on native species and indirect effects due to the increased dominance of introduced species.

Acknowledgments

A. Fuller, M. Cockrell, and M. Evans provided essential help with the "TempUp" experiments. We thank C. Bowles, M. Bracken, C. Bracken-Sorte, J. Byrnes, K. Edwards, K. Menard, A. Newsom, and J. Stachowicz for assistance and feedback. Comments from M. Bracken, J. Byrnes, E. Sanford, J. Stachowicz, D. Wethey, and two anonymous reviewers greatly improved this manuscript. Funding was provided by an AAUW American Fellowship to C. J. B. Sorte, a CEQI Fellowship to C. J. B. Sorte from the California Ocean Protection Council, and the National Science Foundation (DGE-0114432 for the UC–Davis Biological Invasions IGERT Program and OCE-0549944 to S. L. Williams and M. Bracken). This publication is a contribution of the Bodega Marine Laboratory, University of California–Davis.

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APPENDIX A

Supplementary methods for the fouling community census and mesocosm experiments (*Ecological Archives* E091-153-A1).

APPENDIX B

Predicted change in abundance over time of species at +4.5°C increase relative to ambient temperature (*Ecological Archives* E091-153-A2).

APPENDIX C

Change in relative proportion of native species during the survival experiment (*Ecological Archives* E091-153-A3).