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Permalink

<https://escholarship.org/uc/item/4hn0c4r0>

Journal

Global Change Biology, 28(8)

ISSN

1354-1013

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Publication Date

2022-04-01



DOI

10.1111/gcb.16080

Peer reviewed

RESEARCH ARTICLE

Local adaptation in a marine foundation species: Implications for resilience to future global change

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Funding information

Division of Ocean Sciences, Grant/Award Number: 1234345 and 1829976

Abstract

Environmental change is multidimensional, with local anthropogenic stressors and global climate change interacting to differentially impact populations throughout a species' geographic range. Within species, the spatial distribution of phenotypic variation and its causes (i.e., local adaptation or plasticity) will determine species' adaptive capacity to respond to a changing environment. However, comparatively less is known about the spatial scale of adaptive differentiation among populations and how patterns of local adaptation might drive vulnerability to global change stressors. To test whether fine-scale (2–12 km) mosaics of environmental stress can cause adaptive differentiation in a marine foundation species, eelgrass (*Zostera marina*), we conducted a three-way reciprocal transplant experiment spanning the length of Tomales Bay, CA. Our results revealed strong home-site advantage in growth and survival for all three populations. In subsequent common garden experiments and feeding assays, we showed that countergradients in temperature, light availability, and grazing pressure from an introduced herbivore contribute to differential performance among populations consistent with local adaptation. Our findings highlight how local-scale mosaics in environmental stressors can increase phenotypic variation among neighboring populations, potentially increasing species resilience to future global change. More specifically, we identified a range-center eelgrass population that is pre-adapted to extremely warm temperatures similar to those experienced by low-latitude range-edge populations of eelgrass, demonstrating how reservoirs of heat-tolerant phenotypes may already exist throughout a species range. Future work on predicting species resilience to global change should incorporate potential buffering effects of local-scale population differentiation and promote a phenotypic management approach to species conservation.

KEYWORDS

common garden experiment, introduced species, local adaptation, macroalgal bloom, ocean warming, reciprocal transplant experiment, *Zostera marina*

[†]Deceased.

1 | INTRODUCTION

Climate change, pollution, and species invasions are ranked among the most severe facets of global change currently threatening biodiversity (Brondizio et al., 2019). Species experience many of these threats simultaneously (Crain et al., 2008; Halpern et al., 2008), and the worldwide redistribution of species is a direct result of synergistic interactions between global-scale climate change with local anthropogenic stressors (Auffret & Thomas, 2019; Gissi et al., 2021; Guo et al., 2018; Northrup et al., 2019; Russell et al., 2009; Wernberg et al., 2011). However, species' responses to global change are not limited to dispersal to more favorable environments; plasticity of individuals and local adaptation of populations can also play an important role (Gienapp et al., 2007; Kroeker et al., 2020). Together plasticity and local adaptation determine the geographic distribution of phenotypes throughout a species range, and consequently, the response of species to novel conditions (Sanford & Kelly, 2011). Thus, it is critical to describe the spatial scales of and ecological factors underlying population differentiation to understand how patterns of adaptive differentiation among populations might lead to differential sensitivity to global change (Hice et al., 2012).

Global warming can differentially affect populations of marine species due to extreme variation in regional-scale warming (Brierley & Kingsford, 2009). Marine heatwaves (defined as periods when daily temperature exceeds the 90th percentile of climatological observations for at least five consecutive days) have become increasingly common, causing rapid and catastrophic damage to local ecosystems (reviewed in Smale et al., 2019). Trailing and leading-edge populations of marine species are shifting poleward at an average rate of 7.2–19 km year⁻¹ (Poloczanska et al., 2013; Sorte et al., 2010a) in response to long-term warming, and by 100's of kilometers within a few months in response to marine heatwaves (Sanford et al., 2019; Smale & Wernberg, 2013). However, the severity of warming experienced by range-center populations can be equal to that of trailing edge populations. This is because latitudinal trends in ocean warming are modified by local-scale factors causing mosaics of thermal stress or "hot spots" throughout a species range (Helmuth et al., 2006). Populations located along local environmental gradients that include hot spots may be exposed to much higher temperatures than expected given their latitude. Consequently, some populations may be closer to thermal limits than expected based on their latitude, potentially increasing their susceptibility. Alternatively, if populations and individuals have responded to persistent hotspots by adaptation and plasticity, this might create local reservoirs of stress-adapted individuals throughout a species range (Kuo & Sanford, 2009), potentially providing resilience to warmer temperatures at the regional scale (Matz et al., 2020).

A wide variety of marine species demonstrate intraspecific variability in thermal niches across geographic spatial scales, including macrophytes (reviewed by Hollarsmith et al., 2020; King et al., 2018), corals (Howells et al., 2012; Palumbi et al., 2014), and many other invertebrates (reviewed by Sanford & Kelly, 2011). Additionally, population differentiation in marine systems can also exist on fine spatial

scales (meters to kilometers) because of strong and persistent along-shore variation in environmental factors (Sanford & Kelly, 2011), as is demonstrated for corals (Bay & Palumbi, 2014; Kenkel et al., 2015; Oliver & Palumbi, 2009). However, there is a complete lack of investigation of local adaptation to temperature variation on fine spatial scales in marine macrophytes (Hays, 2007; King et al., 2018), which is problematic as many marine macrophytes have limited dispersal and demonstrate strong population structure on fine spatial scales (Kamel et al., 2012; Kinlan & Gaines, 2003; Reynolds et al., 2017). Therefore, the ability to accurately predict the response of this prominent group of foundation species to rising temperatures may depend on knowledge of population differentiation (Wernberg et al., 2018), which could occur on fine spatial scales (i.e., kilometers or less).

Global change encompasses more than rising temperatures, and the total effects of global change can only be understood in the context of multiple interacting stressors (Côté et al., 2016; Crain et al., 2008). However, the simultaneous effects of multiple selective agents on local adaptation is poorly understood (Egea-Serrano et al., 2014; Rogell et al., 2009). Ecological processes in marine systems are synergistically impacted by water quality and invasive species (Crooks et al., 2011; Piola & Johnston, 2008) and their interactions with global warming (Rabalais et al., 2009; Sorte et al., 2010b). Pollution resulting in poor water quality (i.e., eutrophication, algal blooms, sedimentation) is one of the leading causes of decline in marine foundation species because of light attenuation and smothering (Pandolfi et al., 2005; Waycott et al., 2009). Similarly, invasive macrophytes are replacing natives on massive spatial scales (Inderjit et al., 2006; Lyons & Scheibling, 2009), and invasive consumers can decimate entire trophic levels (Kindinger & Albins, 2017). These co-occurring stressors can also impose selection on populations threatened by rising temperatures (Ritter et al., 2010; Moran & Alexander, 2014; Connolly et al., 2018; Jin et al., 2020, reviewed in Sanford & Kelly, 2011), either by constraining the adaptive potential of natural populations through genetic trade-offs or by facilitating rapid adaptation through correlated evolution (Bijlsma & Loeschcke, 2005; Kawecki & Ebert, 2004).

Here, we investigate how multiple facets of global change are linked to local differentiation of a marine foundation species (Eelgrass, *Zostera marina*) on a fine spatial scale (<12 km). Eelgrass is a clonal plant that is broadly distributed along coastlines throughout the Northern Hemisphere and provides invaluable ecosystem services in terms of supporting fisheries (Tuya et al., 2014), stabilizing and enhancing accretion of coastal sediments (Bos et al., 2007), and sequestering blue carbon (Röhr et al., 2018). Poor water clarity and associated light limitation is often attributed as the primary cause of seagrass loss worldwide (Waycott et al., 2009), however seagrass meadows are increasingly impacted by marine heatwaves (Smale et al., 2019) and invasive species (Williams, 2007). Across populations, there is some evidence that the eelgrass is adapted to temperature along latitudinal gradients (Bergmann et al., 2010), and reciprocal transplants of populations separated by 50 km demonstrate the home-site advantage (Hämmerli & Reusch, 2002). There

is often strong genetic structure in this species among bays and also within bays at the scale of a few kilometers (Kamel et al., 2012; Reynolds et al., 2017), which reflects the relatively small estimated genetic neighborhood size of 0.5 km² based on eelgrass pollen and seed dispersal capabilities (Ruckelshaus, 1996). Within populations, controlled mesocosm studies have found individual-level genetically based variation in temperature susceptibility (DuBois et al., 2019; Ehlers et al., 2008; Reynolds et al., 2016), response to light limitation (DuBois et al., 2019; Salo et al., 2015) and consumption by herbivores (Reynolds et al., 2018; Tomas et al., 2011). However, we do not know how these traits are distributed in the field or whether populations demonstrate fine-scale adaptation or acclimation to environmental conditions. To investigate how gradients in multiple selective factors influence genetic and phenotypic variation among populations and the potential for this variation to enhance species' response to environmental change, we combined results from a year-long reciprocal transplant experiment with environmental data and a survey of population genetic structure across sites. We then used common garden experiments and feeding experiments to test the contribution of site differences in temperature, light availability, and grazing by an introduced species on population differentiation.

2 | METHODS

2.1 | Three-way reciprocal transplant experiment

We selected three eelgrass (*Zostera marina*) meadows within Tomales Bay, CA for our reciprocal transplant experiment. Tomales Bay is a 16 km-long and 2 km-wide drowned river estuary characterized by strong environmental gradients (see Smith & Hollibaugh, 1998). Our three sites spanned the entire length of Tomales Bay: Nick's Cove near the mouth of the bay (38°12'18.2"N, 122°55'34.7"W), Blakes Landing mid-bay (38°10'43.2"N, 122°54'31.1"W), and Millerton Point at the head of the bay (38°06'21.5"N, 122°50'44.6"W). These sites were all located along the east side of Tomales Bay, where gently sloping bathymetry and mudflat allows for extensive eelgrass meadows. Our sites were located in the low intertidal zone, only exposed to air when tidal heights were less than -0.5 ft MLLW.

During July 2017, we transplanted a total of 120 eelgrass ramets to each of our three sites: Nick's Cove, Blakes Landing, and Millerton Point. Of these 120 ramets, 40 ramets originated from each of these three sites (i.e., 40 from each of the two foreign populations and 40 from the home-site population). We collected ramets every meter along two 100 m transect lines placed parallel to shore well within the continuous eelgrass meadow in the low intertidal zone. Spacing collections by one meter greatly reduces the probability of collecting multiple ramets from the same genet (Abbott et al., 2018; Reynolds et al., 2016), ensuring that our collections represented the genotypic diversity at each site. We standardized all ramets to one terminal shoot (i.e., removed all clonal side shoots), gently cleaned shoot leaves, and standardized the rhizome length to 3 cm. We kept these ramets overnight in an indoor flow-through seawater tank at

the Bodega Marine Lab (BML) in Bodega Bay, CA, and transplanted ramets to the field the following day.

Our planting design comprised two parallel 60 m transects, spaced two meters apart. We placed the transects parallel to shore, located exactly where we had collected the ramets from the previous day. At 1-m intervals along each transect, we embedded a Sterilite plastic container (22.9 × 20 × 15.6 cm; with perforated walls lined with 2 mm mesh) within the sediment and then filled these containers with coarsely sieved and homogenized sediment from the site. One ramet was planted in the center of each container (here after referred to as "plots"). Ramets were planted in randomized blocks, with half of the replicates randomly assigned to a position along each transect. Using the Sterilite container allowed us to unambiguously identify our planted individual over the course of the next 12 months.

We surveyed plots quarterly, during November 2017, January 2018, May 2018, and July 2018. During surveys, we counted clonal shoot production, flowering, and ramet survival. We also recorded the presence of macroalgae (a potential competitor) and obvious grazing scars on the shoots' leaves. We counted flowering shoots and then removed them to prevent introduction of foreign genotypes into local meadows.

2.2 | Abiotic and biotic characterization of sites

To characterize abiotic and biotic differences among sites across seasons, we conducted quarterly surveys starting in November 2017 and repeated surveys during January 2018, May 2018, and July 2018. To assess eelgrass productivity and structure, we took five 20 cm diameter cores along a 50 m transect at each site. From each core, we measured shoot density, shoot length, aboveground biomass, belowground biomass, and macroalgal biomass.

To determine difference in epifaunal community composition across our three sites, we took five samples along a 50 m transect line at each site quarterly. For each sample, we carefully placed an open-mouthed fine-mesh drawstring bag over a clump of shoots (when seawater depth was about 30 cm deep) so that the mouth of the bag was flush with the sediment surface. We then broke-off the shoots where they emerged from the sediment and quickly closed the drawstring to capture the shoots and associated animals. We preserved the epifauna in 70% ethanol and later identified the epifauna species under a dissecting microscope. We measured the dry mass of eelgrass from each sample to standardize epifaunal abundances by the amount of habitat sampled. We assessed grazing on eelgrass by the introduced amphipod, *Ampithoe valida*, at two time points at Millerton Point only (we did not observe grazing at Nick's Cove or Blakes Landing). *A. valida* preferentially inhabits and grazes on flowering shoots (Reynolds et al., 2012). To assess *A. valida* abundance and grazing on flowering shoots, we haphazardly collected 50 flowering shoots along two 60 m transect adjacent to the transplant plots. In the lab, we counted *A. valida* abundance and surveyed seed spathes for grazing scars. We made our second assessment of

A. valida grazing during the May surveys, during which we recorded grazing scar presence on the leaves of transplants. *A. valida* grazing scars on seed spathes (seeds eaten directly out of spathe) and leaves (approximately 0.5 cm half-ellipses eaten from edge of leaf) are distinct (Reynolds et al., 2012) and unlike scars made by other eelgrass grazers in Tomales Bay eelgrass meadows.

We measured sediment characteristics by taking three sediment cores (7.8 cm diameter to a depth of 15 cm) at each site. We cut the middle 5 cm from the core and analyzed this center sample in three ways. We characterized grain size by sand and clay fractions using a wet sieving method and a 63 μm sized sieve. We measured total organic matter (TOM) by burning 5 g of dried sediment in a Barnstead Thermolyne 1500 muffler furnace at 550°C for 5 h. Finally, we measured total carbon and nitrogen using a Thermo Finnigan FlashEA112 series elemental analyzer.

We recorded temperature at each site every 15 min using Onset Hobo Pendant Temperature Data Loggers. Loggers were placed level with the sediment in the low intertidal zone, one at each end of the two 60 m transects from the reciprocal transplant experiment.

2.3 | Temperature common garden experiment

During May 2019, we collected 12 eelgrass genets from each site using the same collection method (see above). We standardized genets to one terminal shoot (removing all clonal side-shoots) with a rhizome length of 3 cm before planting in square plastic flowerpots (8.9 \times 8.9 \times 8.9 cm) filled with coarsely sieved and homogenized sediment collected from the Bodega Harbor. We placed four shoots from each population in a glass aquarium (30.5 \times 50.8 \times 40.6 cm) for a total of 6 aquaria, each containing 12 shoots. We arranged these aquaria in a cold room set to 16°C, under 45W UNIFUN LED grow lights (378.7 \pm 72 PAR, mean \pm SE) set on a 13.5 h light cycle that mimicked light conditions during August when peak summer temperatures occur in Tomales Bay. We built a partially recirculating seawater system, in which sand-filtered seawater was recirculated from aquaria to two sump tanks. Fresh seawater was fed into the sump tanks at a rate of 180 L hour⁻¹, with the entire system consisting of about 600 L total. We maintained the system salinity at 33 ppt. We acclimated ramets to aquaria for 10 days at 16.3 \pm 0.15°C (mean \pm SE), and then slowly increased the temperatures in three aquaria over 14 days at an average rate of 0.38°C day⁻¹ by warming one sump tank with three Process Technologies 1000 W titanium immersion heaters. The final warm temperature treatment of 21.7 \pm 0.49°C matched the average temperature at Millerton Point during July 2018 (21.5 \pm 2.29°C). The three remaining “cool” aquaria were stabilized at a temperature of 17.7 \pm 0.81°C. We based the temperature treatments on average July temperatures at each site, because this is when the greatest temperature differentiation across sites occurs throughout the year. After 1 month, we measured the following response variables: leaf growth rate using the “hole punch” method (see Dennison, 1987), leaf length, and above and below-ground dry biomass.

2.4 | Shading common garden experiment

During August 2018, we collected 72 eelgrass genets from each site using the same collection method, standardized the genet size, and planted them in pots, as described before. We placed 12 shoots from each population in an outdoor tank (60 \times 60 \times 60 cm, 216 L), for a total of 6 tanks each containing 36 shoots. Tanks were supplied with coarsely sand-filtered flow-through seawater at approximately 288 L hour⁻¹. We acclimated the shoots to these tank conditions for two weeks, after which we shaded three of the tanks using shades made of layered window screen. Shading treatment reduced the light conditions within tanks by 77% (under midday full-sun conditions, PAR values in control tanks were approximately 1300 $\mu\text{mol m}^2 \text{s}^{-1}$ and shaded tanks were approximately 200 $\mu\text{mol m}^2 \text{s}^{-1}$).

We based our shading treatment on estimated light attenuation by macroalgal (*Ulva* sp.) cover at Nick's Cove. We retrospectively estimated light attenuation using quarterly site survey data on *Ulva* sp. dry mass per m², by determining a linear relationship between PAR and equivalent wet weights of *Ulva* sp. biomass. To do this, we added *Ulva* sp. incrementally to one of our outdoor mesocosms at BML and measured PAR below the *Ulva* sp. (see Figure S2). Our shading treatments did not account for other drivers of light attenuation (such as phytoplankton blooms, which occur seasonally at the mouth of Tomales Bay; see Cole, 1989), and it is also likely that our control tanks experienced higher light conditions than those found in the field due to reduced average water depth. However, *Ulva* sp. blooms reduce eelgrass biomass (Hauxwell et al., 2001; Olyarnik & Stachowicz, 2012) and are significant driver of differences in light availability across our three sites. We ran the experiment for 1 month, after which we measured photophysiology of each shoot's leaves using a Waltz Diving Pulse-Amplitude Modulation (PAM) fluorometer.

To measure photophysiology, we selected a subset of 12 shoots per population per shading treatment (four subreplicates for each population from within each common garden). We assigned shoots to a random order, and we measured 24 shoots per day during early morning hours over the course of 4 days. For each shoot, we used a Kimwipe to gently clean the outer surface of the 2nd ranked leaf approximately 20 cm above the sediment surface. We dark acclimated this section of the leaf using a 4 mm diameter leaf clip for 30 min. After dark acclimation, we measured the dark acclimated yield immediately followed by a rapid light curve (Ralph & Gademann, 2005).

2.5 | Introduced herbivore feeding trials

The introduced amphipod, *Ampithoe valida*, was abundant at Millerton Point and rare or absent at other sites (see Section 3). To assess whether this could contribute to the outcome of the reciprocal transplant experiment, we tested the feeding by *A. valida* on eelgrass in choice and no-choice experiments. We collected fresh eelgrass shoots at one-meter intervals along a 50 m transect adjacent to the reciprocal transplant experiment plots at each site. We collected *A. valida* by collecting 50 flowering shoots from the

meadow adjacent to the transplant plots at Millerton Point because these had high densities of amphipods; we standardize the assays by using males placed in 100 ml seawater cups and acclimated for 48 h in a Percival Intellus incubator set to 21°C and a 12 h day/night cycle.

We tested whether *A. valida* preferentially consumed leaves from one population by offering a simultaneous choice of a 3 cm-long leaf section from each population ($N = 20$). We also tested feeding rates on each population in separate no-choice trials in which *A. valida* were offered three sections of leaves from the same population ($N = 20$ each). Each leaf section was taken from the 3rd rank blade to standardize the leaf age. We exchanged the 100 ml of seawater in each cup for fresh seawater at the beginning of each trial, placed the leaf sections in each cup with an amphipod, and returned the cups to the incubator for 48 h. We photographed the leaf sections before and after the trials. We measured the area of each leaf section in ImageJ and calculated the rate of leaf consumption based on area removed during the feeding trial.

2.6 | Population genetic structure

We determined the population genetic structure of eelgrass for our three sites in Tomales Bay based on 45 individuals collected at each site. During summer 2018, we collected shoots at one-meter intervals in the meadow adjacent to the reciprocal transplant experiment plots. We extracted genomic DNA using a modified Qiagen/Genra Puregene protocol for marine tissue. We delineated genotypes using 11 microsatellite loci developed for *Z. marina* and previously used on populations in this region (see Abbott et al., 2018) and analyzed Genescan results through the program STRand to determine allele peaks. We identified genetically unique individuals based on the probability that repeated genotypes originated from distinct sexual events using the Round-Robin method in the R-Package “RClone” (Arnaud-Haond & Bailleul, 2021).

2.7 | Data analyses

We conducted all analyses in R Version 3.6.2 (R Core Team, 2021). For the three-way reciprocal transplant experiment, we assessed the effect of being a local versus foreign genotype on clonal shoot production (i.e., shoot count within plot) of surviving plots using a generalized linear mixed effects model. We specified a fixed effect of genotype (local or foreign), a random effect for site, a random effect for time, and a crossed random effect of plot and time (to account for repeated measures). We specified a Poisson error distribution to account for non-normality of count data. To understand how the strength of home-site advantage differed among sites and time points, we compared the distributions of the conditional modes for the random effects site and time. We ran all mixed effects models, the R-packages “lme4” (Bates et al., 2015), and “emmeans” (Lenth, 2020).

We analyzed differences in multivariate meadow characteristics by the site and season (growing season—May and July—or nongrowing season—November and January). We incorporated the following variables into a principal component analysis (PCA) of meadow morphology: eelgrass aboveground biomass, eelgrass belowground biomass, above to belowground eelgrass biomass ratios, shoot density, canopy height, and *Ulva* sp. biomass. We used nonmetric multidimensional scaling (nMDS) plots based on abundance of 59 species (square-root transformation and using a Bray-Curtis similarity matrix) to visualize differences in epifaunal community composition across sites and seasons. On the square-root transformed data, we performed a permutational multivariate ANOVA (PERMANOVA) with 999 permutations to test for differences in epifaunal community composition across sites. At Last, to identify which species drove community-level differences, we performed an analysis of similarity percentages (SIMPER). All visualization and analyses of epifaunal community composition were done using the “vegan” package in R and following methodology in Clarke (1993).

We analyzed differences in macroalgal biomass across sites with a linear model, specifying an interaction between the predictor variables: survey date and site. We also analyzed differences in *Ampithoe valida* abundance using a linear model, specifying independent effects of survey date and site. For each linear model, we confirmed that model residuals were normal.

For the common garden experiments, we used linear mixed effects models to analyze the impact of temperature and shading treatments. In the temperature common garden experiment, our response variable was the leaf relative growth rate, we specified an interaction between the fixed effects of temperature and site, and we included a random effect of tank. In the shading common garden, our response variable was a measure of photosynthetic capacity: maximum electron transport rate (ETR_{max}). For this model, we specified an interaction between the fixed effects of shading and site, and we included a random effect of measurement date. We incorporated a random effect of date into our model as PAM fluorometry measurements can be influenced by daily differences in irradiance. For each linear mixed effects model, we used a Tukey's test to evaluate differences among estimated marginal means. We confirmed that all models had normally distributed residuals.

For the choice feeding trial conducted with *Ampithoe valida*, we used a one-sample Hotelling's T^2 test (using the R-package “ICSNP”; Nordhausen et al., 2018). For the “no choice” trials, one each for Nick's Cove, Blakes Landing, and Millerton Point, we used a linear model in which leaf consumption was predicted by one variable: site. We checked that the residuals for this model were normal.

We calculated clonal richness (R) at each site as $R = (G - 1) / (N - 1)$, where G is the number of unique genotypes and N is the total number of shoots analyzed. To estimate the degree of genetic structure across sites, we used Nei's estimator of pairwise F_{st} , followed by a G-test to determine the significance of the effect of site on genetic differentiation (a likelihood-ratio test, using 100 permutations). We performed genetic structure analyses using the R-packages “adegenet” (Jombart, 2008) and “hierfstat” (Goudet & Jombart, 2020).

Additionally, we performed PCA on allele composition data to visualize genetic structure across sites.

3 | RESULTS

3.1 | Three-way reciprocal transplant experiment

Local genotypes outperformed foreign genotypes at all sites (Figure 1). At each location, home-site genotypes always had the highest survival, whereas the genotypes with lowest survival were always from a foreign site at the end of the experiment (Figure 1b,e,h). Among survivors, local genotypes produced more clonal offspring shoots (i.e., shoot counts within plots) than foreign genotypes (model estimate: 0.24 ± 0.09 , $p = .007$, number of observations: 498) and this positive effect increased over time (Figure 1c,f,i, also see Figure S1a). Overall, the detection of home-site advantage emerged 9 months after planting (Figure 1c,f,i; Figure S1a). Home-site advantage effects were greater at Nick's Cove and Blakes Landing compared to Millerton Point (Figure 1c,f,i also Figure S1b), likely

because of the overall high mortality experienced at Millerton Point (Figure 1h). By the end of the experiment, at all three sites, local genotypes produced approximately four times more shoots than foreign genotypes (Figure 1d,g,j).

3.2 | Biotic and abiotic variation among sites

Eelgrass morphology, epifaunal community, macroalgal abundance, temperature, and sediment characteristics all contributed to site differentiation, and for many characteristics, this differentiation varied by season (Figure 2). For the PCA of eelgrass morphology (Figure 2a), PC1 accounted for 38% of the variation among sites by season and primarily reveals strong seasonality in Blakes Landing eelgrass, where eelgrass shoot density and belowground biomass increase greatly during the growing season. PC2 accounted for 28.2% of the variation in eelgrass morphology and was positively associated with canopy height, *Ulva* sp. biomass, and above to belowground biomass ratio. Nick's Cove and Millerton Point were more positively associated with PC2 than Blakes Landing, especially during the growing

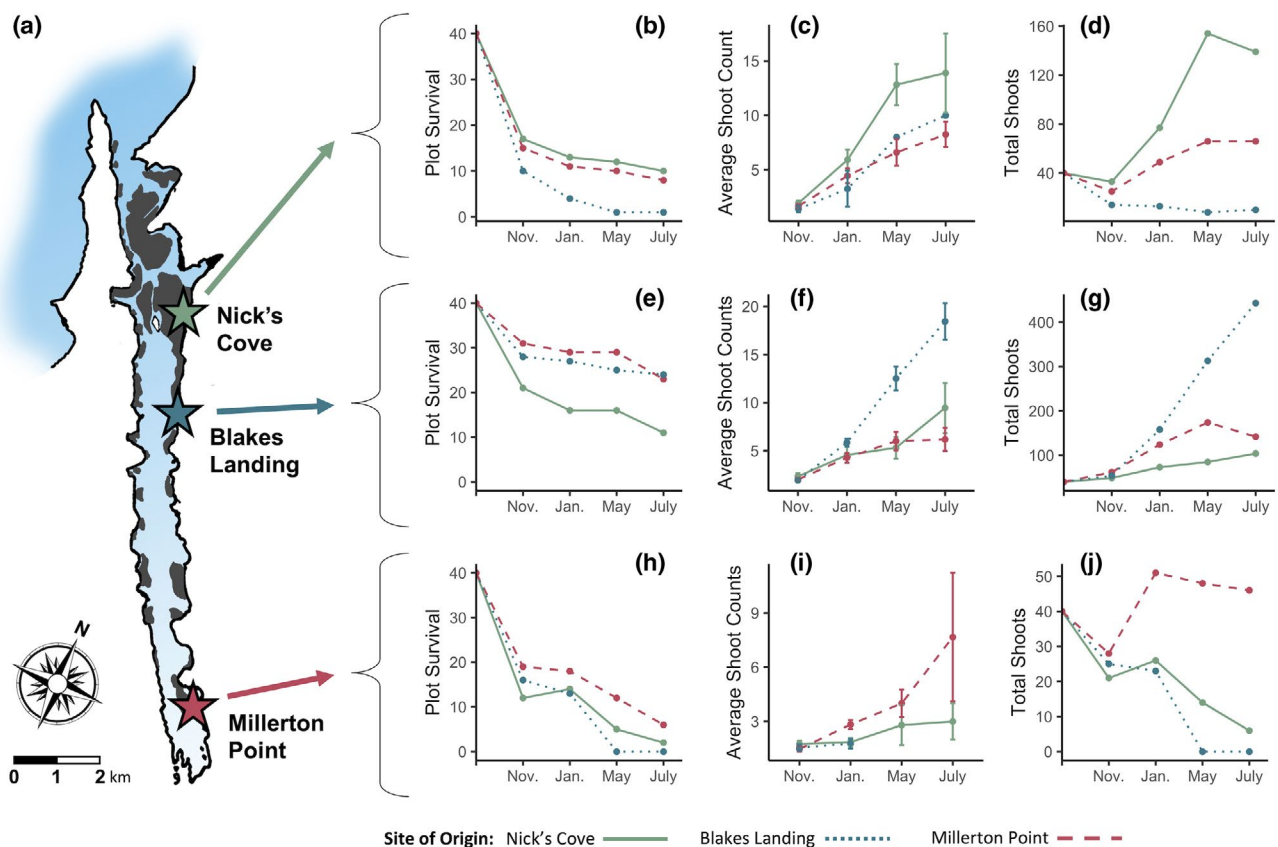


FIGURE 1 (a) Map of Tomales Bay, CA showing locations of eelgrass meadows (shaded in gray, adapted from Fourqurean et al., 1997) and field sites for reciprocal transplant experiment: Nick's Cove, Blakes Landing, and Millerton Point. Results of the reciprocal transplant experiment at Nick's Cove (b–d), Blakes Landing (e–g), and Millerton Point (h–j) for shoots originating from Nick's Cove (solid line), Blakes Landing (dotted line), and Millerton Point (dashed line). (b, e, h) Plot survival at each site through time. (c, f, i) Average shoot counts through time (calculated using surviving plots only); we used these data to statistically compare local and foreign genotype performance (values are mean \pm SE. $N = 40$). (d, g, j) The total number of shoots produced by each population at each site through time

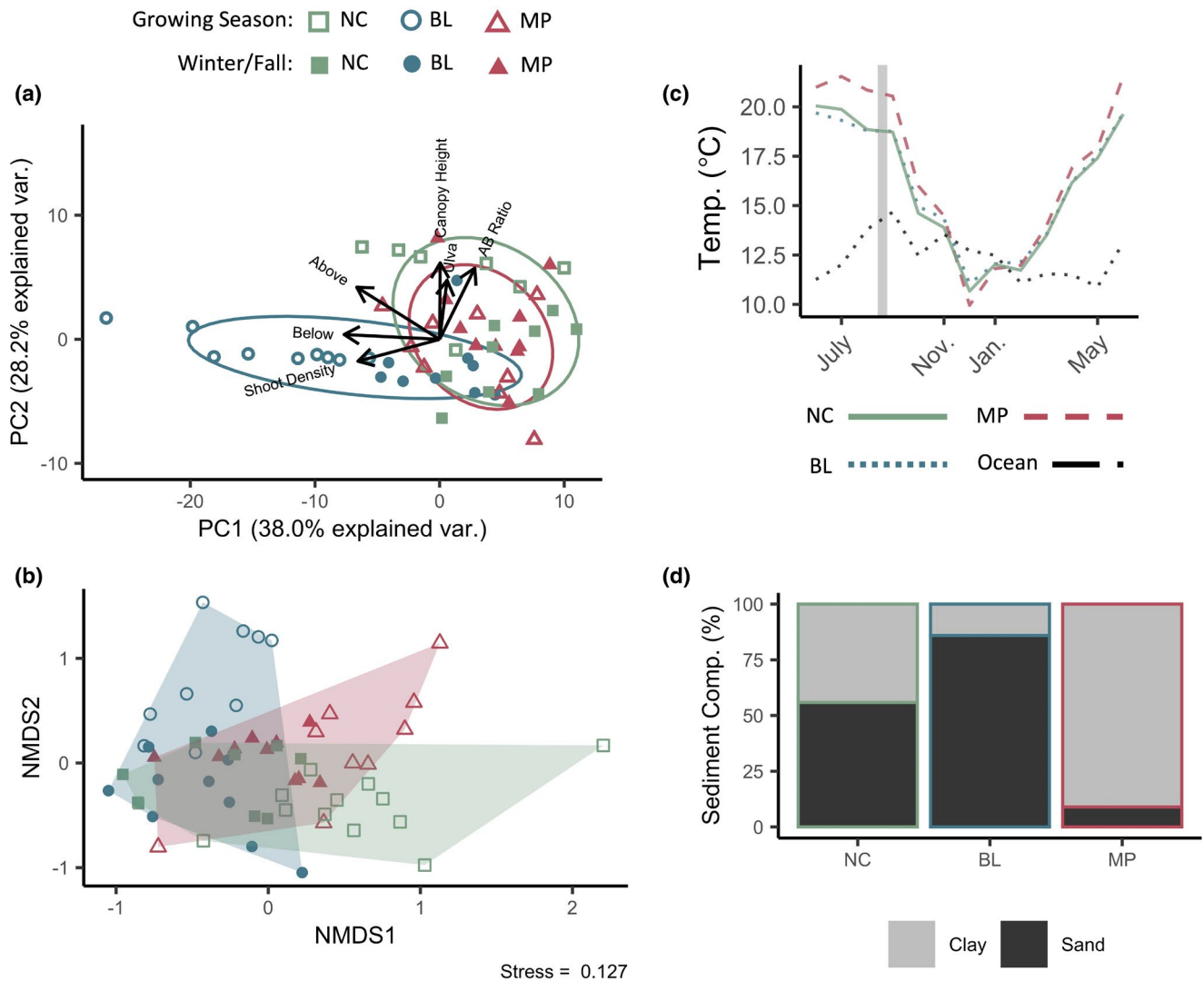


FIGURE 2 Biotic and abiotic variation among sites. (a) Principal components analysis depicting eelgrass morphological differences among sites (Nick's Cove, squares; Blakes Landing, circles; and Millerton Point, triangles) by growing season (open symbols) and non-growing season (filled symbols). (b) Nonmetric multidimensional scaling plot depicting epifaunal community differences among sites (Nick's Cove, squares; Blakes Landing, circles; and Millerton Point, triangles) by growing season (open symbols) and nongrowing season (filled symbols). (c) Daily average temperatures at all three sites (Nick's Cove, solid line; Blakes Landing, dotted line; and Millerton Point, dashed line) and the open ocean adjacent to Tomales Bay (dotted-dashed line) for 1 year. Gray shaded bar denotes dates used for summer temperature profile detail: See Figure 3a. (d) Differences in average sediment grain size composition at each site (N = 3)

season. In general, sites were more similar during the fall and winter, while site differences in eelgrass morphology were greater during the growing season (May and July).

Epifaunal communities differed by site (Figure 2b, PERMANOVA; $df = 2$, $MS = 1.681$, $Pseudo-F = 5.477$, $R^2 = 0.164$, $p_{perm} = 0.001$), particularly in the growing season. SIMPER analysis reveals that no single species had a dominant influence on differences among epifaunal communities, but the introduced amphipod *Ampithoe valida* was more abundant at Millerton, distinguishing it from the other two sites. Three native species, the amphipod *Ampithoe lacertosa*, the isopod *Paracerceis cordata*, and the polychaete *Platynereis bicaniculata* also distinguished Millerton from the other two sites. Each of these species contributed to approximately 6%–13% of the difference

between Millerton Point and both Nick's Cove or Blakes Landing. Differences between Nick's Cove and Blakes Landing were driven by *Platynereis bicaniculata* (12%), the snail *Lacuna marmorata* (8%), *Ampithoe lacertosa* (9%), and the amphipod *Caprella californica* (7%).

Temperature differences among sites also varied seasonally (Figure 2c). Millerton was the warmest site 9 months out of the year, but temperatures at all three sites converged during winter months. From July through September, Millerton temperature was 2°C warmer on average than Blakes Landing or Nick's Cove (Millerton $20.6 \pm 0.9^\circ\text{C}$ vs. $18.7 \pm 0.3^\circ\text{C}$ and $18.8 \pm 0.34^\circ\text{C}$ for Blakes Landing and Nick's Cove, respectively). However, during peak temperatures in August and September, Millerton Point was about 5°C warmer than Blakes Landing and Nick's Cove during daytime high tides

(Figure 3a). Temperatures at all sites were considerably warmer than the offshore average sea surface temperature (up to 10°C warmer during the summer; Figure 2c).

Sediment grain size varied among all three sites (Figure 2d). Millerton Point sediments were almost completely composed of clay; in contrast, Blakes Landing sediments were almost completely composed of sand. Nick's Cove sediments were approximately half sand and half clay.

3.3 | Temperature variation among sites and temperature common garden

In common garden, the pattern of population response to our temperature treatments was consistent with patterns of home-site advantage in the field (Figure 3b). The relative growth rates of shoots from the warmest site, Millerton Point, did not differ among temperature treatments ($p = .424$). In contrast, Nick's Cove and Blakes Landing shoots grew 40% less under the elevated temperatures characteristics of Millerton Point, relative to the cooler temperature treatment characteristic of their home-site environment ($p = .032$ and $p = .029$, respectively).

3.4 | Macroalgal variation among sites and shading common garden

Macroalgae (*Ulva* sp.) were always present and covering the eelgrass at Nick's Cove; however, they were never present at Millerton Point, and only present during the spring survey at Blakes Landing (Figure 4a). For the last 6 months of the transplant experiment, biomass of macroalgae at Nick's Cove was at least double the amount found at Blakes Landing or Millerton Point (May: $p = .04$ and $p < .0001$, July: $p < .0001$ and $p < .0001$ respective contrasts), and average macroalgal biomass was estimated to attenuate approximately 40% of ambient light at Nick's Cove (Figure 4b). The high

macroalgal biomass at Nick's Cove recorded during the final two surveys ($154 \pm 33 \text{ g m}^{-2}$ and $143 \pm 25 \text{ g m}^{-2}$) was estimated to reduce light availability to eelgrass by 60%–87% (see Figure S2). In the common garden, the pattern of population response to our shading treatment was consistent with the patterns of home-site advantage in the field. The photosynthetic capacity (maximum electron transport rate in the Photosystem II, ETR_{max}) of shoots from Nick's Cove did not change in response to a 77% reduction in light ($p = .654$, Figure 4c). However, the photosynthetic capacity of shoots from Blakes Landing and Millerton Point was reduced by approximately 20%–30% ($p = .004$ and $p = .021$ respectively, Figure 4c).

3.5 | Introduced herbivore abundance at sites and feeding trials

Abundance of the introduced amphipod, *Ampithoe valida*, ranged from 5–33 times higher at Millerton Point compared to the other two sites ($p < .001$), with exceptionally high numbers of *A. valida* at Millerton Point during the spring (Figure 5a). We documented severe damage to eelgrass leaves due to *A. valida* grazing at Millerton Point twice during the transplant experiment. Approximately 75% of shoots were grazed in the meadow adjacent to the transplant experiment during September and in the transplant plots during the May survey (Figure 5b; see Figure S3). When *A. valida* were given no choice and offered tissue from only one site at a time (likely more relevant to patterns of herbivory on transplants), 30% more of the Blakes Landing tissue was consumed compared to Millerton Point or Nick's Cove ($p = .006$, Figure 4c). Multichoice experiments showed higher grazing on Millerton Point and Nick's Cove tissue and slightly less on Blakes Landing tissue ($T^2 = 120$, $df = 3,17$, $p < .001$; see Figure S4). The high grazing rates at Millerton Point likely contributed to low biomass accumulation and high mortality of plants from all sites there. Based on feeding trial grazing rates (from the no-choice trials) as well as field survey data on *A. valida* abundance and eelgrass biomass, during May *A. valida* could have consumed approximately

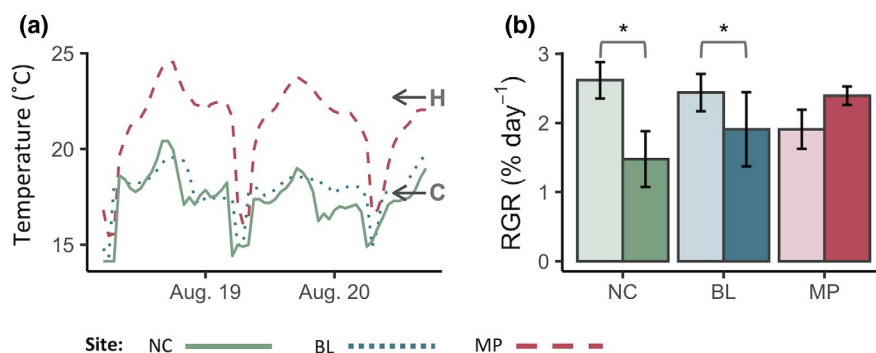


FIGURE 3 (a) Representative detail of temperature differences that occur across all three sites (Nick's Cove, NC, solid line; Blakes Landing, BL, dotted line; and Millerton Point, MP, dashed line) during the summer. Arrows indicate hot (H) and cold (C) temperature treatments used in the temperature common garden experiment. (b) Leaf relative growth rate (RGR) for eelgrass individuals from each transplant site grown in a common garden under hot (dark bars) and cold (light bars) treatments (mean \pm SE). Asterisks indicate model contrasts below the threshold of $p = .05$. $N = 12$

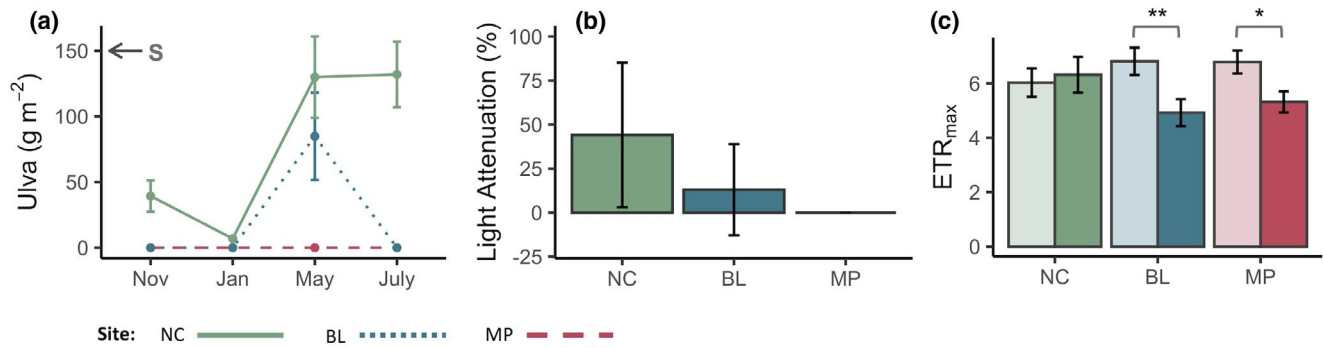


FIGURE 4 (a) Seasonal variation in *Ulva* sp. (i.e., macroalgal) abundance at all three transplant sites in Tomales Bay: Nick's Cove (NC, solid line), Blakes Landing (BL, dotted line), and Millerton Point (MP, dashed line). Arrow (S) indicates *Ulva* sp. abundance mimicked in the shading common garden experiment. (b) Estimated annual light attenuation (mean \pm SD) at each site, calculated based on *Ulva* sp. biomass at each site (see Figure S2). (c) Photosynthetic capacity (maximum electron transport rate within Photosystem II: ETR_{max}) for each eelgrass population, grown in a common garden under shaded (dark bars) and unshaded (light bars) treatments. Asterisks indicate model contrast thresholds (* $p < .05$; ** $p < .01$). $N = 12$

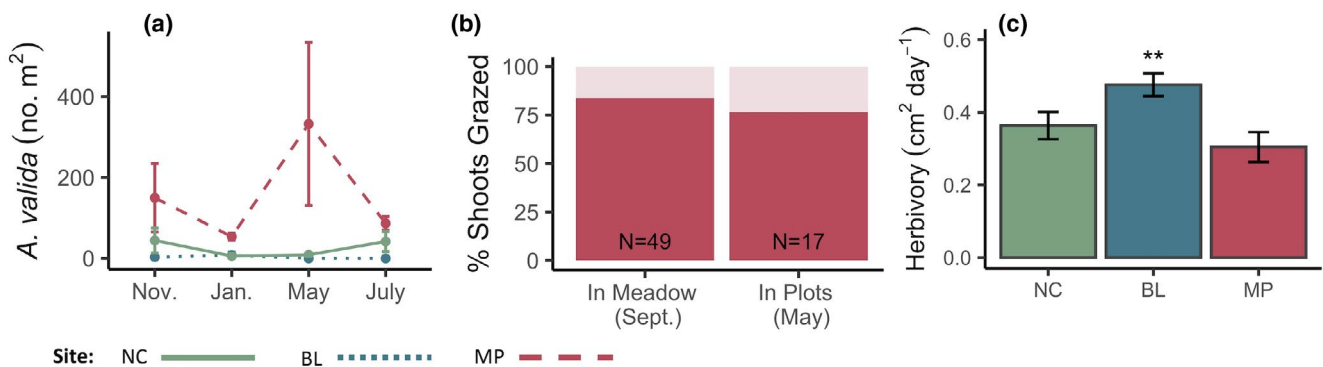


FIGURE 5 (a) Seasonal variation of *Ampithoe valida* abundance at all three transplant sites in Tomales Bay: Nick's Cove (NC, solid line), Blakes Landing (BL, dotted line), and Millerton Point (MP, dashed line). (b) Percentage of shoots with *A. valida* grazing scars on their leaves at Millerton Point during a survey of meadow flowering shoots in September 2017 and the May survey of transplant plots (dark bars, see Figure S3 for photos of grazing scars). (c) Average (mean \pm SE) daily herbivory per individual *A. valida* when offered eelgrass leaf clips from one eelgrass population at a time (i.e., "no choice" feeding trial). Asterisks indicate model contrast thresholds (** $p < .01$). $N = 20$

2.60% of eelgrass biomass per day at Millerton Point. This consumption rate exceeds the daily relative growth rate of $1.91 \pm 0.3\%$ (mean \pm SE) measured for Millerton Point shoots at our temperature common garden under the 17.7°C treatment (field temperatures at Millerton Point averaged 17.9°C during May).

3.6 | Population genetic structure

We detected genetic structure at neutral markers among the three eelgrass populations (Table 1, $p = .01$), suggesting limited gene flow across these eelgrass meadows within Tomales Bay (Figure 6; Table 1). Millerton Point and Nick's Cove, located on opposite ends of the bay, are more greatly differentiated. Nick's Cove and Blakes Landing, separated by only a few kilometers, were the most closely related populations. Millerton Point had the lowest genotypic richness out of the three sites (Table 2), suggesting each unique genotype covered a larger area at this site.

TABLE 1 Pairwise F_{st} for Nick's Cove (NC), Blakes Landing (BL), and Millerton Point (MP), $p = .01$, $N = 22-27$

	NC	BL	MP
NC	0	–	–
BL	0.026	0	–
MP	0.052	0.042	0

4 | DISCUSSION

Collectively, our results provide strong evidence that fine-scale (2–12 km) environmental mosaics can drive local differentiation of eelgrass populations. Local genotypes outperformed foreign genotypes at all three sites during our reciprocal transplant experiment, a pattern that was evident by 6–9 months after transplanting (Figure 1; Figure S1). Common garden experiments provided evidence that differences in temperature and shading between sites

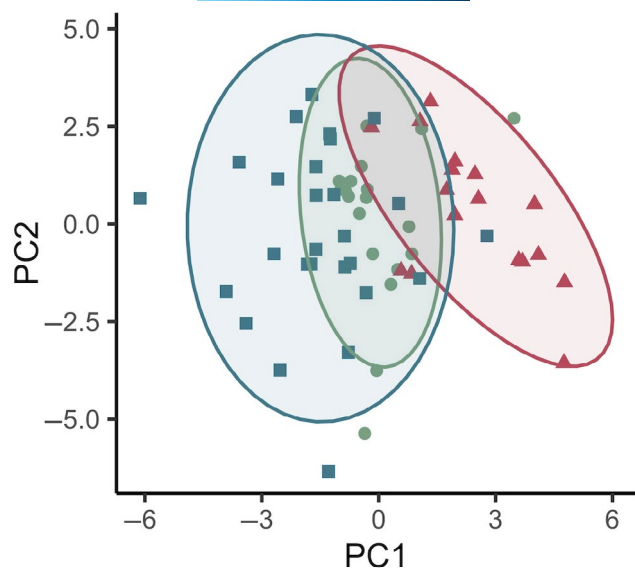


FIGURE 6 Principal component analysis demonstrating genetic differentiation of eelgrass populations from transplant sites in Tomales Bay: Nick's Cove (squares), Blakes Landing (circles), and Millerton Point (triangles) using 11 microsatellite loci developed specifically for eelgrass ($p = .01$)

TABLE 2 Clonal richness (R) at Nick's Cove (NC, $N = 28$), Blakes Landing (BL, $N = 22$), and Millerton Point (MP, $N = 27$)

	NC	BL	MP
R	0.96	0.86	0.63

likely contributed to the phenotypic differences among populations that led to home-site advantage for all three populations (Figures 3b and 4c). Populations tolerant of stressful environments failed to increase growth under more benign conditions, suggesting some cost to tolerance of high temperatures and light limitation. Further, the low overall survival of transplant plots at Millerton Point (Figure 1h) can be attributed to grazing by the introduced amphipod *A. valida*, which outpaced rates of eelgrass productivity. At Millerton Point, slightly higher *A. valida* grazing rates on foreign genotypes (Figure 5c) could also contribute to the low survival of foreign genotypes. We discuss the possible mechanisms underlying this surprisingly fine-scale population differentiation as well as the implications of our results for restoration and conservation of natural populations in the context of changing environmental conditions.

Because we did not raise generations in a common environment, we cannot unequivocally distinguish the extent to which the population differentiation that we observed is caused by genetically based adaptation versus long-term plastic effects. Long-term acclimation to previous experience via provisioning and/or epigenetic changes may be especially important in clonal plants (Dodd & Douhovnikoff, 2016; Verhoeven & Preite, 2014). For example, eelgrass exposure to heatwave conditions leads to phenotypic changes that persist across several clonal generations (DuBois et al., 2020). Yet, our previous

work with genotypes raised for dozens of clonal generations in common garden does provide evidence for genetically based variation in traits related to photosynthetic physiology and temperature tolerance (Abbott et al., 2018; DuBois et al., 2019; Hughes et al., 2009; Reynolds et al., 2016), suggesting a role for genetic adaptation in the population differentiation that we observed. Further, significant genetic structure at neutral markers suggests that gene flow among populations is sufficiently limited that local selection could produce the patterns of eelgrass population differentiation observed (Figure 6; Table 1). Because cumulative performance differences increased through the experiment (Figure 1; Figure S1), it suggests that individuals failed to acclimate in the field. Acclimation to temperature and shading treatments in common garden did not occur after a month (Figures 3b and 4c), also indicating that patterns of home-site advantage in the field and in common garden likely have some genetic component. Indeed, in a separate analysis of whole-genome sequencing of eelgrass from populations in Tomales Bay, we found signatures of natural selection at several loci that were associated with temperature differences among sites (L. Schiebelhut, R. Bay, R. Grosberg, & J. Stachowicz, unpubl. data).

Based on predicted changes in long-term climate averages, average temperatures at Millerton Point are not projected to occur at the mouth of Tomales Bay for the next several 100 years (Burrows et al., 2011), demonstrating how microclimate gradients can be larger than the predicted pace for regional climate change (Oldfather & Ackerly, 2019). The extent to which populations are locally adapted yet remain partially connected through dispersal will determine the timescales over which individuals from pre-adapted populations may be able to rescue populations exposed to new stressors. The distance between our sites (2–12 km; see Figure 1a) is greater than typical maximum dispersal distance for eelgrass pollen and seeds (15 and 50 m respectively, genetic neighborhood area about 0.5 km²; Ruckelshaus, 1996), yet occasional long-distance dispersal occurs in eelgrass via rafting of reproductive shoots with mature seeds (Harwell & Orth, 2002). Thus, Millerton Point eelgrass could act as a reservoir of warming resilient alleles that have ample time to spread to other Tomales Bay populations and to eelgrass in neighboring bays (Kamel et al., 2012), possibly increasing the adaptive capacity of these connected range-center eelgrass populations to continued global warming. Similar patterns occur in corals where naturally high-temperature microclimates harbor populations pre-adapted to future climate conditions (Bay & Palumbi, 2014) and connectivity between populations adapted to different temperature regimes is predicted promote survival of coral populations over the next 200 years (Matz et al., 2020). More generally, incorporating population differentiation into ecological niche models not only improves predictions of species response to climate change but can alter the direction and magnitude of predictions (Bothwell et al., 2020; Kelly et al., 2012; Kuo & Sanford, 2009; Sanford & Kelly, 2011).

We argue that local-scale environmental heterogeneity causing mosaics of persistent thermal hot spots throughout a species range could allow for populations pre-adapted to warmer temperatures to

exist at much higher latitudes than expected (e.g., Kuo & Sanford, 2009) and could greatly enhance adaptation to warmer temperatures at high latitudes. Previous studies demonstrate that dispersal from central populations could limit adaptation of populations in extreme conditions (Pironon et al., 2017); however, there is growing evidence that adaptation of populations to extreme conditions at distributional limits is common (Kottler et al., 2021). Conversely, some dispersal from populations at the edge of the distribution (or from mosaics containing range edge-like environments) back to range center populations could speed adaptation to a changing climate.

Selection for eelgrass phenotypes associated with adaptation to warmer temperatures could have cascading impacts on ecosystem function and community dynamics. Genotypes characteristic of our warmest site (Millerton Point) had reduced shoot density and invested more in belowground biomass, potentially reducing habitat quality (Ralph et al., 2013; Sirota & Hovel, 2006). We did find that epifaunal communities were distinct among sites, but the extent to which this is a direct effect of temperature versus habitat characteristics is unclear. Long rhizomes and large intershoot distance (up to 1 m) combined with selection may have contributed to lower genotypic richness at Millerton Point compared to our other sites (Table 2). Such differences in genotypic and trait richness can alter the structural quality of the habitat influencing community dynamics (Abbott et al., 2017), biogeochemical cycling (Holmer, 2019), and meadow resilience to disturbance (Hughes & Stachowicz, 2011; Reusch et al., 2005).

Our results also illustrate how multiple stressors can concurrently drive population divergence on local scales, giving rise to the possibility that adaptation to one selective agent could constrain the adaptive capacity of a nearby population to a secondary selective pressure through negative genetic correlations (Kawecki & Ebert, 2004; Peterson et al., 2018; Rogell et al., 2009). For example, eelgrass traits that favor increased performance under winter light limited conditions are negatively correlated with traits that favor increased performance during summer marine heatwaves (DuBois et al., 2019). Similarly, eelgrass traits predicting greater competitive ability under warming or intense herbivory (simulated with leaf clipping) were not the same (Kollars et al., 2020). Negative correlations among only a few key traits can be sufficient to slow evolutionary response to changing climates (Etterson & Shaw, 2001). Results from our common garden and field experiments do not support the idea that trade-offs exist between tolerance to warming and light limitation. There was also no evidence for trade-offs in terms of interactions between warming and herbivory, as home-site genotypes were impacted the least by both high temperatures and intense herbivory at Millerton Point. For all three interacting stressors considered here (temperature, light limitation, and herbivory), the strength of environmental gradients varied seasonally, requiring a full year for multifaceted site differentiation to be fully expressed. Millerton Point was only warmer than other sites during the summer (Figures 2c and 3a); *Ulva* sp. cover and shading stress intensified at Nick's Cove during the spring and summer (Figure 4a), and *A. valida* abundance

(as well as entire epifaunal communities) differed across sites only during the spring and summer (Figures 2b and 5a). Thus, evaluation of the importance of trade-offs among multiple stressors should also consider the temporal variation in selective agents and the order that multiple stressors are experienced (Kollars et al., 2020). Instead of evidence for trade-offs among specific stressors, we observed a strong trade-off between maintaining performance at stressful sites (Millerton and Nick's Cove) and inability to increase growth under more benign conditions (Blakes Landing). We observed high performance of Blakes Landing individuals under benign home-site conditions and complete mortality of Blakes Landing plants at both stressful sites (Figure 1). Taken together, these results underscore the idea that prior exposure to disturbance or stress can promote population persistence, whereas populations from benign sites may be highly vulnerable to changing conditions (Connolly et al., 2018; Hoffmann & Sgró, 2011; Matz et al., 2020).

Describing population differentiation is the first step toward incorporating evolutionary processes into species management and conservation (Bible & Sanford, 2016; Gaitán-Espitia & Hobday, 2020; McKay et al., 2005). Fine-scale local adaptation of eelgrass populations could contribute to the high rate of transplant failure in seagrasses (van Katwijk et al., 2016) and suggests that managers might need to consider using multivariate data to match donor sites to restoration sites (Figure 2), or alternatively obtain transplants from a wide variety of sites to ensure adequate genetic diversity in the plantings. Similarly, identifying sites with persistent exposure to high temperature (such as Millerton Point) and the distribution of warming resilient phenotypes throughout a species range is the first step in developing a phenotype management approach for restoration (Watters et al., 2003). When planning for future warming, it will also be important to consider how multiple facets of global change impact systems simultaneously causing not only immediate phenotypic response and/or stress but also potentially altering the rate of adaptation (Etterson & Shaw, 2001; Gaitán-Espitia & Hobday, 2020). The spatial scales of local adaptation and local environmental change must be incorporated into model predictions of species resilience (Bothwell et al., 2020; Urban et al., 2016) and must be accounted for when considering conservation avenues such as assisted gene flow (Aitken & Whitlock, 2013; Gaitán-Espitia & Hobday, 2020).

Species' response to global change is greatly influenced by complex local-scale dynamics. Organisms respond to climate on the scale at which they experience it, and there is increasing evidence that geographic and climate gradients are decoupled at scales that determine population-level processes (Helmuth et al., 2002; Oldfather & Ackerly, 2019; Pironon et al., 2017). Here, we determined that local-scale estuarine gradients in temperature and light limitation are linked to population divergence, and that local gradients in temperature mimicked those found over 10 degrees of latitude. In coastal ecosystems where local environmental gradients are strong and dispersal distances for many foundation species (i.e., seagrasses and macroalgae) are relatively small (Kinlan & Gaines, 2005), local adaptation on extremely fine

spatial scales could be the norm. Predictions of species' responses to global change should strive to incorporate information on such local-scale population differentiation (Bay et al., 2017; Urban et al., 2016) and determine how interactions between multiple co-occurring anthropogenic stressors contribute to population differentiation (Egea-Serrano et al., 2014; Rogell et al., 2009). In cases where local-scale abiotic and biotic mosaics enhance phenotypic diversity across networks of connected populations, it is possible that species resilience to changing environmental conditions could be much greater than currently appreciated.

ACKNOWLEDGEMENTS

This research was funded by NSF OCE 1234345 to JJS, SLW, and Richard Grosberg; OCE 1829976 to JJS, Rachael Bay, and Richard Grosberg; the Russell J. and Dorothy S. Bilinski Fellowship at the Bodega Marine Laboratory, and the UC Davis Graduate Group in Ecology Fellowship. Nicole Kollars provided invaluable mentorship to KNP; we thank Nicole for her generous contribution to this project. We are grateful to Eric Sanford and Ted Grosholz for valuable feedback on this manuscript. Isabelle Neylan, Hannah Nelson, Collin Gross, Cale Miller, Grace Ha, Jordan Hollarsmith, Gabriel Ng, Ben Rubinoff, Emily Longman, Alisha Saley, Karolina Zabinski, Claire Murphy, Sarah Merolla, Josh Chow, Daniel Yim, Liz Allen, Audrey Deutsch, Fabricio Gomez, Deana Villagomes, Megan Ma, Lauren Lebo, Ismena Jameau, Naomi Murray, Rylee Alexander, Zoe Brumbaugh, and many other volunteers assisted with fieldwork and sample processing.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings as well as the R-script detailing data visualizations and analyses of this study are openly available in Dryad at <http://doi.org/10.25338/B8433W> (DuBois & Stachowicz, 2021).

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How to cite this article: DuBois, K., Pollard, K. N., Kauffman, B. J., Williams, S. L., & Stachowicz, J. J. (2022). Local adaptation in a marine foundation species: Implications for resilience to future global change. *Global Change Biology*, *00*, 1–15. <https://doi.org/10.1111/gcb.16080>